# Tree demography in the tropical rain forest of Guyana

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Cover: Greenheart forest in inserted in a stamp from former British Guiana, 'Felling Greenheart'.
Photo by Roderick Zagt; image-processing by Bart Landman.

# Tree demography in the tropical rain forest of Guyana

# De demografie van bomen in het tropische regenwoud van Guyana

(met een samenvatting in het Nederlands)

Proefschrift

ter verkrijging van de graad
van doctor aan de Universiteit Utrecht
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geboren op 2 mei 1964, te Leiden

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# Contents

chapter 1

# Introduction

Over history, western civilisation has built up and maintained an ambiguous relation with the tropical rain forest. Ever since Fransisco Orellana in 1541 made his involuntary trip over the River Amazon, the Amazonian rain forest has attracted or repelled, but certainly enchanted the western mind. The words tropical rain forest and Amazon evoke images of strange, unseen creatures, riches which abound but often remained elusive, rubber booms and gold rushes, hidden cities and lakes, great endeavours and vast failures, opera houses and railroads, stone-age tribes and lost civilisations, poisoned arrows and plenty of mosquitoes which have all conquered their place in the western mind. Amazonia is a magnifying glass which seems to reject mediocrity. The rivers are wider, the beauty is greater, the heroes more heroic, the scoundrels worse, the forest denser and packed with more species than anywhere else. In these days mediocrity has easy access to Amazonia, but the fascination for its myths remains.

Biologists working in the rain forest have not escaped this mystifying force. Scientists turn poets once they set foot into it (examples in Whitmore 1990), and even those scientists who rhyme with numbers find inspiration (Erwin 1982, WCMC 1992). The rain forest stands for the most diverse ecosystem on Earth (Connell 1978), where on 6% of the land area more species are found than in the rest of the world (WCMC 1992), of which 3 species go extinct each hour (Wilson 1989). Keystone species support extensive and intricate foodwebs (Terborgh 1986). Mast-fruiting is related to black-water rivers (Janzen 1974). Rain forests are growing on sterile soil (*cf.* Brouwer 1996). Seedlings and saplings survive deep shade for up to 30 years (Fanshawe 1947), after which they can still respond to gap opening. Seventy-five percent of all species need gaps to reach the canopy (Hartshorn 1978). Herbivores regulate species richness through distance-dependent mortality (Janzen 1970).

Gradually, misconceptions have been corrected, and scientists have increasingly set to quantify these and other aspects of the rain forest, not only in Amazonia. The 1980s and 1990s have become decades of demythologisation of the biological aspects of the rain forest, and although it has lost little of its attraction, at present it is possible to discuss its enigmas on the base of facts and well-argued theories.

The study of the population biology of tropical trees has seen a strong development since the 1960s, when Richards (1952) and Schulz (1960) had just published their pioneering work. While it is not justified to say that it is now possible to understand the population biology of tropical trees, its study has become a mature ecological undertaking. There are two important reasons for this emphasis. Biologists have always been intrigued by the enormous diversity of species in tropical rain forests, and the mechanisms that make them coexist in apparently homogeneous areas. Population biology of these species is thought to provide a key to the understanding of this fundamental biological issue. A second reason for this emphasis is the increasing pressure that tropical rain forests have come to bear from increasing human populations and from economic exploitation, and the realisation that only the management of these forests for timber and other products will be able to diminish this pressure. Sustainable management is only possible with a proper knowledge of the population behaviour of the species to be managed.

By far the most significant contribution to the development of the population biology of tropical trees since the early days has been the creation and census of very large permanent sample plots, first and foremost on Barro Colorado Island (Panama), later also in other countries (Condit 1995). These studies have produced an incessant stream of publications, in which new and existing hypotheses were critically assessed using the enormous data-sets that these plots provide. This is a significant improvement, because tropical population biology is an area in biology where traditionally the formulation of hypotheses and paradigms have run far ahead of the field work and experiments to test them (Janzen 1970, Connell 1971, Hartshorn 1978, Hubbell 1979). Still, what these studies gain in scale, they loose in detail, and therefore other, smaller studies, however sometimes encumbered by the consequences of the same species richness that they study (small sample sizes, taxonomic uncertainty), provide invaluable detail to the knowledge generated in the large plots.

This dissertation is based on the results of a (comparably) small population study of three tree species from the rain forest of Guyana. It describes the population dynamics of three species differing in regeneration strategy, and links this to timber exploitation. While the objectives quite specifically concentrate on assessing the consequences of exploitation on the population dynamics of these species, a large part of the dissertation is spent on quantifying and understanding specific components of the life cycle of these species, and on reviewing their population dynamics in the light of the main hypotheses that are put forward to explain species coexistence and succession in tropical rain forests.

A fully documented introduction of hypotheses concerning species coexistence in tropical rain forests, and an identification of parameters that are thought to shape the course of succession in rain forests is provided in Chapter 2 of this thesis. The ideas forwarded in this Chapter are the fundament of much of the work reported elsewhere in the thesis.

The following introduction is, therefore, limited to a clarification of some concepts and choices that have shaped this thesis, and an introduction to Guyana and the Tropenbos Programme that have coloured it.

chapter 1

# Population biology and tropical trees

Demography is the study of the quantitative aspects of populations; the population biology investigates the factors that govern these aspects (Harper 1979). The number of individuals in a plant population changes as a result of birth and death, and in the seed stage by immigration and emigration. Between birth and death plants grow and only if sufficient individuals grow enough to reach the reproductive stage, the population is perpetuated. Hence, the population dynamics of the species in this study are studied by measuring and interpreting their rates of growth, survival and reproduction.

Nature offers many ways to grow to maturity. Trees in the rain forest, like anywhere else, tend to differ in the way they achieve maturity. Inter-specific differences in exigency for water, nutrients and light, in ways to meet the requirements of pollination, seed dispersal, and to ward off predation, disease and disaster, cause variation in growth and mortality rates, and thus in their demography - in seed production, germination and establishment, in growth and survival rates, and also in the variation in growth and survival with time. Therefore, groups of species with similar 'solutions' to the same environmental problems can be distinguished (Condit *et al.* 1996b), and these are called functional groups of plants with the same strategy. For example, tropical tree species can more or less clearly be classified as light-demanding pioneer species or shade-tolerant climax species (Swaine & Whitmore 1988, Whitmore 1996). The large diversity of species has greatly stimulated the search for functional groups of rain forest species. It shows the way out of the bewildering diversity of species, and puts core ecological and environmental issues like coexistence of species, succession, forest management and global change into a perspective with at least a horizon.

Coexistence, succession, and forest management are all concerned with the differential ability of individuals and species to grow and reproduce, and with the environmental conditions which determine if, where and when individuals achieve this. Mechanisms that explain why two species can grow up together in one canopy opening in the forest may provide a tool for a forest manager to manipulate the composition of a forest.

## The struggle for light

Light is a major determining factor of plant growth in the tropical rain forest. Not only does less than 1-2% of the light penetrate to forest floor environments but light environments vary drastically over short horizontal and vertical spatial scales, and in time (Chazdon *et al.* 1996). This long and complex resource gradient in forests provides ample opportunity for forest plants to differentiate in their requirement for light and their response to variation in light availability. Efforts to classify rain forest species in functional groups have always taken their response to light as a starting point (Popma & Bongers 1988, Swaine & Whitmore 1988, Favrichon 1994, Condit *et al.* 1996). The effects of exploitation on the growth of the remnant vegetation are, to a major extent, the consequence of an altered light regime caused by the change in vegetation structure.

Apart from light, water and nutrients limit plant growth in the rain forest (Raaimakers 1994, ter Steege 1994a, Mulkey & Wright 1996, Grubb 1996). The availability of water and nutrients also is variable, and growth responses to variation in water and nutrients may sometimes be substantial (Swaine 1996), but this variation is often less than variation in light over the spatial scale where plants interact, and these responses are only clear if light availability is high (Burslem 1996). Therefore, in this study the emphasis is on the effect of light on growth and survival of plants. The potential role of water and nutrients in structuring rain forest communities is acknowledged here, but is not addressed in the study.

Forest dynamics, and especially the formation of canopy gaps play a central role in theories explaining species coexistence (Denslow 1980). Gaps create large environmental gradients in the forest, and are foci of forest rejuvenation. The gap is attractive because it is gracious as a concept and tells a story in one word. However, in the field it loses its attraction because gap shape and size are difficult to quantify (van der Meer 1995), and gap size is an unsatisfactory way to define the growth conditions of a plant. Therefore, the assertion that 75% of all plants need a gap to reach the canopy (Hartshorn 1978) is conceptually correct, but factually wrong. In this thesis I have carefully avoided to give a gap definition, and where it was necessary, it was understood as any place in the forest where rapid plant growth is possible. It is used as a concept throughout, but where quantification of environments for plant growth was required, this was achieved by measuring light.

Population ecologists struggle with light as much as plants do. The proper measurement of rain forest light environments has proven to be a major obstacle to the study of tropical plant demography. There is a strong negative correlation between the accuracy and repeatability of the method of measuring light and the number of plants that can be measured. Precise radiation measurements with photo-sensitive diodes are precluded to experimental situations, or to measurements of a few individuals in the field (*e.g.* Oberbauer *et al.* 1988). Large population studies use considerably cruder and more subjective ways to determine light environments, such as canopy height (Welden *et al.* 1991) or the Dawkins index (Clark & Clark 1992). The recent history has brought advances such as hemispherical photography (Whitmore *et al.* 1993, ter Steege 1996) and plant canopy analysers (Hanan & Begue 1995), which permit to quantify light environments of relatively large numbers of individuals in the field. In the present study the light environment of several thousands of seedlings and saplings was quantified using a range of methods. The Dawkins index was used for rapid and large scale assessment of general light environments of seedlings. For a field experiment and a detailed study of seedling distribution more quantitative and repeatable methods were used, viz. hemispherical photography and plant canopy analysis.

## Seedlings

This thesis places much emphasis on the demography of seedlings and saplings in order to understand the composition of the adult community. An oft-heard argument against the study of seedlings is that practically all seedlings die, so that differences in individual demographic rates are not important. This high mortality however just shows that strong selective forces may be at work (Swaine 1996) and that great advantages are bestowed on individuals that possess an adequate strategy to cope with the constraints imposed by the environment. Any functional explanation of the composition of a forest community should encompass all the stages of the life cycle, not only the large ones. Large individuals in the canopy were successful in surviving the vagaries of life in the understorey and in gaps. Although it is valid to say that seedlings which are better adapted to the local environment have a higher probability of reaching the canopy, it is not valid to reverse this argument. Successful recruitment into the canopy (maturity) is not necessarily a sign of optimal adaptation to the local environment, but it merely indicates that the environmental constraints were not sufficient to prevent the individual from being successful. Therefore, more insight in demographic constraints is to be gained from studying juvenile stages than from mature stages.

Formally, seedlings are plants that depend on their seed reserves for growth (Kitajima 1996). In this thesis I use a more colloquial and practical, field-based definition: a seedling is a plant of which no diameter (at 1.30 m above soil level) can be measured, while this is possible with a sapling. This puts the practical border between the two at *c.* 1.60 m height. The distinction between seedlings that depend on seed reserves and that don't is important in demographic terms, but this period is hard to distinguish, covers a short period in the life of plant, and excludes many plants of similar stature, hence I preferred to use the definition given above. A great variety of terms is used (also in this thesis) for plants larger than seedlings: saplings, juveniles, poles, pre-adults, pre-reproductive plants, subcanopy trees. As far as they belong to canopy species, these are all plants that are not yet reproducing, and have their crown below the main canopy.

## Exploitation

Exploitation has large consequences for the population dynamics of a species. A direct effect of exploitation is the removal of a part of the reproductive population of the harvested species from the forest, and the damage to smaller individuals of these and many other species due to the logging operation. Exploitation alters the structure and micro-environment of the forest, and therefore growth, survival and reproduction rates of plants. It is expected that these effects are large just after logging, but that with the gradual closure of the vegetation the demographic rates return to normal values. The impact of exploitation varies with its intensity, frequency and spatial extent (*cf.* Waide & Lugo 1992), and species with different regeneration strategies respond differently to exploitation.

It is hard to describe 'the' effect of logging on the population dynamics of a species, because these effects differently affect growth, survival and reproduction, are dependent on the size of the individual, and change with time after logging. Some effects are 'positive' compared to a natural reference, others are negative. In order to overcome this problem it is proposed to express the combined effect of all demographic changes in terms of the population growth rate, which can be calculated with a population model. In this dissertation, matrix population models are used to describe the population dynamics of species, and to assess the impact of logging on it. These models describe the population dynamics of a species organised in size classes. The demographic rates of each class are organised in a matrix where they are expressed as transition probabilities, the contribution of any individual in one size class to any other size class during one time step. The mathematical properties of these matrices are well known (Caswell 1989) and allow not only to calculate the population growth rate, but also to compare species with widely varying life-history attributes.

Large parts of the present study were carried out in undisturbed forest. This seems a strange place to study the effects of logging. However, unlike exploited forests where rapid changes occurred and continue to occur in microclimate, forest structure and vegetation composition, in undisturbed forest the present-day conditions of individuals are broadly representative for the conditions under which they established and have grown during their lives. Most individuals in exploited forest established in another environment, and much biological information that is contained in a population (*e.g.*, the structure of the population) is caused by an unknown mixture of pre- and post-logging demographic pressures.

## Sustainable management

The concept of sustainable management of tropical rain forests has focused many minds and stimulated much research, but has not produced a workable definition on which to base a population dynamical study. By definition a population dynamical study addresses single species and is therefore limited to produce some ingredients rather than the recipe for sustainable management of tropical rain forest, which in its turn is only one dish in the meal of the sustainable development of a country. Most definitions of sustainable forest management are much wider. They usually contain criteria concerning the quality and quantity of the forest ecosystem (extent, conservation of biodiversity, health and vitality), its functions (protection and production) and social and economic needs (Lanly 1995). Given the fact that this study was limited to the life and death of three rain forest species, a much more limited working definition for 'sustainable management' needed to be adopted. The matrix modelling approach provides an attractive approach: sustainable management of a tree species is that management that maintains a positive (or rather non-negative) long-term population growth rate (*e.g.*, Usher 1966, Peters 1996). This growth rate can easily be calculated from the demographic rates of a population with a matrix model, and the effect of changes in the demographic rates can also easily be determined. The simplicity of this

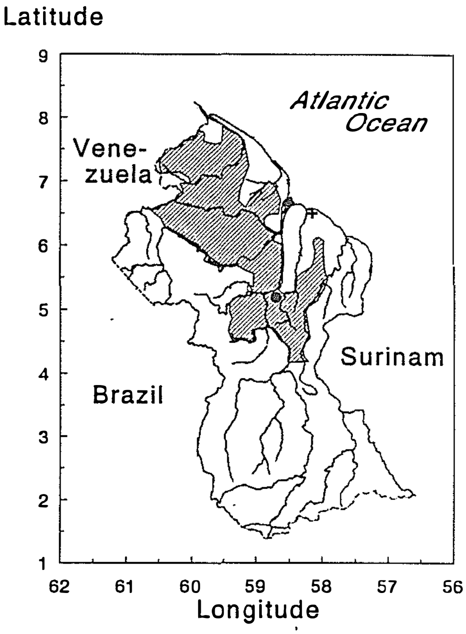


**Figure 1**
Guyana and the location of the study area at Mabura Hill (dot), the capital Georgetown (cross) and the approximate extent of logging concessions (hatched). Source: WRI (1997).

definition is its main attraction, and also the main reason for suspicion: it is hard to imagine that trees characterised by a complex life cycle lasting several centuries, modelled by the interaction of multi-faceted biotic and abiotic forces on many temporal and spatial scales can be satisfactorily summarised by something as simple as one single statistic. Apart from this, it should be noted that sustainable management is not equivalent to maintaining the status quo of the forest. Each forest will change under management, and therefore a definition based on non-negative population growth rate has its limitations. In chapter 9 I will consider slight variations on this approach of sustainability, applied on the species that is being exploited.

## Guyana and tropical rain forest in a nutshell

Guyana, ‘land of many waters’, is situated at the north-eastern margin of the South-American continent (Fig. 1), on the Guiana Shield which forms a distinct phytogeographic province from the Amazonian rain forest proper (Berry *et al.* 1995). The population is strongly concentrated in a narrow strip along the coast (Table 1), and the Interior has long remained without major human influence.

The climate of Guyana is tropical, with a mean temperature of 26°C and a rainfall which is concentrated in two periods: the long rainy season (May-August) and the short rainy season (December-February). The rainfall varies with the orogeography of the country between 1700-4400 mm annually. No month receives less than 100 mm on average, although periods of drought occur at times (ter Steege 1993).

**Table 1**

**Guyana: key statistics. Not all statistics are compatible because they are from different sources. All amounts of money are in US$.**

| | | |
|---|---|---|
| **Guyana: country and economy** | | |
| State form | Co-operative Republic | • independent from UK since 1966 |
| Area | 214.970 km$^2$ | |
| Population (1992 est.) | 739.000 | • East Indian (51%), African (29%), Mixed (14%), Amerindian (4%), rest (2%) |
| Capital | Georgetown | • 284.000 inhabitants |
| Population density | 3.4 km$^{-2}$ | • 115 km$^{-2}$ in the coastal plain |
| Annual net population increase (1992) | 1.4% | • more than compensated by emigration rate (2.0%) |
| GDP (1992) | $375 million | • $500 per capita |
| Annual growth of GDP (1992) | 7.8% | • inflation 14% |
| Debt to GDP Ratio (1996) | 392% | • debt $2.1 billion; $2825 per capita |
| Debt service (% of current revenue) (1995) | 71.6% | • projected to fall to 40% in 1999 |
| Trade (1992) | exports $322 million<br>imports $307 million | • gold (32%), sugar (29%), bauxite (19%), rice (14%) |
| **Forest and forestry** | | |
| Forest cover (1990) | 187.550 km$^2$ | • 87% of land area |
| Annual change (1981-1990) | -0.09% | • one of the lowest world-wide |
| Contribution of timber to export | 2% | |
| Log production (1995) | 425.000 m$^3$ | • average 1955-1990 *c.* 190.000 m$^3$ |
| Proportion *Chlorocardium* (1995) | 10-15% | • average 1955-1990 *c.* 50-70% |
| Government revenue from logging (1995) | $1.000.000 | • acreage fee $0.15/acre; royalties $0.58-2.70/tree |
| Sales price for rough, dressed sawnwood (1995) | $318-412 m$^{-3}$ | • volume of a *Chlorocardium* in the forest *c.* 2 m$^3$ |
| Forest concessions (1996) | 51.000 km$^2$ | • equivalent to *c.* 55% of land suitable for forestry |
| National Parks | 117 km$^2$ | • plus 3600 km$^2$ Iwokrama International Rainforest Project |

Sources: General data from Guyana info pages on Internet (http://www.guyana.org/backgrou.htm); Inter-American Development Bank evaluation reports (http://ww2.iadb.org/eval/GY-sint.htm). Forestry data from WCMC (1992), Sizer (1996) and WRI (1997). Original sources are mentioned in these publications.

Pristine rain forests cover Guyana for *c.* 87%, and deforestation rates rank among the world's lowest: 0.1% annually (WRI 1997). The regional variation in composition and structure of the rain forest in Guyana is large, and led already early to classification schemes (Davis & Richards 1933, 1934; Fanshawe 1952). Classifications are based on physiography (*cf.* Huber *et al.* 1995), soil type, inundation (Ter Steege et al 1993, Jetten 1994), and they are in many cases strongly characterized by the occurrence of dominant species. Dominance by few species and, to Amazonian standards, a moderate species richness (*cf.* Ek & van der Hout *in prep.*) set the Guyanese forests apart from most other forests in South America.

The Guyanese rain forest is very much the cradle of tropical forest ecology. In Guyana (then British Guiana) Davids and Richards did their work on forest structure and composition, that, published in 1933 and 1934, became one of the pillars under Richards influential textbook on the tropical rain forest (first published in 1952). After that, knowledge of the ecology of Guyanese forests has progressed slowly. Most research was concentrated on the ecology and silviculture of *Chlorocardium rodiei*, the main timber species of the country (Fanshawe 1947, Clarke 1956, Prince 1973). While botanical exploration continued at a steady pace from 1981, systematic ecological research was resumed only in 1989 with the Tropenbos Programme (with predecessors and associated projects; ter Steege *et al.* 1996), soon to be followed by the Iwokrama International Rainforest Programme. This surge in scientific research accompanied a similar increase in the activity of the Guyana forest industry, and although certainly not limited to forestry related research, most of these research projects take sustainable exploitation of the forest as their *raison d'être.*

While logging, mainly for Greenheart (*Chlorocardium rodiei*), has been ongoing for most of this century, forestry is recently increasing, and a number of large, mostly Asian loggers have been granted large forest concessions (Colchester 1994, Sizer 1996). This increase comes at a time that the Forestry Commission, the supervising and regulating body of forestry in Guyana, is vastly under-staffed and under-financed (the British Overseas Development Agency has recently started a large support programme). This has fed rising concern over the future of the Guyanese rain forests, not only in Guyana but world-wide (Sizer 1996).

## The Tropenbos Programme

The Tropenbos Foundation, funded by the Dutch Government, carries out multidisciplinary research programs in collaboration with research institutions and Governments of tropical countries. Its main objectives are (Tropenbos 1995):

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

These objectives are realised at five main sites scattered over the tropical zone: Indonesia, Cameroon, Côte d'Ivoire, Colombia, and Guyana.

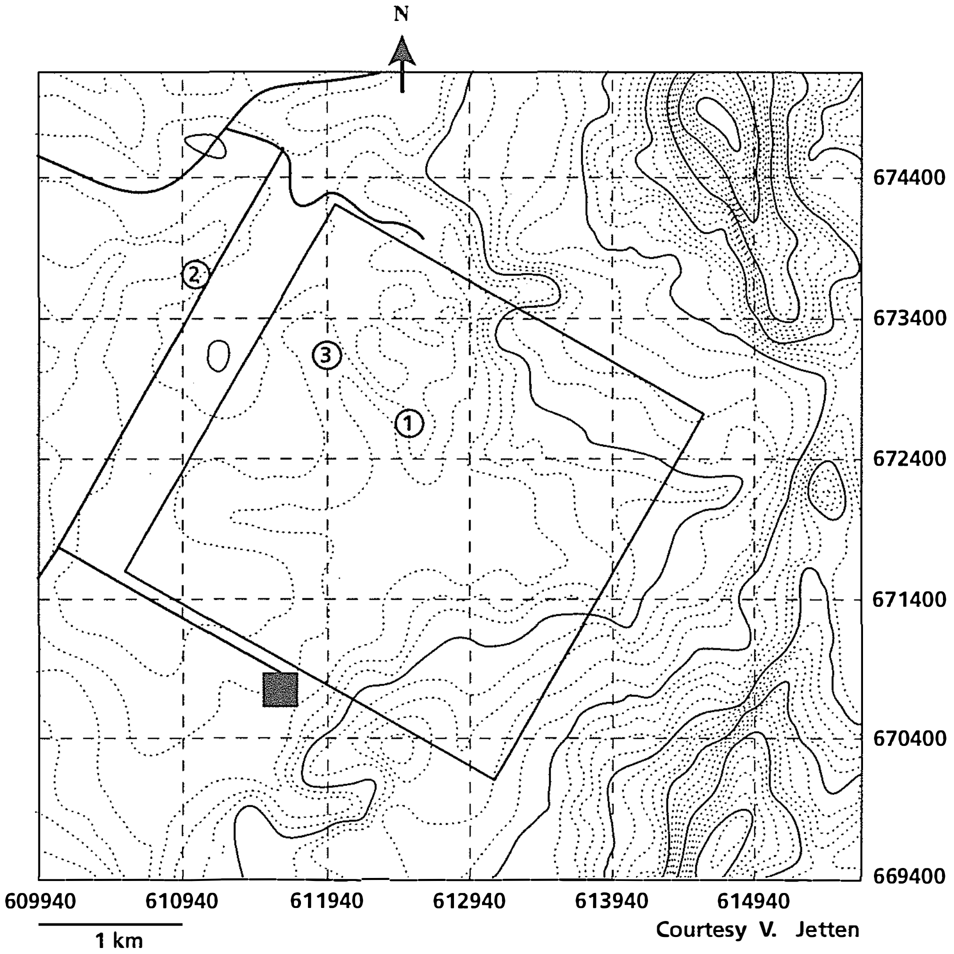
The aims of the Tropenbos-Guyana Programme are 'to achieve an understanding of the lowland tropical rain forest ecosystems in the area to such a degree that timber harvesting (and possibly non-wood products) under a sustainable forest management system can be achieved without it leading to biodegradation and loss of proper hydrological functions of the exploited system, while at the same time a satisfactory level of biodiversity is maintained and an appropriate area of rain forest can be conserved' (ter Steege *et al.* 1996).

It is based at Mabura Hill (5° 13' N 58° 48' W), *c.* 230 km South of the capital Georgetown (Fig. 1). Mabura Hill is a logging community (population *c.* 1000) established on the concession of Demerara Timbers Ltd. (DTL), which is presently owned by Primegroup Investments (Singapore). Exploitation of timber resources in DTL's 5.500 $km^2$ timber concession started in 1986. In 1988 a 900 ha Ecological Reserve with Field station was created in primary rain forest for the Tropenbos-Guyana Programme (ter Steege *et al.* 1996). In the Reserve the major forest types present in the concession area are represented.

The Programme set out in 1989 as a co-operative effort between various Guyanese, Dutch and English institutions. A multi-disciplinary and integrated research programme was designed including:

- inventory of soils and vegetation (van Kekem *et al.* 1997);
- a set of handbooks of the 100 major timber species of Guyana: recognition, timber characteristics, a lens key and anatomical characteristics (Polak 1992, Brunner *et al.* 1994, Gérard *et al.* 1996);
- hydrological study (Jetten 1994);
- nutrient cycling study (Brouwer 1996);
- population dynamics study (this study);
- growth in relation to environmental constraints (ter Steege 1993, Boot 1994, Raaimakers 1994);
- plant-animal interactions (Hammond & Brown 1995, Hammond *et al.* 1997);
- logging intensity study (ongoing);
- biodiversity study (ongoing);
- radar and remote sensing study (ongoing).

A comprehensive review of results of the First Phase of the Programme (1989-1993) and recommendations for management have been compiled by ter Steege *et al.* (1995, 1996). Currently the Second Phase (1993-1996) of the Programme is under way, with new research projects.



Courtesy V. Jetten

**Figure 2**
The Ecological Reserve with the plots used in this study. 1 = undisturbed plot; 2 = exploited plot; 3 = white sand forest plot (used in Chapter 4).

## Objectives and means

The general objectives of the present study are:

1 to describe and understand the population dynamics of tropical rain forest tree species, with an emphasis on its relation with light;

2 to explain the impact of timber exploitation on the demography of these species, and

3 to construct a population model that can be used to assess the consequences of exploitation on these species.

The main timber species of Guyana (at the time the study started), and therefore the focal species of the Tropenbos-Guyana Programme was *Chlorocardium rodiei* (Schomb.) Rohwer, Richter & v.d. Werff (syn. *Ocotea rodiaei* (Schomb.) Mez.; Lauraceae, Greenheart). *Chlorocardium* is a shade-tolerant, dominant species of the main canopy in the forest types described above, and is reputed to require small gaps for regeneration. It is the only species of the three study species which is commercially exploited. Two other species were selected for study, on the basis of their abundance, their different regeneration requirements, their importance as potential competitor of *Chlorocardium*, and their biologically interesting features. *Dicymbe altsonii* Sandw. (Caesalpiniaceae, Clump Wallaba), is a co-dominant of the canopy, a shade-tolerant that responds strongly to canopy opening and has the peculiar habit of producing stem suckers as a means of vegetative reproduction. *Duguetia neglecta* Sandw. (Annonaceae, Yarri yarri) is a treelet of the understorey which is probably capable of completing its life-cycle in the shade.

The objectives were addressed by means of a field study in permanent sample plots. The growth and survival of tagged and mapped individuals of the three study species were monitored over 3 years (4 censuses between 1991-1995) in plots of 2-4 ha. The effects of logging were studied by comparing an undisturbed plot with a plot which was logged (for *Chlorocardium* only) in 1988.

All research reported in this study was carried out in the Ecological Reserve (undisturbed plots) or just outside it (plot exploited in 1988). The study limited itself to the forest type that is dominated by Greenheart, which was one of the three species studied. Greenheart forest is a colloquial name for one of several *Chlorocardium*-rich forms of the *Eschweilera-Licania* association (Fanshawe 1952). Descriptions can be found in Davis & Richards (1933, 1934), Fanshawe (1952), ter Steege *et al.* (1993, 1996), Ek & van der Hout (*in prep.*) and in Chapter 6. This forest type is associated with extremely nutrient-poor, well drained brown sands of varying clay content (see Brouwer (1996) and van Kekem (1997) for precise classifications and descriptions) in gently sloping terrain.

## A sneak preview

This thesis is organised along two main lines. After an introductory chapter (chapter 2) the study moves gradually, from flowers, via germination and vegetative reproduction to seedlings and finally adolescent and adult trees. The integration in population models is last, just before the general discussion. The second line of organisation carries from undisturbed forests (chapters 3-6) to exploited forests (7-8).

Chapter 2 is a general introduction on population biology and its relation with biodiversity. The role of seedlings for determining forest composition is discussed, and the major factors that affect the course of succession are evaluated.

Chapter 3 focuses on demographic processes that occur even before seedlings are produced: the floral stage of *Dicymbe.* The mast-flowering behaviour of this species is investigated, and the relation between floral demography and nutrient dynamics is studied.

Chapter 4 unveils another reproductive peculiarity of *Dicymbe* : its potential for rejuvenation through stem suckers. These may grow out to trees after the death of the parent. In this chapter the contrasting occurrence and potential of suckers for regeneration is compared between different forest types.

Chapter 5 shows that *Chlorocardium* also has remarkable regenerative capacities. Its seeds fall over many months, and they may take between 3 and 36 months to finish their germination. The relation between the timing of germination events and rainfall is discussed, and it is considered whether this behaviour could act as a mechanism to spread the risk of germination.

Chapter 6 compares the distribution, growth and survival of seedlings of *Chlorocardium*, *Dicymbe* and *Duguetia*, and is concerned with factors that may affect this, such as light and seedling size. It is tested whether there is a relation between demographic behaviour in deep shade and in well-lit environments, and whether this might explain the co-occurrence of these species.

Chapter 7 continues where 6 stopped, by studying seedling demography of *Chlorocardium* in exploited forest. It is shown that for *Chlorocardium* seedlings exploited forests are not light at all, and how they cope with the gloom.

Chapter 8 finally integrates growth, survival and reproduction of these species in matrix models. Exploited and non-exploited populations are compared, and it is tried to estimate the age of tropical trees. To conclude, promising ways are identified to increase the growth of *Chlorocardium*, for the benefit of future harvests.

chapter 2

# Community structure and the demography of primary species in tropical rain forest

*Roderick J. Zagt & Marinus J.A. Werger*

## Abstract

Equilibrium and non-equilibrium theories have been proposed to explain the high species richness in tropical rain forests. Equilibrium theories suggest that species differ in their regeneration requirements and partition the available space over resource gradients. Non-equilibrium theories propose that most species have similar resource requirements and emphasise chance as the major factor determining the species composition of tropical rain forests.

Close inspection of the literature reveals that support for non-equilibrium theories comes from studies on large (diameter >10 cm) or at least well established trees, whereas support for equilibrium theories comes from studies on seedlings.

In inter-specific comparisons, large trees are more likely than seedlings to be classified as generalists that do not show habitat specificity. This is because their growth and mortality responses are too slow and insensitive; the methods of measuring growth are too inaccurate; current methods are capable of measuring only part of the spectrum from very negative to very positive plant responses; and the abiotic environment cannot be quantified with sufficient precision as to detect small but significant differences between species. The growth and survival of seedlings are in a number of ways more easy to quantify with accuracy. However, large scale seedling studies are scarce and often only quantify seedling numbers, not size.

The contributions of chance and determinism to successful regeneration are not constant during the different stages of the regeneration cycle. Processes occurring before gap formation partly determine the result of interspecific competition after a gap has formed. Even though the spatially and temporally stochastic availability of seedlings, and stochastic seedling mortality may dominate seedling dynamics in the understorey, interspecific differences in growth and mortality and variation in resource availability may affect the size and condition of the seedlings at the onset of the gap phase. Therefore seedling studies should not limit themselves to gaps, but also address the understorey.

Owing to a higher availability of resources, species-specific differences in growth are more pronounced in the gap phase than in the understorey, and the contribution of chance factors to regeneration is less.

Among generalist tree species, species that differ in competitive ability, and in the abundance of seedlings and their spatial distribution may maintain themselves in the community at different population size distributions, which represent different pathways towards successful regeneration. Species which are weak competitors in gaps may locally recruit through chance by being common as a seedling.

In efforts to resolve the issue of species maintenance in rain forests, seedlings should be included in large scale, long-term demographic studies, and the full variability of their biotic and abiotic environment should be addressed

chapter 2

# Species richness and guild delimitation

Tropical rain forests are characterised by a remarkably high species richness (Whitmore 1984; Gentry 1988; Valencia *et al.* 1994). A number of theories have been advanced to explain the coexistence of large numbers of species with apparently similar regeneration requirements in the same area. These theories are generally grouped as equilibrium and non-equilibrium theories (Connell 1978).

Equilibrium theories emphasise a differential adaptation of species to specific conditions of growth, survival, or reproduction that occur from time to time during the life cycle of the species (Clark & Clark 1987). 'Gap partitioning', and 'compensatory mortality' are two applications of equilibrium theories. Gap partitioning occurs when species are niche-differentiated, and, through different requirements of growth, survival and reproduction, regenerate optimally in gaps of different sizes (Hartshorn 1978, 1980; Whitmore 1978, 1984; Denslow 1980; Orians 1982; Brokaw 1985, 1987). Compensatory mortality in the form of frequency, density or distance-dependent mortality is seen as promoting species coexistence because it prevents self-replacement of species at a location. This mechanism is most often considered in the context of parent-offspring relations as in the Janzen-Connell model (Janzen 1970; Connell 1971), but density-dependence of growth and mortality among established individuals fits also in this category (*cf.* Condit *et al.* 1994).

The evidence for the Janzen-Connell model is mixed (Condit *et al.* 1992; Hammond & Brown, *in press*). Augspurger (1983a, 1984), Clark & Clark (1984), Connell *et al.* (1984); Howe *et al.* (1985) and Schupp (1988a,b) found either distance or density dependent depression of growth and/or survival among seedlings around adult conspecifics; however, in other cases the expected decrease of seedling mortality rates with increasing distance from the parent tree, or with decreasing seedling density was not found (Hubbell 1979; Forget 1989, 1994; De Steven 1994; Hart 1995; Itoh *et al.* 1995), *e.g.*, as a result of predator satiation. Negative density-dependent relations among larger individuals have been demonstrated for some species (Hubbell & Foster 1987a, 1990; Barros-Henriques & Elias Girnos de Sousa 1989; Condit *et al.* 1992, 1994; Alvarez-Buylla 1994).

In contrast, non-equilibrium theories do not emphasise differential specialisation in species; rather it is pointed out that many species show large similarities in their life histories and functional responses to environmental conditions, and that chance factors and frequency rhythms of environmental disturbance largely explain species co-occurrence. Owing to the unpredictable identity of competing neighbours of an individual in species-rich communities, there is no constant selective pressure that fosters niche-differentiation. Instead, the neighbours exert a competitive pressure which is, at a population level, close to the spatial and temporal average of the community, thereby preventing the development of niche-specificity (Hubbell & Foster 1986b). The composition of the community is considered a 'random walk without a stable composition', determined by chance and historical effects (Hubbell & Foster 1986b).

In both views, gap dynamics play an important role in regulating the species composition of tropical rain forests. The sudden occurrence of an opening in the forest canopy, and its large variation in size, greatly changes micro-environmental conditions below the original canopy (Hartshorn 1978; Brokaw 1982). Furthermore, within each gap a spatial pattern in environmental conditions develops which is related to gap size, form and orientation. This allows, in principle, gap partitioning among colonising species. Germination and the response of pre-established seedlings and saplings to the sudden opening of the forest canopy strongly determine their success in reaching reproductive size. Based on differences in response to these gaps, species are often grouped as long- and short-lived pioneers, gap-dependent, and gap-independent species (or equivalents; Aubréville 1938; van Steenis 1958; Lieberman *et al.* 1985a; Lieberman & Lieberman 1987; Clark & Clark 1987; Bongers *et al.* 1988; Swaine & Whitmore 1988). The extent to which the species show life-history differentiation within these groups is widely debated (Connell 1978; Hubbell & Foster 1986b).

A large body of evidence, gathered mainly at the 50 ha plot on Barro Colorado Island (BCI), Panama, and at La Selva, Costa Rica in Central America (Hubbell & Foster 1990; Clark & Clark 1992; Lieberman *et al.* 1995) over the past decade and a half, has led to the belief that the forest is not at equilibrium, and that most species possess a wide ecological amplitude with large interspecific overlap instead of narrow tolerance and high specificity (Lieberman *et al.* 1995). Only a few (usually four) large and broad guilds are recognised, depending on the criteria used. The largest is usually a group of generalists or indifferents (Hubbell & Foster 1986a: 57 out of 81 species studied; Hubbell & Foster 1987b; Welden *et al.* 1991: 79 out of 104). Responses to light vary somewhat, but the variation is so large that only a limited number of species are shown to significantly prefer lighter or darker sites (Hubbell & Foster 1986a: 24 out of 81 species studied; Welden *et al.* 1991: 9 out of 104, Lieberman *et al.* 1995: 14 out of 104). Virtually all species may occur under gap and non-gap conditions (Lieberman *et al.* 1995).

Direct evidence of gap partitioning is available for pioneer species which appear to respond to gap size by differential germination and establishment (Brokaw 1987, Raich & Gong 1990), but is weak for climax species. In experiments, the seedlings of a number species have been demonstrated to respond differentially to high light conditions (Popma & Bongers 1988; Osunkoya *et al.* 1993; Boot 1996). In the field many other factors, such as the variation in light availability within gaps and size differences, also determine success in a gap, and this may contribute to the absence of gap partitioning (Barton 1984; Brown & Whitmore 1992).

On the basis of these data, the current view seems to be that a small number of guilds can be distinguished among rain forest species (Lieberman *et al.* 1985a; Hubbell & Foster 1986a, 1987b; Lieberman & Lieberman 1987; Bongers *et al.* 1988; Welden *et al.* 1991; Clark & Clark 1992; O'Brien *et al.* 1995; Newbery *et al.* 1996), but that most species fall into a broad, generalist group.

From careful consideration of these studies, it seems that the support for theories that assume randomness to be the force organising communities is usually derived from research on trees which are either large (as in Lieberman *et al.* 1995: dbh ≥10 cm) or at least well established, as in the BCI-studies (Hubbell & Foster 1990: dbh ≥1 cm). Few of these studies include seedlings and saplings (Clark & Clark 1987, 1992: seedlings of 50 cm height and up).

In contrast, support for theories that assume species-specific differences in growth and survival frequently comes from studies on seedlings (Clark & Clark 1984; Popma & Bongers 1988; Osunkoya *et al.* 1993, 1994; Kitajima 1994). A striking illustration of this point is that *Quararibea asterolepis, Tetragastris panamensis* and *Trichilia tuberculata* are three of the many generalist, undifferentiated tree species of the 50 ha plot on BCI in terms of their established plant dynamics (Welden *et al.* 1991), whereas these species, in exactly the same plot, showed 'large differences in seedling and sapling recruitment', which were 'directional, rather than stochastic' (De Steven 1994, p. 380), when their smallest life stages were considered.

In this paper, we will address the balance between species-specific (directional) and random processes in the determination of successful regeneration in the forest against the background of the methodology of studying trees and seedlings. In order to avoid drawing this discussion into an analysis of well established differences between pioneers and non-pioneers, we will focus on the large group of generalist species that germinate in the understorey; require gaps for regeneration, reach the canopy, and appear to coexist without apparent life history differences or apparent habitat segregation. We will pay special attention to the relation between plant performance and the light climate, even though we acknowledge that species may show differential responses to variation in water and nutrient availability, and that these factors thus contribute to the composition of communities. However, comparably few studies focus on these factors (but see recent papers by Huante *et al.* (1995), Burslem (1996) and Veenendaal *et al.* (1996) for large comparative studies of the influence of nutrient availability on growth in tropical tree seedlings).

We use 'species richness' to mean the number of species per unit of homogeneous forest area, that is homogeneous in meso-climate, hydrology and soil. We define a gap as any patch which is suitable for rapid plant growth, independent of the exact delineation of the canopy opening or the quantity of available resources. In regeneration we include the entire process of the establishment of a seedling until the emergence of a reproducing individual (although we will generally refer to the initial phase of that process). In the term 'seedling' we include saplings up to about 3 m height, and consider trees over 10 cm dbh as 'large trees'. Speaking about chance factors, we mean those factors that work in a probabilistic fashion, the occurrence of which can not be influenced by the plant and the effect of which on regeneration processes is thus unpredictable. We choose a phytocentric view. So, for example, although many herbivores will find and attack plants according to a certain search strategy rather than chance, for individual plants it is unpredictable whether it will be attacked or not, and thus we consider herbivory a chance factor. Deterministic factors, as used here, encompass those characteristics in plants which lead to a predictably different response of different species which are subject to the same conditions.

## Why do large trees always appear generalists?

The reason for the apparent discrepancy in results between seedling and 'large tree' studies is found in a number of methodological and conceptual limitations in the latter, when compared with seedlings (Table 1):

**Table 1**
**Aspects of the measurement of responses to environmental factors in large trees and seedlings.**

| Feature | Large trees | Seedlings |
|---|---|---|
| **Response of growth and survival to environmental factors** | limited, slow | strong, rapid |
| **Mortality rate** | low, largely stochastic | potentially high, partly stochastic |
| **Measurement of plant size** | difficult, inaccurate | relatively easy, accurate |
| **Measurement of negative response to unfavourable conditions** | nearly impossible | possible |
| **Light climate during the history of the individual** | usually highly variable | usually limited variability |
| **Measurement of the light climate in the crown area** | difficult, inaccurate | easier, often also inaccurate |

### Tree responses are slow and insensitive

Functional responses in large trees are often very small, or very slow. Changes in stem diameter in many species take a long time to become sufficiently large to be measurable. Death which is caused by potentially specific mortality agents, such as pathogens or drought, is often delayed until after a long period of decline. This hinders detection of this causal relationship. Random responses however, which are not very informative about species-specific differences, may be very strong, such as is the case with stochastic mortality due to wind-, tree- or branch-fall (Uhl *et al.* 1988; Yavitt *et al.* 1995; van der Meer & Bongers 1996). Furthermore, mortality among large trees is low (generally between 1 and 3% per year (Lieberman *et al.* 1985a; Clark & Clark 1992; Condit *et al.* 1995a), and this makes accurate determination of species-specific mortality rates difficult.

Seedlings, on the other hand, die quickly, in large numbers, and from a variety of causes. They show more sensitivity to levels of pathogen infestation and herbivory (Augspurger 1984; Augspurger & Kelly 1984; Clark & Clark 1985; Osunkoya *et al.* 1992; Itoh *et al.* 1995) than larger trees. Mortality rates of seedlings drop rapidly with increasing size (Hartshorn 1972; Clark & Clark 1992), and in most species survival of

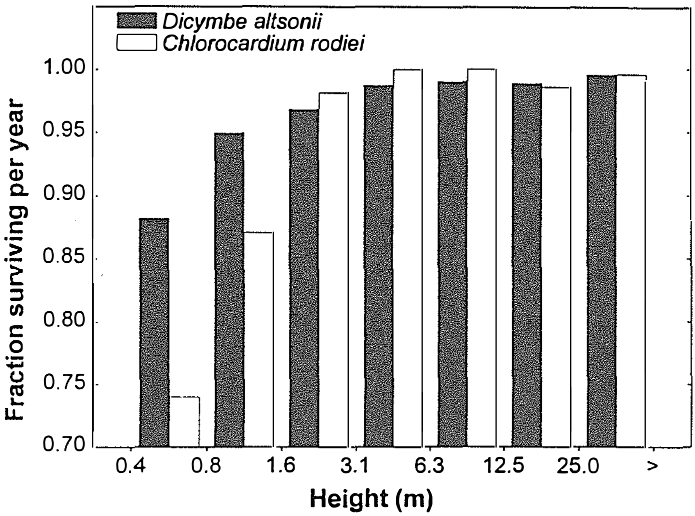


**Figure 1**

**Average yearly survival of the climax species *Dicymbe altsonii* and *Chlorocardium rodiei* in rain forest near Mabura Hill, Guyana. Data is from individually tagged individuals in two 1 ha demographic study plots in tropical rain forest near Mabura Hill, Guyana, which were monitored yearly during 1991-1995. Seedlings <1.3 m height were monitored in a 5% sample. The individuals were classified in categories of doubling height (for individuals below the canopy) and for individuals in the canopy (height >25 m). The population size per size class varied between 20 (larger trees) and 1015 (seedlings).**

individuals above 1 cm diameter is already more than 97% (Welden *et al.* 1991; *cf.* Fig. 1). Seedling growth also responds strongly to variations in resource availability, such as light (Augspurger 1984; Popma & Bongers 1988; Osunkoya *et al.* 1993; Boot 1996).

### Diameter measurements are inaccurate

It is hard to accurately measure the size of a large tree. Diameter at breast height (dbh) is the most common measure of tree size since it generally correlates well with other dimensions, such as height, crown diameter and crown area (Alvarez-Buylla & Martínez-Ramos 1992; O'Brien *et al.* 1995; Condit *et al.* 1995a; King 1996) and biomass, which is the variable of real interest. However, the allometry of these dimensions to dbh is far from perfect, *e.g.*, as a result of branch loss due to senescence or falling trees. The measuring error in dbh is of a comparable magnitude to the annual diameter growth in many tree species. Moreover, the dbh of large trees does not respond promptly and accurately to changes in biomass over the short time given to most demographic studies. Therefore, measurement of dbh increments is convenient, but not very suitable to detect small differences in growth between species, except in long-term studies. In seedlings and saplings it is easier to determine dimensions, including biomass (through allometric relationships which include more parameters), and hence responses to environmental variations.

### Negative performance can not be quantified

Height or diameter measurements are better at detecting positive than negative performance. Reductions in height or diameter are usually the result of damage, and not a functional response. Generally, negative responses under adverse conditions are difficult to quantify in large trees. In seedlings height or diameter measurements are also inadequate to register negative performance, but changes in biomass or leaf loss are easier to quantify.

### The measurement of the light climate of a tree crown is difficult

The light climate is among the most variable environmental factors in the tropical rain forest and may be expected to cause clear plant responses. Its precise measurement is difficult, however. The present light climate in the crown of a large tree, which is sometimes used to demonstrate (the absence of) species-specific responses to crown light environments (Clark & Clark 1992; Lieberman *et al.* 1995), is not necessarily a proper reflection of the crown light environments under which the tree grew up. The physical environment around and above each individual is subject to continuous change, as gaps close and new ones form. The older a tree, the lower probably is the correlation between its present light climate and the light climate in which it grew up. For seedlings this is less of a problem as their history is shorter. Moreover, seedlings are small and thus cover a short distance at the lower end of the vertical light gradient in the forest.

The larger a tree, the more difficult it is to adequately quantify its light climate. Many methods have been applied. There are indirect, qualitative methods such as the classification of sites in gaps (defined as areas with a canopy less than 10 m high) and non-gaps (canopy higher; Hubbell & Foster 1986a; Welden *et al.* 1991). Also indirect, but quantitative methods are the determination of the number of tree crowns above an individual (Clark & Clark 1987, 1992), the canopy closure index of Lieberman, Lieberman & Peralta (1989) and Lieberman *et al.* (1995), and gap size (Brokaw 1982). These methods have in common that they are based on the size or extent of vegetation around or above a plant, rather than the amount of light that the plant is receiving.

Other methods are more directly concerned with the amount of light received by the plant. The Dawkins crown position score (Dawkins & Field 1978; Clark & Clark 1992; Oberbauer *et al.* 1993) is a semi-quantitative measure, while hemispherical photographs (Chazdon & Field 1987; Whitmore *et al.* 1993; ter Steege 1994b), diffuse light (LAI meter) measurements (Machado, Zagt & Reich *unpublished data*) and radiation measurements with light sensors (Oberbauer *et al.* 1988; Brown 1993) are quantitative. Not all of these methods are equally easy to use in large trees, although most can be employed in some way (see *e.g.*, Sterck 1997 for hemispherical photographs taken in tall trees).

Correlations between the scores obtained by these methods and measured irradiance are rarely determined (but see Chazdon & Field 1987; Clark & Clark 1992; Whitmore *et al.* 1993; ter Steege 1994b), but these are likely to be low in the case of the qualitative and semi-quantitative methods as these have limited resolution and large inherent measuring errors. This hampers the detection of subtle interspecific differences in light requirements with some methods to such an extent that it cannot even be expected to find differences between species.

It seems realistic to assume that there is a significant negative correlation between the size of the tree and the accuracy of the light measurement in its crown. Moreover, light availability has been shown to be highly variable within crowns (Oberbauer *et al.* 1988). Therefore the value of single determinations of light is limited for large crowns. For seedlings, appropriate light measurements remain cumbersome and laborious, but less so than for large trees, and they are likely to achieve higher accuracy.

In conclusion, the problems associated with the study of large trees alone may have led to a failure to distinguish more than a few broad species groups and an overemphasis of the importance of random processes governing regeneration. However, this is not to say that random processes are unimportant, nor that a high degree of specialisation occurs among climax species. The matter is simply not exhaustively explored with the most commonly applied research strategy of studying large trees alone. As shown, seedlings have clear advantages for demographic studies and are more suitable to evaluate the existence of species-specific regeneration strategies.

## Why have seedling studies so far not demonstrated species-specific differentiation?

In spite of the advantages seedlings have for the study of species richness, and interspecific differences, this has not yet led to firm conclusions. Apart from practical problems of seedling identification and usually high seedling densities, three factors have contributed to this situation: the lack of large-scale studies on seedling dynamics; the difficulties in quantifying dose (such as light) and effect (such as growth) for large populations of plants under field conditions; and contribution of chance factors to regeneration.

### Scarcity of seedling studies

For seedlings, there are, hitherto, few if any studies of the same scale and scope as the large plots in Central America for the study of large trees. The number of species that is studied is much less, and the time-span of the studies is usually short (*e.g.*, Howe *et al.* 1985; De Steven 1994; but see Li *et al.* 1996). Also, many results are obtained under experimental conditions, in artificial treatments and in absence of competition from other species (*e.g.*, Popma & Bongers 1988; Boot 1996).

### Quantifying plant responses in seedlings

The methodological problems of quantifying environmental heterogeneity and plant responses are much easier to overcome in seedlings than in large trees. A suitable set of size parameters should ideally reflect as closely as possible the underlying mechanisms of plant performance, *e.g.*, the parameters used for growth analysis (Lambers & Poorter 1992). Unfortunately, it is difficult to measure relative growth rate (RGR), leaf area ratio (LAR) and net assimilation rate (NAR) non-destructively (even for above-ground parts). For this reason, in many demographic studies only the number of seedlings and their stem length is determined (*e.g.*, Brown & Whitmore 1992; De Steven 1994; Li *et al.* 1996), and the opportunities for more precise quantification of resource availability, plant size and plant responses are lost. The stem is hardly involved in the acquisition of resources, by itself not very informative about the condition of the seedling, and not necessarily correlated with plant growth (Whitmore & Brown 1996).

As leaves are the principal light intercepting organs, it seems essential to determine the leaf area in demographic studies. Moreover, leaf area appears to be a highly responsive variable explaining interspecific differences in performance. Height growth was correlated with leaf area for *Dipteryx panamensis* and *Lecythis ampla* saplings, even in understorey conditions, at La Selva, Costa Rica (Oberbauer *et al.* 1988); for the same *D. panamensis* it was shown that seedling survival was correlated with leaf length, and with the number of leaves per seedling at 7 months after germination (Clark & Clark 1985). In *Pithecellobium elegans* and *L. ampla* at La Selva, height growth correlated with leaf area and the diffuse site factor (or ISF, Whitmore *et al.* 1993) in understorey conditions (Oberbauer *et al.* 1993). Also, in seedlings of 5 out of 10 pioneer species in light gaps on BCI, leaf area was correlated with survival (Garwood 1986).

In interspecific comparisons LAR correlates well with RGR as long as the light gradient is not too long (as may be assumed to be the case in the forest understorey; Kitajima 1994; Osunkoya *et al.* 1994; Huante *et al.* 1995; Boot 1996). Although the amount of leaf-area per unit stem length is probably the best correlate for LAR, it is a time-consuming exercise to determine it at a large scale in the field. In species with a largely constant leaf size the number of leaves per unit stem length, or leaf density, can be used as an easy and satisfactory approximation of LAR that can easily be quantified in the field (Ashton 1990). In practice, however, this relation holds true for only a small fraction of the species (Fig. 2). Nevertheless, leaf density may prove to be a useful measure as it provides a performance index which can assume negative values, *e.g.*, as a result of leaf abscission under unfavourable conditions such as deep shade, drought, or sudden increases in light.

### Chance-effects

Even if competitive exclusion among climax species in the rain forest affects regeneration, it may still be difficult to demonstrate it because of chance factors. Chance processes such as mortality from branch falls (Hartshorn 1972; Aide 1987; Clark & Clark 1991), and the occurrence of gaps in relation to the temporal and spatial constraints associated with seed rain and seedling persistence (Hubbell & Foster 1986a; Brokaw 1986; De Steven 1994; van der Meer & Bongers 1996) may obscure the patterns resulting from species differentiation.

The contributions of chance and determinism to successful regeneration are not constant during the different stages of the regeneration cycle. Therefore, in studies of seedling dynamics, the importance of chance and determinism must be evaluated for each of the various stages that characterise the regeneration process.

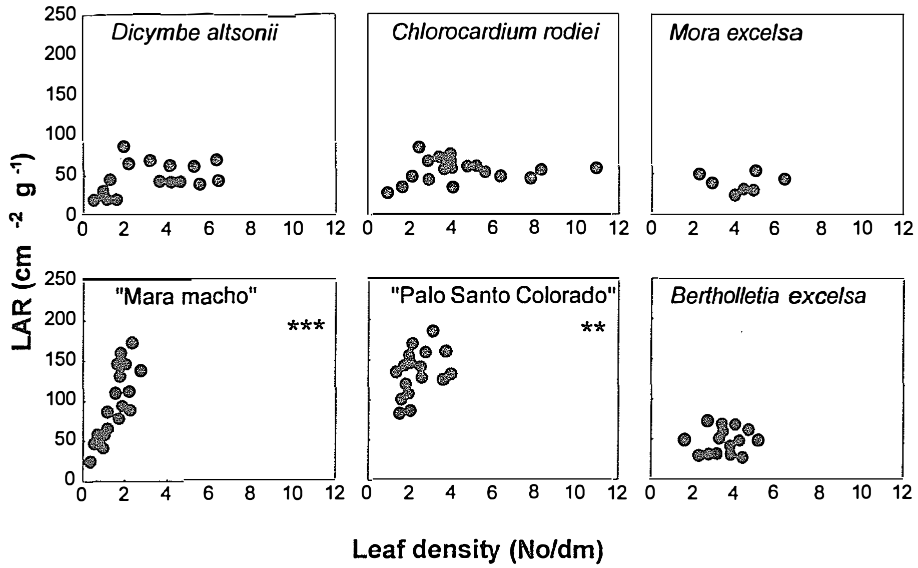


**Figure 2**

**The relation between leaf density (the number of leaves per decimetre stem length) and the leaf area ratio (leaf area per unit plant weight; $cm^2$ $g^{-1}$) for six species of rain forest seedlings from Bolivia and Guyana. Not all species are identified by their scientific name. All seedlings were grown in pots under experimental conditions, in medium and low light (<12% of full sunlight). Stars denote significant correlations (** $p \leq 0.01$; *** $p \leq 0.001$); in the remaining species the correlations were not significant. Sources: R. Boot, *unpublished data* (top row); L. Poorter, *unpublished data* (bottom row).**

## Factors determining successful regeneration in climax species

The recruitment to maturity of a climax species is dependent on its success in two consecutive phases of regeneration. During the first phase seedlings must become established and survive until a gap is formed. During the second phase the seedlings must be successful after the gap has formed, given the initial species composition of that site. Hence, in the first phase the sites of eventual regeneration are unpredictable, so the relevant spatial context is the entire forest understorey (Burslem 1996). In the second phase the foci of regeneration are determined, so then the relevant spatial context is the gap. Only with the start of this phase will competition become an important determining factor.

These two phases are different in terms of resource availability. During the pre-gap phase the seedlings need to be tolerant towards environmental conditions which are close to their physiological minimum requirements, whereas during the gap phase the major constraints to success are likely to arise from the presence of competing neighbours. These phases require different responses in terms of survival and growth from the seedlings. In the next two sections we argue that the presence of a species in a gap

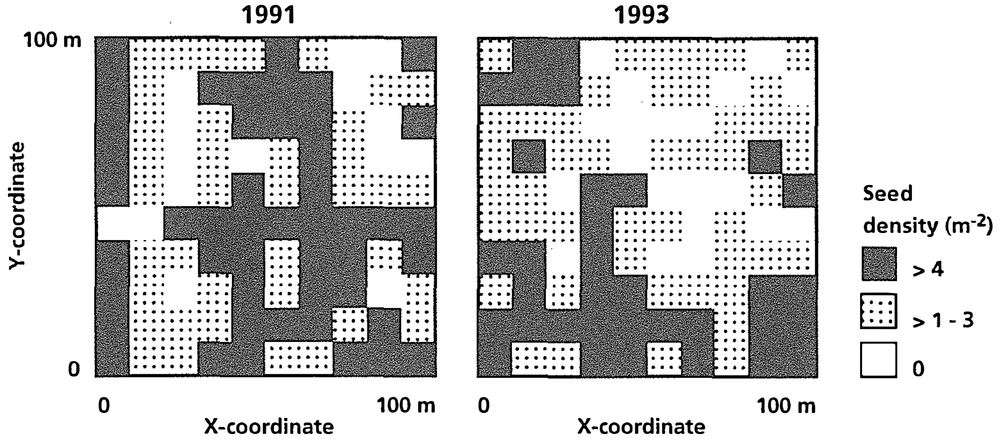


**Figure 3**
**The density per 100 m² of freshly fallen seeds of *Dicymbe altsonii* in 1991 (left) and 1993 (right) in a 1 ha plot in tropical rain forest near Mabura Hill, Guyana. Although the distribution of reproductive adults did not change between those years, the two seed distribution patterns differ considerably between the two years.**

depends more on chance than determinism; and that the success of a seedling in a gap depends more on determinism than on chance.

## Factors affecting seedling abundance of climax species before gap formation

The first phase, the presence of a species as a seedling in a patch at the moment a gap is created, depends on (see also Grubb 1977): the quantity of available seeds in time and space, and on survival and growth of seedlings in the understorey. As a result the composition of the species pool at a given patch fluctuates in time. For a seedling it is important to be in the patch at the moment a gap is created: no gap can be colonised by species whose seedlings have not reached it.

### Seed- and seedling distribution in the understorey

The quantity of seeds and seedlings varies in time (Frankie *et al.* 1974; Garwood 1983; De Steven 1994; Li *et al.* 1996) and in space (Forget 1989, 1994; Bariteau 1992; Fig. 3) In the past, the dispersal of seeds into newly created gaps was considered an important feature (Denslow 1980; Connell 1989). This may be important for pioneers, but less so for climax species, as suitable conditions for their seedling establishment also occur outside the strict boundaries of gaps (*cf.* Popma *et al.* 1988; Lieberman *et al.* 1989, 1995; Schupp *et al.* 1989). In San Carlos (Venezuela), seedlings established prior to gap formation accounted for 83 to 97% of the vegetation at four years after gap formation, and their mortality in the gap was lower than the mortality of newly established seedlings (Uhl *et al.* 1988). Nevertheless, as both the formation of gaps and the distribution of seeds in time and space are independent random processes, chance does play a dominant role in this aspect of regeneration. Shmida & Ellner (1984) have shown theoretically that non-uniform seed dispersal is an important mechanism for the coexistence of (herbaceous) species with similar niches in species rich communities.

### Growth and survival in the understorey

Potential growth in the understorey differs between species. Inter- and intraspecific differences in seed size (Foster & Janson 1985; Hammond & Brown 1995) contribute to differences in seedling size (Howe & Richter 1982; Osunkoya *et al.* 1993, 1994; Boot 1996). Relative growth rates, biomass allocation patterns and leaf dynamics vary between species and between individuals of the same species (Kohyama 1987; Popma & Bongers 1988; Bongers & Popma 1990; Osunkoya *et al.* 1993). Small differences in light availability may lead to differences in inter- and intra-specific growth (Canham 1989): variations in growth rate at light levels below 2-4% of above canopy light levels were shown by Howe *et al.* (1985), Oberbauer *et al.* (1988), Boot (1996) and Burslem (1996). Our own data from Guyana indicate that the growth rates of *Dicymbe altsonii* seedlings were correlated with the diffuse light environment in 22 understorey sites (Fig. 4). Similarly, survival may vary between species at these low light levels (Osunkoya *et al.* 1992; Li *et al.* 1996).

Owing to species-specific growth and survival in the understorey, patterns that form as a result of dispersal may be adjusted or even reversed, as was shown for seedlings of *Gilbertiodendron dewevrei* and *Julbernardia seretii* in Zaire (Hart 1995). *Gilbertiodendron* dominates the canopy, while *Julbernardia* is less common. After seed dispersal more seedlings of *Julbernardia* became established because it was more successful than *Gilbertiodendron* in satiating seed predators. Later, however, *Gilbertiodendron* more than compensated for the initial disadvantage through a much higher 10-year survival in the understorey and it re-established its dominance by the time it reached a diameter of 2.5 cm (Hart 1995).

Therefore, although species-specific differences in growth and survival in the understorey may be small compared to gaps, they do contribute to predictable changes in the composition of seedling communities.

Stochastic aspects of survival in the understorey concern mortality due to falling debris (Itoh *et al.* 1985; Clark & Clark 1991), disease (Augspurger 1983b) and herbivory (Coley 1983). However, species may differ in their ability to defend themselves against pathogens or herbivores (Coley 1983; Augspurger & Kelly 1984).

### Variation in resource-availability in the understorey

Resource availability varies on a small-scale (Chazdon & Fetcher 1984) that may be relevant for seedling establishment and growth. Light availability is heterogeneous at scales of metres (Machado, Zagt & Reich, *unpublished results*; Becker & Smith 1990; Clark *et al.* 1996). Water infiltration rate and other soil-hydrological properties vary at a scale between 2 and 20 m in Guyana (Jetten *et al.* 1993); for nutrients no tropical

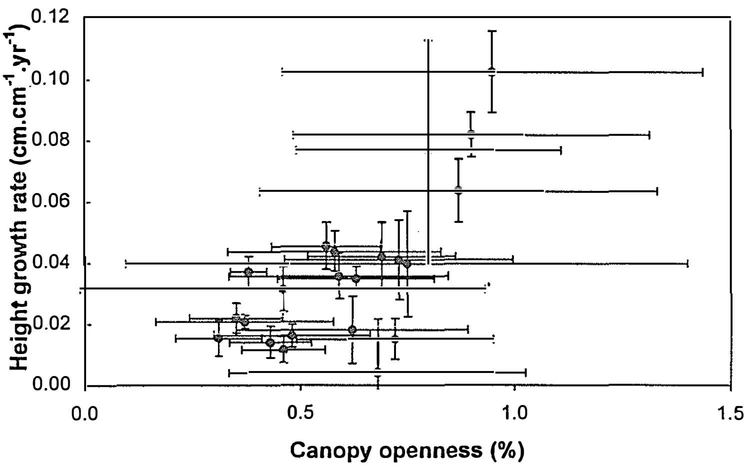


**Figure 4**
**Relation between light environment and mean relative height growth rate of *Dicymbe altsonii* seedlings in 22 understorey plots of 5 m by 5 m (defined as plots with canopy openness <1%) near Mabura Hill, Guyana (see Figure 1 for details). Light was determined with a LiCor LAI-2000; 10 samples per plot. Relative height growth rate is $(\ln h_{t=1} - \ln h_{t=0})/(t_1 - t_0)$, where $h$ is height in cm and $t$ time in days. Only seedlings with leaf density of 0.5-1.0 leaves dm$^{-1}$ that showed no sign of physical damage after 3 years are included in the analysis (n=264). Seedling growth correlated with canopy openness at r=0.60 (p<0.01).**

data are available, but in temperate forest variation of soil pH, potassium and nitrate concentrations was in the range of 2 m (Lechowicz & Bell 1991). This means that in most species appreciable differences in resource availability exist within the dispersal range of single individuals. Hence the conditions that seedlings encounter after germination in the understorey depend more on chance than on determinism, especially for species without directed dispersal mechanisms (Howe & Smallwood 1982).

Seedling dispersal, survival and growth in the understorey determine which seedlings are present at the moment a gap is formed. The distribution of seeds in space, the availability of resources at the site of germination and the formation of canopy openings are all stochastic factors which are likely to have a larger impact on seedling performance than species-specific differences.

## Factors affecting the success of climax species in gaps

Soon after a gap is created, the composition of the pool of competing seedlings is determined; few seedlings that establish after the first few months can compete with the rapidly growing saplings that established earlier (Uhl *et al.* 1988). The success of a species in a gap then depends on: the abundance of the species in the patch, the size hierarchy at the moment of gap formation, differences in growth responses and in mortality, and on the variability in within-patch resource availability. The presence of a species in the gap, or even eventually 'winning' a canopy position does not imply that this species is optimally adapted to the conditions in the gap, or that it is the best competitor, but it means no more and no less than that it did not die out. As long as a species is still present, it is in principle capable of capturing a canopy position.

### Abundance of the species in the gap

The abundance of the species in the gap is a chance process, depending on the location and timing of gap formation relative to the pre-gap seed and seedling dynamics of the species at that site. Having a high abundance in a gap increases the probability for a species of recruiting into the canopy through chance processes. One may argue that in forests where gaps are formed at a slow rate, seedling persistence in the understorey (which is deterministic) plays a more important role in the initial composition of a gap than in highly dynamic forests. In the first case it may take a long time before a gap is formed, so seedlings of persistent species have a higher chance than less persistent species of surviving until a gap is formed. In the second case, the probability of gap formation soon after seed dispersal is higher and seedling persistence is of less importance.

### Size-differences at the moment of gap formation

One determinant of successful regeneration is the hierarchy of size and vitality at the onset of competition (Connell 1989; Brown & Whitmore 1992; Garwood 1986 for pioneer species). Based on an allometric model, Kohyama (1991) emphasised height growth as the main criterion of sapling success, and showed that 'the effort to maximise height growth on the dim forest floor has a critical meaning for the survival and competitive ability of saplings'. Seedling size at the moment of gap formation is partly a function of age and growth conditions in the understorey and partly of species-specific differences in seed size and seedling growth. Larger individuals have a head-start over smaller ones; also, at a given RGR, larger individuals gain biomass faster than smaller individuals (Hartshorn 1972; Uhl *et al.* 1988). Boot (1996) argued that it may take a long time before small individuals with a high potential RGR grow sufficiently to catch up with larger individuals with a lower potential RGR. However, the result of competition between species differing in potential RGR is not only dependent on differences in size, but also on plant density in the competing stand and light availability (Whitmore & Brown 1996).

### Growth and survival in gaps

Among similar sized individuals of different species, the success of a seedling depends on differences in growth and survival at prevailing conditions of light, water and nutrients. Species have been shown to differ in RGR and allocation patterns at the different light levels that can be found in gaps of different sizes (Popma & Bongers 1988; Osunkoya *et al.* 1993; Boot 1996; Burslem 1996), and also in the capacity to acclimate to gap-related environmental conditions (Fetcher *et al.* 1987; Popma & Bongers 1991). Therefore, given similar size, and similar environmental conditions, predictable changes will occur in the size hierarchy between species, and eventually also in species composition due to competitive exclusion.

Mortality in gaps may be related to competitive exclusion or poor acclimation to the gap environment, but mortality due to chance still occurs. Like in the understorey, this concerns pathogens, herbivores and falling debris. The impact of minor damage due to these chance factors is likely to be less than in the understorey, as the improved carbon balance of plants in gaps increases their recovery capacity.

### Variation in resource availability within gaps

The success of a seedling in a gap depends also on the variability of resource availability within gaps, as this determines its ability to compete. Within gaps, a root, bole and crown zone can be distinguished (Orians 1982; Vitousek & Denslow 1986; Brandani *et al.* 1988), each offering a specific combination of resource availability and damage patterns among seedlings. The light conditions within gaps (Clark & Clark 1987), and in their immediate surroundings (Popma *et al.* 1988; *cf.* Lieberman *et al.* 1989) may vary considerably, not only as a result of the gap geometry, but also because of remnant treelets, the fallen tree itself and developing vegetation. Unfortunately, this is rarely quantified (Canham *et al.* 1990), in particular in relation to seedling performance (van der Meer 1995). The relative position of a seedling in a regenerating patch is chance-dependent. On the other hand, competition occurs between direct neighbours, which are submitted to relatively similar environmental conditions. Competition between neighbours is therefore still affected by directional processes. As the seedlings attain a larger size, competitive interactions stretch over an increasingly larger, potentially more variable, neighbourhood.

In conclusion, due to the greater availability of limiting resources, species-specific differences are more pronounced in gaps than in the understorey and more likely to determine the result of competition processes. Nevertheless, chance factors such as stochastic mortality and position within the gap contribute to variation in the result of competition.

## Regeneration strategies

Chance processes and species-specific responses can be expected to have greatly different effects on species recruitment, depending on variation in spatial patterns of seed and seedling abundance. Theoretically, species which are different in competitive vigour (the ability to be successful during the phases of regeneration that were described above), and in abundance at different spatial scales (patch *vs.* entire community) may maintain themselves in the community at different population size distributions, each representing different pathways towards successful regeneration. By capitalising on stochastic processes competitively inferior species may occasionally regenerate successfully at the expense of competitively more vigorous species, and thus maintain themselves in the community. Species characteristics that enhance success of inferior species are for example a long reproductive life, which is advantageous by increasing the number of seed dispersal events; concentration of offspring in space, which increases the probability of success in a limited number of sites, or, alternatively, a specialised dispersal

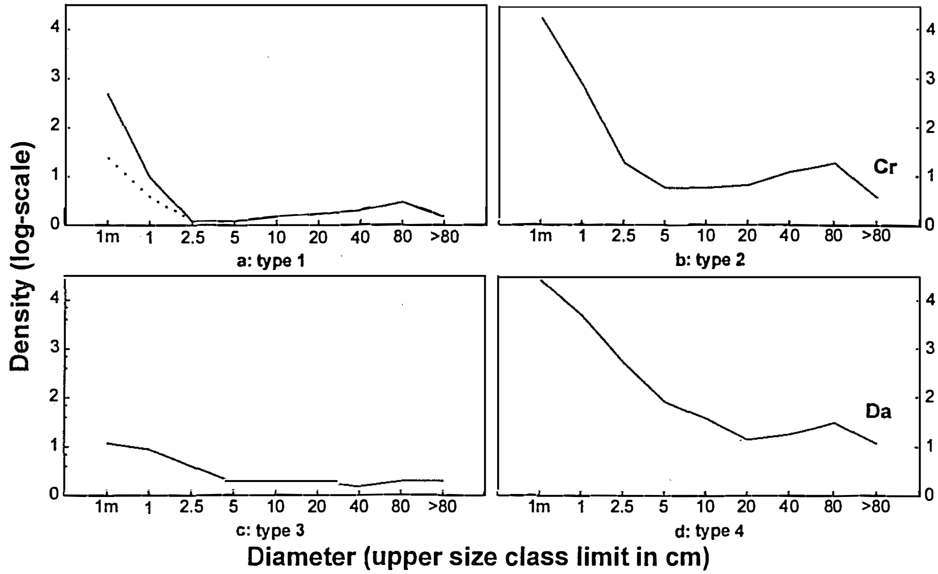


**Figure 5**
Hypothetical population size distributions of species differing in competitive ability and abundance. See text for explanation. The size class marked '1m' concerns seedlings less than 1 m tall. The density scale (No $ha^{-1}$ is based on actual population curves observed for *Chlorocardium rodiei* ('Cr', type 2) and *Dicymbe altsonii* ('Da', type 4) in two 1 ha demographic plots in tropical rain forest near Mabura Hill, Guyana. *C. rodiei* is a slow growing species of low competitiveness; *D. altsonii* is a fast growing, competitive species. Both are common in the canopy.

mechanism which increases the probability for a seed to establish in a favourable microsite (directed dispersal, Howe & Smallwood 1982). Frequent gap formation leads to an increase in the number of opportunities for successful regeneration of inferior species. These considerations lead theoretically to least four different classes of population size distributions, although each of them is subject to modification according to the specific characteristics of the species and site.

A species which is infrequent in a given patch by the time it has a canopy opening formed above it, and also a poor competitor is likely to be excluded from this patch. If such a species is also infrequent in the entire community, then it is likely to be rare and eventually disappear from it, unless its seeds and seedlings are concentrated in space, so that it is frequent in at least some patches. Such a situation was hypothesised by Condit *et al.* (1992) as a mechanism for inferior species to hold onto their canopy sites. We predict that such species are relatively long-lived and have a population structure that is dominated by adults, deficient in larger saplings and spatially very variable as to the amount of juveniles (Fig. 5a).

A species that is more frequent in a given patch but poorly competing is more likely to be retained because there is a higher probability than in the previous case that an individual escapes stochastic mortality, and finds itself in suitable conditions for competition. Successful regeneration is only possible when the seedlings and saplings are very persistent under the unfavourable light conditions which develop at the forest floor during the rebuilding phase of gaps. Lacking competitive vigour, these species require a series of suitable regeneration events to reach the canopy. Mortality due to repeated gap formation and poor competitive ability allow only a few seedlings to reach larger size classes. If these species are also frequent at the community scale, we predict that their population size class distributions are bimodal, with a high amount of adults and small seedlings and saplings, but a low amount of 'advanced regeneration'. Their frequency in the canopy is then explained by a low mortality rate in comparison with the previous 'pole' stage (Fig. 5b).

Strongly competing species that are infrequent in a given patch are in many cases retained by virtue of their competitive abilities. If these species are also infrequent at the community scale, they are predicted to have a relatively uniform population size distribution, *i.e.* with an over-representation of adults and large saplings compared to normal 'reversed J' distributions. Possible reasons for their low abundance in the community are short-livedness as an adult, poor seedling survival in the forest understorey, small seedling stature or infrequent reproduction (Fig. 5c)

Species that are frequent in gaps and competitive are the most likely ones to gain access to the canopy. If they are also frequent in the community, we predict that these species have a well-balanced population structure in the form of a 'reversed J', with a heavy representation of large saplings. These species are likely to dominate the structure of the forest (Fig. 5d).

Other population size distributions have been published (by Knight (1975) and Bongers *et al.* 1988). It is difficult to interpret them without knowledge about the competitive ability of the species for which they were derived. Type I of Bongers *et al.* (1988) and Figs. 6 and 9 of Knight (1975) represent 'reversed J' population size distributions as in Fig. 5d. Knight's Fig. 10 is an uniform distribution reminiscent of our Fig. 5c. Species with irregular size distributions (Bongers type II, Knight Fig. 7 and 8) or a distribution with few adults and saplings but a large seedling bank (Bongers type III) concern species with temporally irregular recruitment or growth rates. This pattern is indicative of poor competitivity under adverse conditions, hence these might be variations of the size distributions presented in Fig. 5b. These population size distributions might show unimodality if adults are less persistent in the canopy than in our example or if the seedlings are very short-lived and thus have low average densities. Pioneers, not considered here, show comparable size distributions.

The species composition of the community and within the gaps influence the shape of the population size distribution of each species. In this respect it is necessary to keep in mind that competitive ability and abundance are both relative measures, and this implies that one species may have different size class distributions in communities with different species compositions.

## Conclusions

Studies into the maintenance of species richness in tropical rain forests have concentrated on the response of large-sized trees to light availability. Canopy trees are the product of successful regeneration, and are not subject to its critical demographic constraints. Their large size and complex form prevent the precise determination of growth and the environmental conditions to which they are subject. Because of this, the results of these studies are likely biased towards the detection of random processes governing forest regeneration.

Seedlings are more sensitive to variations in resource availability, and their responses in terms of growth and mortality are much larger than in large trees. This makes them more suitable for evaluation of mechanisms promoting species coexistence.

The contribution of chance and species-specific factors varies during the stages of seedling regeneration in the understorey and in gaps.

We argue that chance processes contribute highly to the initial species composition of gaps through the random seed density distributions, relative to the availability of resources in the understorey and to the occurrence of gaps. These chance processes are probably in most cases strong enough to even out the effect of species-specific growth and survival characteristics. Once the species composition of a patch is determined (soon after gap formation), regeneration will be dominated by predictable processes based on species-specific differences in growth and survival, and on their initial size. Chance effects such as chance mortality and position of the seedling within the gap will affect but not always cancel out these directional processes.

Seedling studies should be carried out on the scale of hectare plots rather than gaps, on the scale of years rather than months, and should encompass a large fraction of the available species pool. The full variability of biotic and abiotic environmental conditions should be addressed. As ecosystems may differ in important aspects, such as disturbance regime and diversity patterns of species, a comparable approach at different sites would increase our understanding of the relative contributions of chance and directionality to the coexistence of many species.

### Acknowledgements

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# Pre-dispersal and early post-dispersal demography, and reproductive litter production in the tropical tree *Dicymbe altsonii* in Guyana

*Roderick J. Zagt*

## Abstract

The demographic history of a flower-cohort of the tropical tree *Dicymbe altsonii* (Caesalpiniaceae) was studied by collecting litter from flowers, fruits and seeds, and by monitoring 3-month seedling survival. Flower production was estimated at 137 to 172 $m^{-2}$ in a plot of one hectare. Four percent of the flowers yielded a pod, which contained an average of 1.97 seeds. Post-dispersal mortality over three months was 39% of the initial number of dispersed seeds.

Most flowers and fruits were aborted; insect and vertebrate predation in the tree and on the ground was very low. Reproductive litter production of this species was estimated to be equal to leaf litter production; the amount of phosphorus lost in litter from fruits and flowers was much larger than in leaf litter. This implies that the impact of the biennial flowering events on the nutrient dynamics of the trees and of the ecosystem may be large. It is argued that the reproductive cycle and the pre-dispersal demography of *Dicymbe* seem to be determined by a scarcity of nutrient resources, and possibly by pollinator limitation.

## Introduction

Pre-dispersal losses of flowers, fruits and seeds in trees vary widely, but in some species less than one percent of all flowers produces fruits (Lloyd 1980, Stephenson 1981). Two aspects play a major role in determining the success of flowers in producing a surviving seedling. First, many species seem to have an inherently low fruit set (Bawa & Webb 1984). Second, some species suffer high levels of predation of developing fruits or seeds (Bawa & Webb 1984, Crawley 1992, Janzen 1969, 1971), which continue after dispersal, often with different mortality agents involved (Crawley 1992, Janzen 1971).

Predation by insects and vertebrates requires the number of flowers that is initiated to be large enough to compensate for mortality of fruits, seeds and seedlings throughout the predator-sensitive phase. Such predator satiation is thought to lead to selection for large seed crops per tree (associated with a host of other adaptations) and synchronisation of flowering (Crawley 1992, Hart 1995, Janzen 1969).

Although over-production of flowers is common in plants, it has rarely been quantified for canopy trees in the tropical rain forest. The limited accessibility of the rain forest canopy impedes demographic studies of flowering and fruiting demography. *Dicymbe altsonii* is a species that combines a profuse flowering habit with a particularly high stem density in the tropical rain forest of Guyana. Therefore, this species provides an opportunity to reconstruct the demographic history of a flower cohort on a population scale in an indirect way by analyzing the quantity and composition of the litter produced by flowering trees. This is the first objective of this paper.

Most flowers and fruits that abscise do so before large investments in nutrients and energy are made (Lloyd 1980, Stephenson 1981). Nevertheless, a very low fruit set, either caused by overproduction of flowers for pollen production or pollinator attraction, or by high abortion of predator-damaged fruits represents a potentially significant loss to the parent tree in terms of carbon or nutrient resources (Kozlowski 1973).

Through a combination of poor nutrient status of the soil, high tree abundance and massive flowering this species potentially exerts a major claim on the available nutrients in the whole system. The second objective of this paper is to quantify the relative contribution of flower and fruit litter to the total litter production of this species, and of the entire system.

## Study site and species

The study was conducted in the Tropenbos Ecological Reserve, located *c.* 20 km south of Mabura Hill, Central Guyana (5°13' N 58°48' W; altitude *c.* 50 m). The climate is hot (average temperature 25.9°C) with a yearly precipitation of *c.* 2700 mm (Jetten 1994, Khan *et al.* 1980), following a bimodal pattern with maxima in May-July and December (ter Steege & Persaud 1991). The study was conducted in mixed rain forest on well drained Haplic Ferralsol (*sensu* ter Steege *et al.* 1993) also called the

*Dicymbe altsonii* faciation of the *Eschweilera-Licania* association (Fanshawe 1954). Flowering in this community is mainly in September-November, coinciding with the long dry season (ter Steege & Persaud 1991). The soil is derived from the highly weathered Guyana Shield and is considered extremely nutrient-poor (Brouwer 1996), especially in available P (less than 1.3 mg $kg^{-1}$) and exchangeable bases (CEC less than 3.5 cmol+ $kg^{-1}$; van Kekem *et al.* 1997).

*Dicymbe altsonii* (Clump Wallaba, Caesalpiniaceae) is a large tree occurring at high densities in certain rain forest types in Guyana (Fanshawe 1952, ter Steege *et al.* 1993, Isaacs *et al.* 1996). In the study area, it is the most abundant tree >10 cm dbh (diameter at breast height), with a density of 78 trees in the study plot, representing 41.4% of total basal area in this size class (R.J. Zagt, unpublished data). The largest trees have a dbh over 1 m and are 40 m tall. The trees mature once they reach the canopy (30-40 m), at dbh >20 cm.

*Dicymbe* populations in this area flowered abundantly in 1989, 1991, 1993 and 1995, while flowering occurred in less than 1% of the individuals in intermittent years (personal observations H. ter Steege, R.J. Zagt). The flowers of *Dicymbe* are relatively large (approx. diameter 5 cm), yellow and grow in racemes (Cowan & Lindeman 1989). They are hermaphroditic and most likely insect pollinated; no other potential pollinators have been observed. The pods (size approx. 20 x 6 cm) dehisce at maturation, releasing the seeds with some force so they are scattered over a short distance. The seeds are relatively large (fresh weight 14.3 ± 0.5 g; dry weight 7.7 ± 0.2 g, n=96). During the reproductive season the species produces large quantities of litter consisting of flower remnants and aborted fruits.

## Methods

A square 1 ha plot was located randomly within a large expanse (>0.5 $km^2$) of undisturbed, *Dicymbe*-rich *Eschweilera-Licania* forest. The average density of *Dicymbe* (dbh >10 cm) in a 10 ha area surrounding the plot was 69 trees $ha^{-1}$; in the study plot itself it was 78 trees $ha^{-1}$. From March-July 1993 all *Dicymbe* >10 cm dbh were inspected four times with binoculars for flowering and fruiting. In this way most if not all reproductive individuals could be located.

One litter trap was randomly placed in each of twenty 0.05 ha subplots in the plot. The average area per trap was about 0.4 $m^2$. One trap collapsed during the study and was discarded. A sampling intensity of 19 traps of this size for one hectare is considered sufficient for the study of (leaf) litter production (Brouwer 1996, Proctor 1983).

For 1991, data were gleaned from a litter fall study that was carried out in the same area with the same traps (Brouwer 1996). Litter was collected every 10 days and separated into fractions, of which reproductive parts was one. No further distinction of reproductive parts was made, so only total weights can be presented, and all specifications of flowering and fruiting refer to 1993, unless stated otherwise.

In 1993, all litter originating from reproductive parts from *Dicymbe* was collected weekly between 3 March and 21 July 1993, except between 18 May and 22 June, when collections were made fortnightly. This litter is termed 'reproductive litter'. In the laboratory the litter was separated in the following fractions (number normally present per flower): unopened buds (1), bracteoles (2), hypanthia (1), ovaries and developing pods (1), remaining flower parts (stamens 10, sepals 4, petals 5), pod valves (after seed dispersal, 2) and dispersed seeds (variable). The total number of units in each of these fractions (except 'remaining flower parts' and seeds) was counted and converted to flower equivalents, the estimated number of flowers per trap and per collection date. Flower equivalents will be used throughout this paper to compare collections from traps. All fractions were dried for 48 h at 70°C and weighed.

As the flower fractions usually do not drop jointly as complete flowers, two estimates, $F_A$ and $F_B$, were made for the number of flowers (including unopened buds) in the trees:

$F_A$ = (N of buds) + (N of bracteoles)

$F_B$ = (N of buds) + max([N of hypanthia], [N of developing pods]) + (N of pod valves)

Max([N of hypanthia], [N of developing pods]) is the maximum of these values per litter trap at each collection date. These two are usually abscised together and represent one flower, but sometimes a single fruitlet or hypanthium was found.

$F_A$ gives an estimate of the total number of flowers that was formed irrespective of their eventual success. $F_B$ on the other hand gives the total of the number of abortions in flower and pod stage, and the number of successful pods. There were no indications that any fraction disappeared or disintegrated in the traps between collections.

Fruit set and pre-dispersal mortality were defined as the ratio of the number of successfully dispersed and dead, respectively, pods to the total number of flowers (*cf.* Sutherland & Delph 1984). The fraction of flowers that was fertilised could not be determined directly. Instead, as an approximation, the ratio of fruits that had started growth and exceeded 2 cm in length to the total number of flowers was used. These ratios were determined over the total number of flowers over all traps.

To describe the development of the pods, length and width of developing and ripe fruits were measured. The number of dispersed seeds per pod was determined from the impressions of the seeds in the pod wall; the number of non-fertilised ovules and prematurely aborted seeds was counted.

As trapping of pods larger than 5 cm was rare, the development of pod size was studied by collecting and measuring all aborted pods that dropped into 20 randomly positioned 25 $m^2$ sampling plots during the fruiting period. Causes for abscission were classified as abortion (entire fruit abscised without damage), insect damage, parrot damage (triangular bites located at the positions of the ovules), monkey damage (pods ripped open, seeds removed) or unknown damage. In order to determine the seed production per pod, collections were made of pod valves outside the traps on two occasions during the fruiting period. Length, width, number of dispersed seeds and number of undeveloped ovules were determined.

Estimates of seed production per hectare were obtained from seeds trapped in the littertraps. In an alternative calculation, the calculated density of pod valves was multiplied by the average number of seeds dispersed per pod, as determined independently during the fruiting period. These estimates were compared with an estimate of the number of seeds in a systematic sample of 400 1 $m^2$ plots positioned on the intersections of a regular 5 x 5 m grid within the study plot (11 August 1993). A second check was provided by determining the number of seeds in the subplots used for seedling monitoring (see below; Table 5).

Post-dispersal mortality was monitored for natural populations in seventeen randomly distributed subplots of 2.5 x 2.5 m in the study plot. On 30 July 1993, all recent seeds and seedlings in these subplots were labelled, and the dead ones counted. At fourteen day intervals till 7 November 1993 mortality and its probable cause were assessed. The total initial population was 414 individuals.

In order to compare pre- and post dispersal mortality, all parameters were converted to seed equivalents. Flower- and seed equivalents differ from each other by a factor 1.97, the average number of dispersed seeds per pod (Table 4).

The diameter at breast height of *Dicymbe* individuals in the study plot was monitored yearly between October 1991 and October 1994. For all three years, the median growth rates of reproducing and non-reproducing individuals (in 1993) were determined; the differences were tested with Kruskal-Wallis anova. Only individuals larger than 20 cm DBH with reliable growth data in all three years were included in the analysis.

The *Dicymbe* litterfall in the plot, and the amount of phosphorus returned to the forest floor in *Dicymbe* litter were calculated from data of a litterfall study done in the study plot by Brouwer (1996). The contribution of *Dicymbe* to leaf biomass and to leaf litterfall was calculated by multiplying the respective figures given by Brouwer by 0.40, the approximate contribution of *Dicymbe* to the total stand basal area. The amounts of P in leaves and litterfall at community level were taken from Raaimakers (1994) and Brouwer (1996), respectively; the estimated contributions by *Dicymbe* were based on P-concentrations in *Dicymbe* leaf litter (0.23 mg $g^{-1}$; Brouwer 1996), green leaves (0.65 mg $g^{-1}$; Raaimakers 1994), seeds (1.34 mg $g^{-1}$; P. Haripersaud, *pers. comm.*) and flowers (1.19 mg $g^{-1}$; one bulked sample only, analysed following methods described in Raaimakers 1994).

## Results

There were no flowering *Dicymbe* smaller than 20 cm DBH. Of the 61 trees larger than 20 cm, 41 (67.2%) were flowering in 1993. Flowering and fruiting in 1993 lasted approximately 5 months (Fig. 1). Litter produced by flowers was maximal between late March and early April; litter produced by fruits peaked late June. Litter production averaged 1.36 ± 0.37 (SE) g $m^{-2}$ $d^{-1}$ and totalled 2.00 ± 0.54 t $ha^{-1}$ for the whole reproductive period. In 1991 the reproductive litter production was similar to 1993 at 2.16 ± 0.57 t $ha^{-1}$. Flowering was more abundant in 1991 than in 1993; the fruit and seed

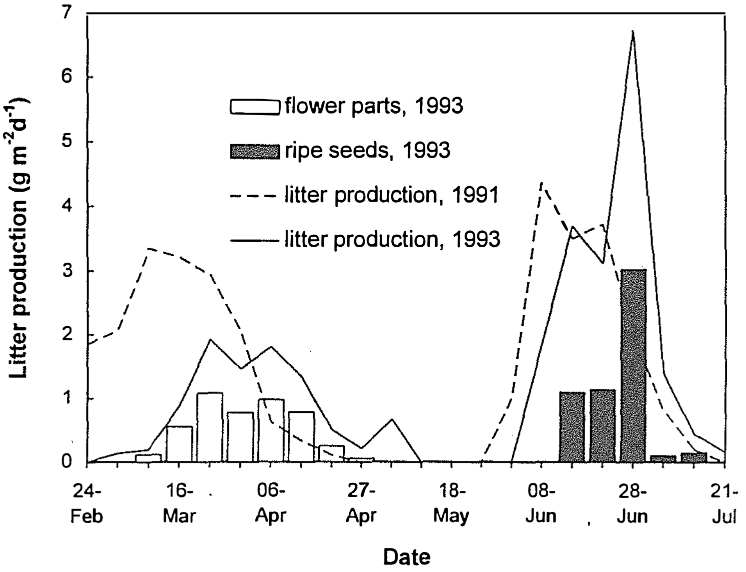

**Figure 1**
Temporal pattern of reproductive litter production by *Dicymbe* in 1991 (Brouwer, *pers. comm.*) and 1993. Based on weekly collections in g m$^{-2}$ d$^{-1}$.

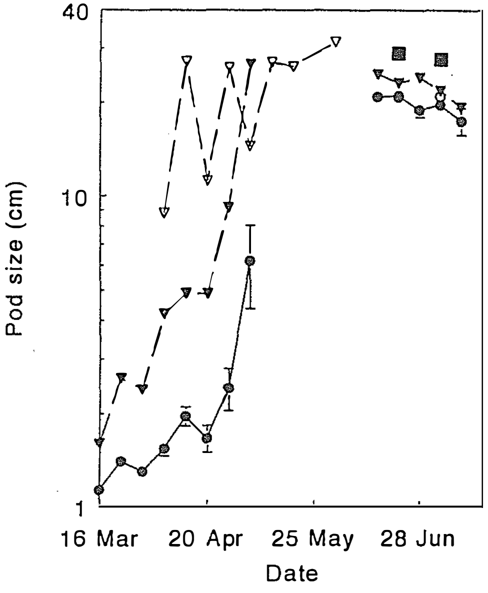

**Figure 2**
Size development of *Dicymbe* pods between fertilization and release of seeds. Combined data from different sources: litter trap collections (● average ± 1 s.e.; (▼ maximum per collection date), collections in 25 m$^{-2}$ sample plots (∇ maximum per collection date) and independent samples of dispersed pods (O average ± 1 s.e., ▨ maximum per collection date). Points before June are unripe pods, after June ripe pods after release of seeds. For sample plots no average was calculated as only pods >5 cm were collected.

production were slightly lower in 1991 (Fig. 1). Fruiting occurred in nearly the same period in the two years whereas flowering in 1991 was slightly ahead of 1993.

The total number of flowers $F_A$ was estimated at 171.9 ± 50.4 m$^{-2}$. $F_B$, the sum of

**Table 1**
**Reproductive litter production of *Dicymbe* and breakdown in fractions from the littertraps in the study plots near Mabura Hill, Guyana. Max(hypanthia; pods) is the maximum of hypanthia and developing fruits per collection date; $F_A$ is the sum of buds and bracteoles; $F_B$ is the sum of buds, max(hypanthia; pods) and pod valves. Remaining flower parts (sepals, petals etc) were not counted, but they are given as a weight. Total is the summed weight of all fractions.**

| Fraction | Number ($m^{-2}$) | s.e | Weight ($g\ m^{-2}$) | s.e |
|---|---|---|---|---|
| Buds | 17.9 | 5.0 | 1.7 | 0.6 |
| Bracteoles | 154.1 | 46.6 | 15.4 | 4.5 |
| Max(hypanthia; pods) | 115.9 | 48.9 | 3.8[1] | 1.6 |
| | | | 9.4[2] | 4.2 |
| Remaining flower parts | | | 33.1 | 9.1 |
| Ripe pod valves | 3.3 | 0.9 | 89.9 | 24.9 |
| Ripe seeds | 5.2 | 1.7 | 47.4 | 17.5 |
| Total: $F_A$ | 171.9 | 50.4 | | |
| Total: $F_B$ | 137.1 | 53.0 | | |
| Total: weight | | | 200.3 | 53.8 |
| Production[3] | | | 1.36 | 0.37 |

**[1] hypanthia**
**[2] ovaries and developing pods**
**[3] in g $m^{-2}$ $day^{-1}$ over 147 days.**

the number of aborted flowers and pods and the number of matured pods, was estimated at 137.1 ± 53.0 $m^{-2}$ (Table 1). The number of flower parts caught varied greatly among traps. There was a significant discrepancy of 34.8 flowers per $m^2$ or 20.3% between the two estimates $F_A$ and $F_B$ (paired t-test on natural log-transformed data). In the following $F_B$ is used as the estimate of the initial population of flowers, as it is based on actually trapped pods and aborted pods.

Fruit set, the number of ripe fruits over $F_B$ averaged over all traps where pods were present, was 2.5% (Table 2). For 1991 no data are available, but Fig. 1 suggests that fruit set was lower. It was not possible to estimate the fertilisation rate because flowers were not investigated for the presence of pollen tubes. The percentage of fruits that had started to grow (length over 2 cm) was 12.8%.

After fertilisation the pods grew rapidly until they reached their mature size. This was reflected by the size of the pods caught in the litter traps (Fig. 2). However, full-grown pods were observed in trees and in the sample plots three weeks before the first observation in the litter traps, suggesting that the probability of abscission for successful, fast-growing and hence, larger pods was less than for unsuccessful pods.

Seed development started much later than pod development. Pods with developing but unripe seeds were hardly ever found; the first ripe seeds were found on June 15, long after the pods reached their maximum size.

**Table 2**

**Mortality per stage in the pre- and post-dispersal phases of reproduction for a *Dicymbe*-population in Guyana. The data are presented as totals over all traps resp. plots, and percentages of these. Results in the pre-dispersal phase refer to the initial number of flower-equivalents; in the post-dispersal phase to the initial number of seed-equivalents. The percentage of surviving pods is an estimate for percentage fruit set.**

| | Flowers/fruits | | Seeds | |
|---|---|---|---|---|
| Stage | Total | (%) | Total | (%) |
| **Before dispersal** | | | | |
| Initial | 982.5 | 100.0 | | |
| Buds, abscised | 137.0 | 13.9 | | |
| Fruits < 2 cm, abscised | 751.0 | 76.4 | | |
| Fruits > 2 cm, abscised | 70.0 | 7.1 | | |
| Surviving pods, dispersed | 24.5 | 2.5 | | |
| **After dispersal** | | | | |
| Initial | | | 414 | 100.0 |
| Seeds, not germinated | | | 84 | 20.3 |
| Seedlings, not established | | | 115 | 27.8 |
| Seedlings, surviving | | | 215 | 51.9 |

The mean number of ripe and dispersed seeds per pod was 1.97, with a range of 0 to 6 (Table 4; in 1991 a fruit with 14 ripe seeds was observed). On average 23.5 ± 1.2% of all ovules that were present in the pod were dispersed as a ripe seed, while an additional 2.7 ± 0.5% of the ovules developed into seeds that were aborted before dispersal.

Seed dispersal started 15 weeks after the first flowers appeared (Fig. 1). The various estimates for seed density (in seed equivalents per m$^2$) just after dispersal were different ($\chi^2_3=16.1$; $p<0.001$; Table 5). This was due to the high estimate based on the number of valves in the traps; the seed-based estimates were not statistically different ($\chi^2_2=2.9$; $p>0.05$).

After dispersal, the seeds germinated within two weeks. Of the original seed population 16.5% failed to germinate, while an additional 22.1% died during the establishment phase (Table 3).

With these data a demographic curve was constructed from anthesis until 4 months after seed dispersal (Fig. 3). The number of flower equivalents was multiplied by 1.97, the mean number of dispersed seeds per pod (Table 4), to yield an estimate of the number of seed equivalents. $F_B$ was taken as the estimate for the number of flowers.

Three phases could be distinguished: the flowering phase (before 4 May), the fruit ripening phase (between 4 May and 21 July) and the seedling phase (after 21 July).

The flowering phase was characterised by a high and fairly constant rate of mortality

**Table 3**
**Causes of mortality in the pre- and post-dispersal phases of reproduction for a *Dicymbe*-population near Mabura Hill, Guyana in % of total mortality observed per stage. N is the total number of dead individuals observed. Refer to Table 3 for percentage mortality per stage.**

| | | Cause of mortality (% of total mortality per stage) | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Stage | N | Abortion | Parrots | Monkeys | Insects | Fungi | Physical | Unknown |
| **Pre-dispersal phase** | | | | | | | | |
| Fruits <2 cm, abscised | 751 | 100.0 | | | | | | |
| Fruits >5 cm, abscised | 87 | 58.6 | 16.1 | 3.5 | 17.2 | | | 3.5 |
| **Post-dispersal phase** | | | | | | | | |
| Seeds, not germinated | 84 | | | | 47.6 | | 47.6 | 4.8 |
| Seedlings, not established | 115 | | | | 1.7 | 83.5 | 6.1 | 8.7 |

once an initial period of low mortality during the period of anthesis was over. The phase of fruit ripening started when no flowers were left. This phase was poorly documented with the litter trap method as it seemed to be characterised by low mortality. No fruits were found in the traps during this period, and elsewhere in the plot they were scarce. Locally, mortality among developing fruits can be much higher, depending on the incidental passage of groups of parrots and monkeys (*personal observations*, R.J. Zagt). Table 3 lists the mortality agents for the fruits as determined in the traps and from the sample plots (for fruits >5 cm).

During the seedling phase, high mortality was caused by harvester ants attacking the cotyledons of germinating seeds and by physical factors such as the failure to become rooted. After germination mortality was lower and mainly caused by a fungus that caused the seedling to wilt and die.

The median growth rate of flowering and non-flowering individuals was not different in the years without mass-flowering, but flowering individuals had a significantly lower growth rate than non-flowering individuals in the flowering year 1993 (Kruskal-Wallis $H = 1.30$ and $0.41$, $p>0.25$ for 1992 and 1994, respectively; $H=4.08$, $p<0.05$ (1993), Table 6). This effect was not caused by a reduced growth rate of flowering individuals, but by a higher growth rate of non-flowering individuals.

The estimated contribution of *Dicymbe* reproductive litter production to the total litter and phosphorus cycle of *Dicymbe* and the entire community is given in Table 7. *Dicymbe* produces in a flowering year about equal amounts of leaf and reproductive litter, but the losses and investments of phosphorus in flowers and fruits are larger than in leaves. The contribution of pod valves to phosphorus losses are unknown.

**Table 4**
Seed set per pod in a sample of N=144 ripe *Dicymbe* pods near Mabura Hill, Guyana.

| | Mean | s.e. | Range |
|---|---|---|---|
| Ripe and dispersed | 1.97 | 0.10 | 0 - 6 |
| Aborted and not dispersed | 0.22 | 0.04 | 0 - 2 |
| Undeveloped ovules | 6.15 | 0.13 | 1-10 |
| Total | 8.33 | 0.09 | 4-11 |

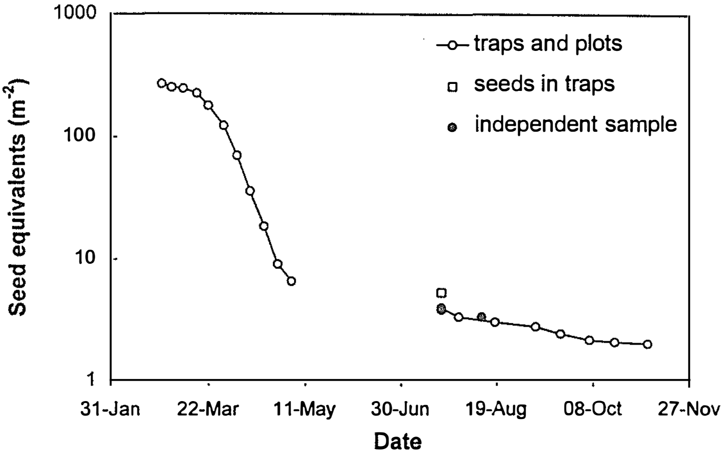

**Figure 3**
Evolution of cohort size of *Dicymbe* between flowering and seedling establishment in 1993. Cohort size is expressed in seed equivalents (see text). Regression lines are: $\ln(Y)=3.073-0.0338.X$; $R^2=0.98$, $p<0.001$, $n=7$ (flowering period, regression of the last 7 points), and $\ln(Y)=0.944-0.0027.X$; $R^2=0.96$, $p<0.001$, $n=8$ (seedling phase). X is the number of days since Feb. 26, 1993.

## Discussion

### Flower production and pre-dispersal demography

*Dicymbe* produces a large amount of flowers during a reproductive event. The total number of flowers in this plot was estimated at $1.37 \times 10^6$. In some species, individual trees produce a similar or larger number of flowers (Chan & Appanah 1980), but in those cases the flowers are not as large as in *Dicymbe*. A proper estimate of the reproductive litter production is complicated by the fact that the production of flowers is spatially very variable, even for an abundant species like *Dicymbe*. Therefore a large standard error must be accepted.

The estimate based on the number of bracteoles ($F_A$) was higher than the estimate based on the number of failed and successful pods ($F_B$). Possible explanations for the difference between the two estimates are: (1) There is a differential trapping probability for the various reproductive parts caused by differences in dispersal range. However, less than 10% of the litter of any fraction was trapped in traps that were more than eight meter away from the nearest reproductive tree (data not shown), so it is unlikely that one of the estimates is too low due to dispersal beyond the range of the traps. (2) The sampling error depends on litter fraction in a different way than mentioned in (1). (3) Substantial amounts of sterile flowers (without an ovary), or of non-abscised flowers that remain in the tree could boost $F_A$ over $F_B$ if these flowers normally dropped their bracteoles. (4) There is predation of entire flowers or pods in the tree. Small scale predation of entire flowers by birds was observed in another dominant Caesalpiniaceae in the area (*Eperua falcata*), but this was not seen in *Dicymbe*, and it is not likely to cause the observed difference. Flower predation by howler monkeys (*Alouatta alouatta*) as described by Jones (1983) for legumes was not observed. Large scale predation of fruits is also unlikely to go unnoticed as most predators are rather messy eaters.

The discrepancy between $F_A$ and $F_B$ cannot be explained with certainty with the littertrap method. However, errors due to possibilities (1) and (4) mentioned above seem too small to explain the difference, leaving the other two as the most likely explanations. No positive evidence of sterile flowers were found, though.

The causes of death vary with the stage of flower, fruit, seed and seedling development. Just as in the legumes *Caesalpinia eriostachys* and *Myrospermum frutescens* (Bawa & Webb 1984), close to 90% of all abortions occurred in the first weeks after flowering (Fig. 3). During the flowering and fruit ripening phase insect predators were rare, and insect-incurred pre-dispersal mortality was very low in *Dicymbe* compared to some other woody tropical legumes (Janzen 1969). This leads to the conclusion that predator satiation does not seem to be a reproductive strategy for *Dicymbe*. Janzen (1969) observed that large and fleshy seeds of legumes are not attacked by bruchid seed predators, due to their fast germination rate. In general, predation of developing pods seemed to be very low in *Dicymbe*, and external mortality agents (predators and pathogens) became important only after nearly 90% of all flowers and fruits had already aborted. Losses of larger pods were very low, consistent with findings of Bawa & Webb (1984). The main factor here was the local occurrence of groups of parrots and especially monkeys (*Alouatta saniculus* and *Cebus apella* have been observed to eat *Dicymbe* seeds). Mortality per tree visited by these animals can be very high (*personal observations*).

### Fruit and seed set

The estimated fruit set of 2.5% was low compared to averages for tropical plants (26.9%: Sutherland 1986) and for woody perennials (19.4%: Sutherland 1986; 18.8%: Ramírez 1993), but comparable with values reported for tropical leguminous trees by Bawa (1974), Bawa & Webb (1984), Sutherland & Delph (1984) and Ramírez (1993). These range generally between 1 and 10%, although lower values are also reported (*e.g.*, Grimm 1995). It must be noted, however, that pod and seed pro-

**Table 5**
**Estimates for *Dicymbe* seed density just after dispersal obtained with different methods, in the study area near Mabura Hill, Guyana.**

| Method | Date (all in 1993) | Sample size | Sampled area ($m^2$) | Mean seed density ($m^{-2}$) | s.e. |
|---|---|---|---|---|---|
| Littertraps: | | | | | |
| seeds | July 21 | 19 | 7.5 | 5.2 | 1.7 |
| valves × 1.97 | July 21 | 19 | 7.5 | 6.5 | 1.7 |
| Demographic plots | July 30 | 17 | 106.3 | 3.9 | 0.8 |
| 1 $m^2$ samples | August 11 | 399 | 399.0 | 3.8 | 0.2 |

duction were very low compared to the flower production, and therefore their density estimates were more prone to sampling error. Fruit and seed production estimates based on the litter trap method appear high in comparison to estimates based on larger sampling schemes (Table 5).

A number of hypotheses have been proposed to explain inherently low fruit set (Bawa & Webb 1984, Stephenson 1981, Sutherland & Delph 1984). First, overproduction of flowers would allow the tree to benefit from variations in resource availability and pollination success (Sutherland 1986). This mechanism would specifically be important for trees, where the period between flower initiation and fruit maturation is long, and hence, the uncertainty about resource and pollinator availability large. Although the length of this period is not known for *Dicymbe*, the biennial flowering cycle implies that the resources needed for the production of fruits are so large that they can only be gathered over a period of more than a year (see below). It is unlikely that variations in resource availability during the few months between flower initiation and fruit maturation would affect the long term build-up of reserves significantly, and there would be no reason to produce a large amount of excess flowers to benefit from rare better-than-usual events. Second, at high fertilisation success low quality fruits may selectively be aborted. Third, in hermaphroditic plants, more flowers may be required to produce the optimum amount of pollen than for producing the optimum amount of fruits. Sutherland (1986), comparing a large number of species, suggested that for self-incompatible, hermaphroditic species, this 'pollen donation hypothesis' is best in explaining low inherent fruit set percentage. Fourth, the pollinator limitation hypothesis is that a high production of flowers would serve to attract pollinators when these are scarce, resulting in a low percentage fruit set.

The data on *Dicymbe* do not provide a test for these hypotheses. Still, even though the pollinator limitation hypothesis is often discarded as a mechanism selecting for excess flowering and, hence, low fruit set in plants (Bawa & Webb 1984), it should be realised that *Dicymbe*, being by far the most common canopy species in the area, causes a short but high peak in flower availability for pollinators in a period outside the normal flowering season in the area (ter Steege & Persaud 1991). It is likely that during the flowering period pollinator densities are limiting for pollination, especially if

**Table 6**

**Median growth rates (cm $yr^{-1}$) of reproducing and non-reproducing *Dicymbe* individuals in flowering and non-flowering years in the study plot near Mabura Hill, Guyana. The bottomline indicates whether growth was different between reproducing and non-reproducing individuals (Kruskal-Wallis anova).**

| | | Growth period | | |
|---|---|---|---|---|
| | N | Oct '91 - Oct '92 | Oct '92 - Oct '93 | Oct '93-Oct '94 |
| Did flowering occur? | | no | yes | no |
| Reproducing individuals | 34 | 0.37 | 0.30 | 0.27 |
| Non-reproducing individuals | 17 | 0.28 | 0.59 | 0.40 |
| | | ns | $p<0.05$ | ns |

the opening time for individual flowers is short. The production of surplus flowers for floral display would then be beneficial if more pollinators could be attracted.

The seed set per dispersed pod (Table 4) was variable, and many pods had more than one seed. The observed seed set value is slightly below those reported for two species with multi-seeded pods from Central America (Bawa & Webb 1984), and well below the value of 4-8 seeds per pod mentioned by Fanshawe (1954) for *Dicymbe.*

### Impact of flowering on carbon and phosphorus cycling

In flowering years, the reproductive litter fall for this single species in this plot (2.0 ± 0.5 t $ha^{-1}$; Table 1) is high compared with values reported elsewhere in tropical rain forests (Proctor 1984). Flower and fruit fall for entire communities reported in Proctor (1984) are below 1.2 t $ha^{-1}$ $yr^{-1}$ (median 0.43, n=34), with the exception of one (apparently unpublished) study on Barro Colorado Island (3.3 t $ha^{-1}$ $yr^{-1}$). All values for flower and fruit litterfall from more or less nearby Amazonian rain forest sites cited in Scott *et al.* (1992) are substantially lower than reproductive litterfall by *Dicymbe* (median 0.45 t $ha^{-1}$ $yr^{-1}$, n=8). No published data were found for Dipterocarp forests in mast years; reproductive litter production should be very high in such years (*cf.* Chan & Appanah 1980, *cf.* Janzen 1974). The values for *Dicymbe* approach those reported for some mangrove forests (Proctor 1984).

The results of the present study can be directly related to those of a detailed study of litterfall which was conducted in the same plot in the period 1991-early 1993 (Brouwer 1996). In good flowering years the reproductive litter production of *Dicymbe* is of the same order as its leafy litter production (Table 7). Nutrient concentrations in flowers and fruits are generally higher than in leaf litter (Brouwer 1996, Franken 1979, Scott *et al.* 1992, Veneklaas 1991). Due to this, losses of phosphorus in reproductive litter vastly exceed losses in leaf litter, and they even represent, in flowering years, a significant however pulse-wise contribution to the total internal P-cycle in this plot (*cf.* Brouwer 1996; compare also to the estimated P pool in living leaf biomass, Table 7).

**Table 7**
**The estimated contribution of *Dicymbe* to leafy and reproductive litterfall during a flowering year, and estimated total leafy biomass in the study plot. Data of the entire community from Brouwer (1996). Reproductive litterfall data for *Dicymbe* from Table 1, for remaining data see methods section. Remaining small litterfall includes flowers, fruits, small woody litter and trash.**

| | Total litter weight (kg $ha^{-1}$ $yr^{-1}$) | | Phosphorus (kg $ha^{-1}$ $yr^{-1}$) | |
|---|---|---|---|---|
| | Entire community | Only *Dicymbe* | Entire community | Only *Dicymbe* |
| Leaf litterfall | 5400 | 2160 | 1.1 | 0.5 |
| Non-leaf litterfall: | | | | |
| *Dicymbe* flowers | | 630 | | 0.7 |
| *Dicymbe* pod valves | | 900 | | ? |
| *Dicymbe* seeds | | 475 | | 0.6 |
| Remaining small litterfall | 3700 | ? | 1.1 | ? |
| Living leaf biomass (kg $ha^{-1}$) | 12000 | 4800 | 7.1 | 3.1 |

It must be noted that not all phosphorus that is released with seeds contributes to the pool in the litter layer, as 52% of the seeds survived until the end of the year. Phosphorus was shown to be limiting at the study site (Brouwer 1996, Raaimakers 1994), as it is in most tropical rain forest ecosystems (Silver 1994, Vitousek 1984). Through the combination of the extraordinary poverty of the soil, especially in available phosphorus (Brouwer 1996, Raaimakers 1994), the abundance of the species and the pulse-wise production of flowers and fruits, *Dicymbe* reproduction must have a large impact on the size and temporal variability of nutrient fluxes, not only in the *Dicymbe* individuals themselves, but also in the entire system. An impact of individual trees on phosphorus levels of the surrounding soil through fruit fall was demonstrated by Rhoades *et al.* (1994) for *Simarouba amara* in Costa Rica.

The biennial reproduction cycle and the large investments in P that are required for reproduction suggest that more than one year is needed to store sufficient resources for one reproductive event (*cf.* Davis 1957, Lloyd 1980). Crawley & Long (1995), in a study on alternate bearing in *Quercus robur*, suggest that reproduction only occurs when a certain threshold level of resources is met. This could explain alternate bearing in trees with a large reproductive investment, and the absence of a negative correlation between growth and fruit production. On the other hand, such negative correlation was demonstrated for conifers and European Beech (*Fagus sylvatica*; Eis *et al.* 1965, Holmsgaard 1956). The results for Dicymbe conform to the latter pattern: reproducing individuals exhibited a lower diametrical growth rate than non-flowering individuals in flowering years, but not in non-flowering years (Table 6).

For oaks (Crawley & Long 1995) and conifers (Eis *et al.* 1965) the lower crop size in 'off' years was at least partly explained by a higher abortion rate of flowers, and not by decreased initiation of flowers. This is in contrast to *Fagus sylvatica* (K.A. Longman, pers. comm.) and *Dicymbe*, where there is no evidence for either high abortion nor for initiation of flowers in off years.

In conclusion, the reproductive cycle and the pre-dispersal demography of *Dicymbe* seem to be determined by a scarcity of nutrient resources, and possibly by pollinator limitation. Predation of seeds, both pre-dispersal and post-dispersal, seems to be too low to constitute a significant factor in determining timing and abundance of flowering. A combination of high abundance and massive flowering causes this species to exert a significant impact on nutrient dynamics in this forest.

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chapter 4

# Stem sprouting of *Dicymbe altsonii* in the tropical rain forest of Guyana: impact of soil type and potential for regeneration

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## Abstract

*Dicymbe altsonii* from the rain forest of Guyana is a rare example of a tropical rain forest tree that carries coppicing shoots (sprouts) on the base of the trunk. The distribution of size and number of these sprouts was investigated in two *Dicymbe* populations occurring in Dry Evergreen Forest on White Sand and Mixed Forest on Brown Sand. More than two thirds of all trees above 10 cm diameter at breast height had at least one sprout. The number and total basal area of sprouts per tree was positively related to parent size and the occurrence of damage in the crown. Sprouts were higher in number, but smaller in size in the Mixed Forest than in the Dry Evergreen Forest. This difference is attributed to differences in the light climate between the forest types. The number of standing dead sprouts was high. Sprout and sapling densities were comparable at both sites, except that small sprouts (1-2.5 cm diameter) had a much higher abundance than small saplings. Sprouts and saplings differed in above-ground biomass allocation, with sprouts having less leaves. It is argued that sprouts and saplings represent alternative regeneration strategies for *Dicymbe*. Saplings are more suitable for the occupation of new sites, whereas sprouts increase the ability of an individual to retain its own position.

## Introduction

Considerable areas of tropical rain forest in Guyana are dominated by two species of the genus *Dicymbe* (Caesalpineaceae), which apart from a prolific generative regeneration (Fanshawe 1954, Zagt (Chapter 3) distinguish themselves by possessing stem sprouts (coppice shoots) as a means of vegetative regeneration (Davis & Richards 1934, Fanshawe 1954, Richards 1996). Vegetative regeneration through root or stem suckering, rhizome production, or layering, while common in temperate forests (Solomon & Blum 1967, Koop 1987, Read & Hill 1988), seems to be scarce among woody species in the tropical rain forest. Palms (*e.g.*, Dransfield 1978, Chazdon 1991), lianas (Peñalosa 1984, Putz & Holbrook 1991) and some African forest understorey shrubs (Richards 1996, Nkongmeneck 1996) constitute notable exceptions. However, coppicing after cutting or damage is more common among tropical woody species (de Rouw 1993).

Although the peculiar habit of *Dicymbe* is frequently mentioned and population size structures have repeatedly been published (Fanshawe 1954, Whitton 1962, ter Steege *et al.* 1993, Isaacs *et al.* 1996, Zagt & Werger (Chapter 2), the contribution of sprouts to the total *Dicymbe* population has never been quantified. Similarly, it is unknown to what extent sprouts actually contribute to regeneration, or, more accurately, rejuvenation or perpetuation of the genet, in *Dicymbe.* The aim of this study is to quantify sprouting in one of the species, *Dicymbe altsonii.* We determined the quantity and size distribution of sprouts in relation to parent size and vigour in a *Dicymbe* dominated vegetation, and we compared these with saplings produced by generative means. In addition, we harvested similar-sized sprouts and saplings in order to assess differences in biomass allocation patterns that may reveal differences in growth constraints.

A second objective of this study was to quantify differences in these characteristics between populations occurring on two contrasting soil types. Variation in soil type leads to variation in forest types in Guyana (Davis & Richards 1934, ter Steege *et al.* 1993). Wallaba (*Eperua* spp.) forest on white sand and Greenheart (*Chlorocardium rodiei*) dominated mixed forest on brown loamy sand represent extremes in floristic composition and physiognomy. *Eperua*-dominated forests tend to be low and possess a high stem density of mainly small-stemmed trees, while *Chlorocardium*-dominated forests are taller and have a lower stem density with a higher contribution of large trees. *Dicymbe altsonii* is one of few species that is common in either forest type, and it is already established that the population size distribution of *Dicymbe* in either forest type varies much in the same way as the size distribution of the entire vegetation (ter Steege *et al.* 1993). We hypothesised that the sprout populations of *Dicymbe* from both forest types showed the same patterns.

## Material and methods

### Study area, soils and study species

The study was conducted in 1993 in the Ecological Reserve of the Tropenbos-Guyana Programme, *c.* 20 km south of Mabura Hill, central Guyana (5°13' N, 58°48'

W). Average rainfall and temperature in the area are 2700 mm and 27°C, respectively (Jetten 1994). Rainfall follows a bimodal pattern with maxima in May-July and in December (Jetten 1994). The soil types in the area belong to one of two major groups: a group of clayey Plinthosols and a group of sandy and loamy soils of various types (Jetten 1994, van Kekem *et al.* 1997). The distribution of species and forest types is well correlated with soil type (Davis & Richards 1934, Fanshawe 1954, ter Steege *et al.* 1993, Jetten 1994).

*Dicymbe altsonii* Sandw. (Caesalpiniaceae, Clump Wallaba) is a canopy tree with a maximum height of *c.* 40 m and a maximum diameter of *c.* 1.50 m. It is distributed in a small area in central Guyana and north-western Brazil (Cowan & Lindeman 1989). In the study area, *Dicymbe* occurs exclusively on sandy and loamy soils, over a broad hydrological gradient, although in the Amatuk region, *c.* 100 km W of the study area, it is also reported from latheritic soils (Whitton 1962). It is dominant or co-dominant in a number of forest types (ter Steege 1993, Jetten 1994, Zagt (Chapter 3). In this study, *Dicymbe* populations from two different forest types are compared: Dry Evergreen Forest (DEF) on Albic Arenosol (white sand) and Greenheart (*Chlorocardium rodiei*) bearing Mixed Forest (MF) on Haplic Ferralsol (brown sand). These forest and soil types differ appreciably (Table 1a,b). Dry Evergreen Forest is low in stature, rich in small trees but poor in large trees when compared to Mixed Forest. Brown sands are more clayey, moister and richer in total nutrient contents than white sands, although the amount of available nutrients is comparable (Brouwer 1996). *Dicymbe* is not a constant species in these forest types. In Davis and Richards' (1934) description of these forest types at Moraballi Creek (*c.* 100 km North of the present site), *Dicymbe* is absent. Also in the study area DEF and MF without *Dicymbe* occurs within *c.* 500 m respectively 3 km from the study plots. The boundaries between the subtypes are sharp.

### Population structures

In DEF and in MF, a square 1 ha study plot was laid out and gridded in 10x10 m subplots. In order to construct population size distributions, the diameter of all *Dicymbe* individuals of 2.5 cm dbh (diameter at breast height, 1.30 m) and more was measured. Individuals in the 1 to 2.5 cm class were tallied but not measured. Crown damage of parent trees was qualitatively assessed in two classes: intact, and crown partially or completely absent. All *Dicymbe* above 10 cm dbh were investigated on the presence of trunk suckers, henceforth called sprouts. Sprouts were distinguished from branches by their orthotropic growth, whereas branches grew obliquely away from the trunk. Root suckers were not observed.

The number of sprouts was determined. Sprout diameter was measured at 0.5 m above the implantation in the parent bole with a calliper (up to 3 cm diameter; two perpendicular measurements that were averaged) or a graduated pi measuring tape (above 3 cm diameter). The choice of a reference height of 0.5 m and not 1.3 m increased the number of sprouts that could be measured in the study. From the diameter measurements the total sprout basal area per tree was determined. The diameter of sprouts that were implanted higher than 4 m above the ground (*i.e.* out of reach of the

**Table 1a**
**Overview of the main differences between the soil types of the two *Dicymbe* study plots near Mabura Hill, Guyana.**

| | Albic Arenosol (white sand) | Haplic Ferralsol (brown sand) |
|---|---|---|
| Colour | white | dark brown-yellowish brown |
| Sand content (mean ± sd) [1] | 89.4 ± 3.1 % | 66.5 ± 10.5 % |
| Clay content (mean ± sd) [1] | 0.0 ± 0.0 % | 19.4 ± 9.3 % |
| Infiltration rate (mm/min) [1] | 27.0 ± 12.3 | 1.2 ± 1.2 |
| pH($H_2O$) [2] | 3.8-4.4 | 3.8-4.7 |
| CEC (cmol/kg) [2,4] | 1.5 | 2-6 |
| Total P (mg/kg) [3] | 8 | 55 |
| 'Available' P [3,4] | slightly higher | slightly lower |
| Associated Forest Type in study plot | Dry Evergreen | Mixed on well drained soil |

**[1] Jetten (1994); [2] van Kekem *et al.* (1997); [3] Raaimakers (1995); [4] Brouwer (1996)**

**Table 1b**
**Overview of the main structural differences between the forest types in the two study populations.**

| | Dry Evergreen Forest (Wallaba forest) | Mixed Forest (Greenheart forest) |
|---|---|---|
| Canopy height | 25-30 m [4] | 30-40 m [1,3] |
| Stem density (dbh >10 cm, $ha^{-1}$) | 617 [2] | 300-519 [1,2,3] |
| Stem density (dbh >55 cm, $ha^{-1}$) | 13 ± 16 [4] | 41 ± 17 [4] |
| No of species >10 cm dbh | 74 [2] | 95 [2] |
| Lianas | relatively scarce [2] | relatively frequent [1,2] |
| Most common canopy species in study plot | *Eperua grandiflora*,<br>*Dicymbe altsonii* [3] | *Dicymbe altsonii*,<br>*Chlorocardium rodiei* [3] |

**[1] Fanshawe (1954); [2] Davis & Richards (1934); [3] Zagt, unpublished data and personal observations; [4] van Zanten (1991)**

ladder used) was estimated, but not used for quantitative analysis. Implantation height of the sprout was measured directly or with a clinometer.

Analysis was performed on sprouts from those parent trees whose diameter could be measured. If the parent itself originated from a sprout, it was omitted if the other sprouts were evidently from the same generation as the 'parent' itself. This was the case if a number of similar-sized trees stood together, sometimes around the remains of an old trunk, and had an irregular stem base indicative of their sprout origin. Except when explicitly mentioned, analysis is restricted to sprout-bearing trees, to living sprouts, and to sprouts implanted below 4 m height.

Population structures of sprouts and saplings were compared over a diameter range of 2.5-20 cm diameter (*i.e.* immature individuals). Due to different reference heights for the diameter measurements, sprout diameters were overestimated compared with saplings. Because saplings were shown to have a larger average diameter than sprouts, this did not affect the qualitative results of the comparison.

### Allocation

Morphological differences between saplings and sprouts were evaluated in a sample of eleven sprouts and eleven saplings from the Mixed Forest. Pairs of one sprout and one sapling growing less than five meter distance from each other were randomly drawn from pairs meeting the following criteria: a height between 1.5 and 2.0 m and growing within the same hectare in mature forest, in understorey environment far from a gap. The ages of the individuals were unknown. Inevitably only above-ground biomass could be sampled. The plants were cut in seven to eight sections of 0.25 m, numbered from one (bottom) to seven/eight (top). The following measurements were taken: diameter at 1.30 (dbh), oven-dry weight of stem and leaves (after 48 h at 70°C), determined on a Sartorius LP 620 S balance; number of leaves and leaflets; and leaf area as determined with a LiCor LI-3100 leaf area meter. From these, Specific Leaf Area (SLA, in $cm^2\ g^{-1}$), Leaf Weight Ratio ($LWR_{above}$, in $g\ g^{-1}$, determined on a sprout basis alone) and Leaf Area Ratio ($LAR_{above}$ in $cm^2\ g^{-1}$) were calculated. The stem weight to volume ratio was determined for segment 6 (the segment where the diameter was taken), where volume (V) was approached with the formula $V = \pi \times (0.5 \times dbh)^2 \times l$ (l=segment length).

### Data analysis

Differences between parent tree and sprout characteristics between the two sites, and differences between sprouts and saplings were tested with Mann-Whitney unpaired rank tests and $\chi^2$ tests. Differences in population structures were tested with the Kolmogorov-Smirnov two sample test. The relation between the number and size of sprouts per parent and parent size, site and damage was studied with stepwise multiple regression. The data were transformed prior to analysis when appropriate. For regression analysis, dead and high (implantation above 4 m) were included as dependent variable (see results).

## Results

### Characteristics of parent trees and the presence of sprouts

The *Dicymbe* populations (trees above 10 cm dbh) showed different size distributions at both sites. Compared to the Mixed Forest population, small individuals were over-represented in the Dry Evergreen Forest, and large individuals were underrepresented (Fig. 1, Table 2). The total tree basal area was larger in the MF plot than in the

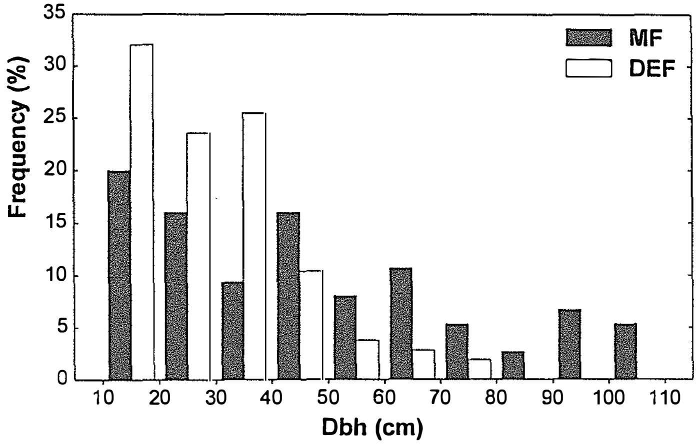

**Figure 1**
**Size class distribution of two *Dicymbe* populations in Mixed Forest and Dry Evergreen Forest near Mabura Hill, Guyana.**

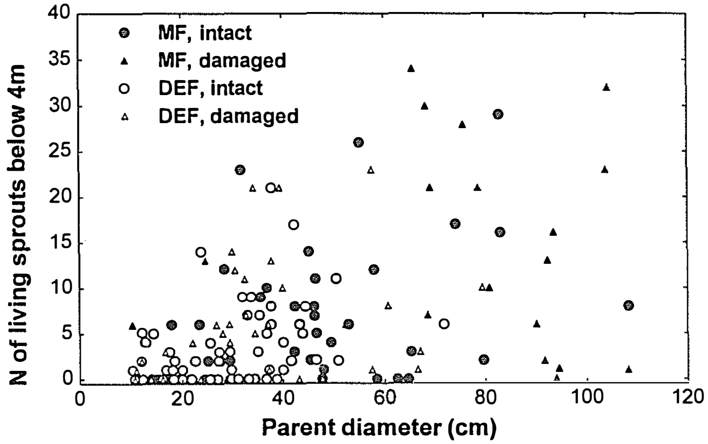

**Figure 2**
**The number of stem sprouts on *Dicymbe* trees as a function of parent diameter, site and crown damage. All data are living sprouts implanted on the basal 4 m of the parent.**

DEF plot. This result is in agreement with the general structural characteristics of these forest types (Table 1b). The fraction of trees with crown damage was the same at both plots (Table 2); damage was more prevalent at larger size classes, increasing from *c.* 20% at 10 cm dbh to *c.* 50% above 50 cm dbh (data not shown)

In both plots, more than two thirds of all *Dicymbe* more than 10 cm dbh had one or more sprouts (Table 2). The number of living sprouts per sprouting tree varied between 1 and 34 (Fig. 2); with the dead ones included the number was much higher (Table 3). The trees at the MF site tended to have more sprouts, but a lower total

**Table 2**

**Descriptive statistics of the tree populations in the 1 ha study plots in Dry Evergreen Forest and Mixed Forest near Mabura Hill, Guyana. N=106 trees for DEF, 77 trees for MF. $\chi^2$ tests were performed on the underlying data. KS means Kolmogorov-Smirnov two sample test.**

| | Dry Evergreen Forest | Mixed Forest | test | p |
|---|---|---|---|---|
| median tree diameter (cm) | 28.4 | 46.1 | KS | <0.001 |
| maximum tree diameter (cm) | 79.5 | 108.4 | | |
| median tree basal area ($cm^2$) | 634 | 1669 | | |
| % damaged trees | 29.2 | 32.5 | $\chi^2$ | ns |
| % trees with sprouts | 76.4 | 66.2 | $\chi^2$ | ns |
| % trees with sprouts below 4m | 67.9 | 63.6 | $\chi^2$ | ns |

sprout basal area, than the trees at the DEF site (Fig. 3; Table 3). The average sprout size distribution per tree is shown in Fig. 4. Sprouts were already present on the smallest trees, but the frequency of sprouting was higher at larger size classes (Fig. 5). Among sprouting trees, damaged trees had more sprouts than undamaged trees (Mann Whitney test, $p<0.05$). The percentage of dead sprouts was higher at the MF site (36.4%) than at the DEF site (22.7%; Mann Whitney test, $p<0.001$). At both sites, about 75% of the sprouts was implanted on the first meter of the parent trunk, but higher sprouts were not rare (Fig. 6).

The independent effects of three potentially important factors, site (MF and DEF), parent damage and parent size, on the number and basal area of sprouts were studied with stepwise multiple regression analysis (Table 4). The interactions between these variables were highly correlated to site or parent size (due to the differences between the parent populations in the two plots), so they were not used in the regressions.

Coefficients of determination for regressions on the number of sprouts were not high. The best regression ($R^2=0.28$) related the total number of sprouts (including dead and high ones) to all three explaining variables. A similar result (at $R^2=0.36$) was obtained with the total sprout basal area per tree (excluding sprouts that were dead, high or shorter than 50 cm). It is concluded that the number of sprouts increases with parent diameter, that it is higher on damaged trees than on undamaged trees and higher at the MF site than at the DEF site. The total sprout basal area per tree increases with parent diameter, is higher on damaged than on undamaged trees, but it is lower on the MF site than on the DEF site. Therefore, contrary to the parent size distribution, the DEF site is characterised by trees with fewer but larger sprouts than at the MF site. This effect is independent of parent condition and parent size.

In trees with many sprouts a size hierarchy was apparent, as was revealed by a positive correlation between sprout number and the coefficient of variation of sprout basal area (Pearson $r=0.64$, $p<0.001$; sprout number was square-root transformed). There

**Table 3**

Characteristics of the sprout populations on *Dicymbe* trees in the study plots in Dry Evergreen Forest and Mixed Forest near Mabura Hill, Guyana. Statistics are calculated per sprout-bearing tree; N=81 trees for DEF, 51 trees for MF. Medians were tested with Mann-Whitney unpaired ranks test, in column marked p: *** p≤0.001; ** p≤0.01; ns: not significant.

| | Dry Evergreen Forest | | | Mixed Forest | | | |
|---|---|---|---|---|---|---|---|
| | Median | Max | Total | Median | Max | Total | p |
| No of sprouts below 4 m per tree | 5 | 31 | 538 | 12 | 66 | 898 | *** |
| No of living sprouts below 4 m per tree | 4 | 23 | 413 | 7 | 34 | 531 | ** |
| Total basal area of living sprouts > 0.5 m below 4 m per tree ($cm^2$) | 38.7 | 824.8 | 365[1] | 15.8 | 655.9 | 434[1] | ns |
| Average basal area per living sprout > 0.5 m below 4 m per tree ($cm^2$) | 5.7 | 113.1 | | 2.1 | 227.0 | | ** |
| Max sprout diameter per tree (cm) | 3.8 | 27.9 | | 2.6 | 26.5 | | ns |
| Implantation height of living sprouts below 4 m (cm) | 24 | - [2] | | 41 | - [2] | | *** |

[1] number of living sprouts taller than 0.5 m.

[2] analysis was restricted to lower 4 m of the stem.

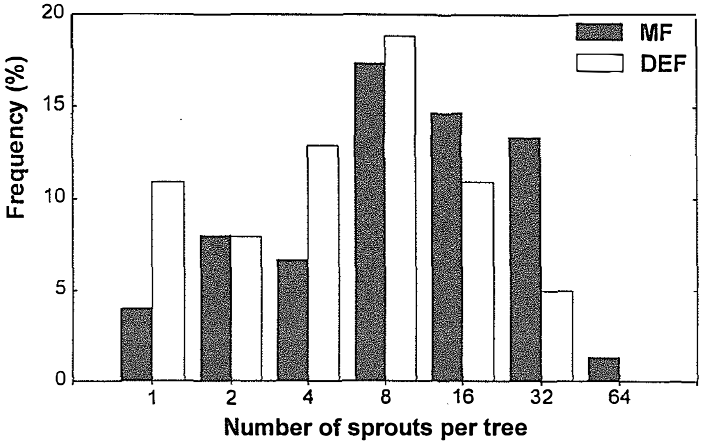

**Figure 3**

The number of stem sprouts per *Dicymbe* tree in Mixed Forest and Dry Evergreen Forest. The categories on the X-axis are doubling classes of sprout number per parent. The category 'without sprouts', not shown, is about 33% in both plots. N = 77 (MF) and 106 (DEF) parent trees.

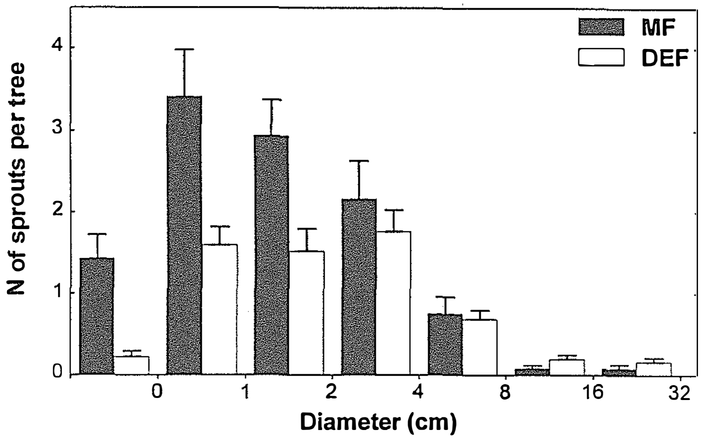

**Figure 4**
**Size distribution of stem sprouts on *Dicymbe* trees in Mixed Forest and Dry Evergreen Forest. The class below 0 cm dbh represent sprouts less than 50 cm length. N = 49 (MF) and 67 (DEF) sprout-bearing parent trees.**

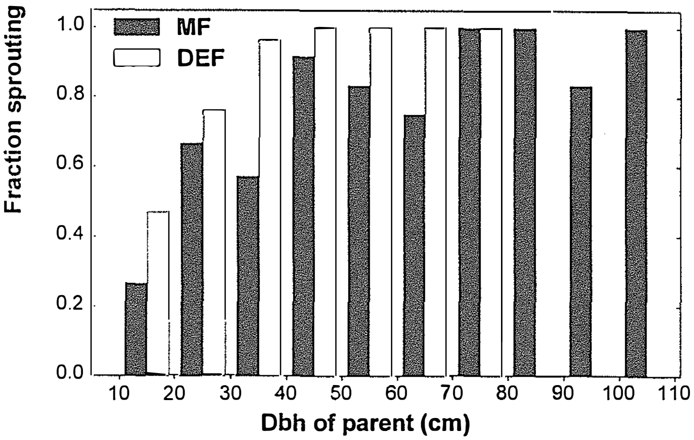

**Figure 5**
**The proportion of sprouting *Dicymbe* trees in Mixed Forest and Dry Evergreen Forest. All sprouts are included, also dead sprouts and sprouts implanted above 4 m on the trunk.**

was no correlation between the number of sprouts per tree and their average basal area (Pearson r=0.08, ns; sprout number was square-root transformed, basal area was log transformed). The correlation between sprout number and maximum basal area was weak and positive (r=0.32, p<0.01) This implies that possible self-thinning among sprouts (which would lead to a negative correlation) could not be demonstrated for this data-set. Although all trees with very large average sprout size had only few sprouts, not all trees with few sprouts had large average sprout size.

**Table 4**

**Summarised results of stepwise multiple regression analysis relating sprout number and size to parent diameter, site and crown damage. Dependent variables were: N of living sprout implanted below 4 m on the parent bole (LIVSPR<4); N of living and dead sprouts implanted below 4 m (ALLSPR<4); N of dead and living sprouts irrespective of implantation height (ALLSPR), and total living sprout basal area below 4 m (LIVSPRBA<4, this excludes sprouts that did not reach the reference height). Sprout basal area and parent diameter were log-transformed; the remaining dependent variables were square-root transformed prior to analysis; site and damage were dummy variables coding 'MF' resp. 'with damage' as 1. Stars indicate the level of significance of the partial regression coefficients: * $p \leq 0.05$; *** $p \leq 0.001$; ns not significant. N=123.**

| | dependent variable | | | |
|---|---|---|---|---|
| Independent variables | LIVSPR<4 | ALLSPR<4 | ALLSPR | LIVSPRBA<4 |
| Intercept | -1.01 ns | -1.06 ns | -1.02 ns | -1.03 * |
| Parent dbh | 2.18 *** | 2.39 *** | 2.37 *** | 1.57 *** |
| Site | | 0.72 * | 0.62 * | -0.53 *** |
| Damage | | | 0.61 * | 0.48 *** |
| F | 21.78 *** | 19.08 *** | 15.24 *** | 20.20 *** |
| $R^2$ | 0.15 | 0.24 | 0.28 | 0.36 |

### Comparisons of sprouts and saplings

At either site the sapling density exceeded sprout density (Table 5). There were many more small saplings than sprouts, but between 2.5 and 20 cm dbh, sprout and sapling density were more balanced, and saplings were significantly larger than sprouts (Table 5, Fig. 7). Sprout and sapling population distributions both differed significantly between the two plots (Table 5). In either case the individuals from the DEF were larger than individuals from the MF.

Saplings and sprouts of similar length and diameter (but unknown age; at the MF site) differed in their above-ground biomass allocation. While stem weight was comparable, saplings had twice as many leaves and three times as much leaf area as sprouts (Table 6, Fig. 8). This caused total dry weight, the number of leaflets, leaf dry weight, $LAR_{above}$ and $LWR_{above}$ per individual to be larger for saplings than for sprouts. Specific Leaf Area tended to be higher for saplings than for sprouts, but this difference was only marginally significant. A difference in SLA was not expected as the light environment was a constraining condition to the choice of the individuals from which the sample was taken. The volume to weight ratio of segment 6 (1.25-1.50 m), where the diameter was measured, was higher for saplings than for sprouts. In saplings the leaves and leaf area seemed to be more concentrated in the top segments (Fig. 8), although this effect was only significant for leaf area (Kolmogorov-Smirnov two-sample test; $p<0.001$), and not for the number of leaves.

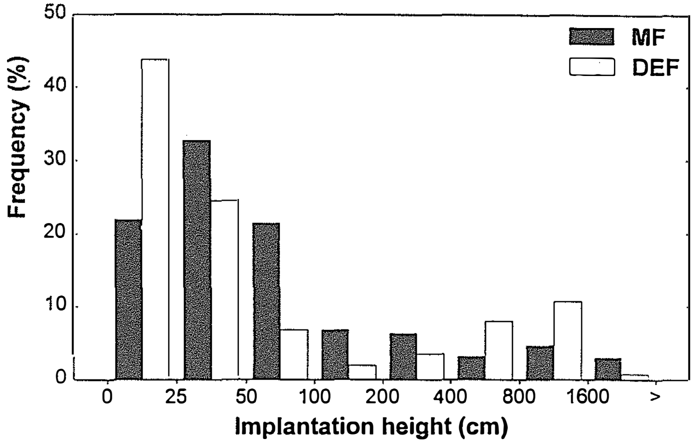

**Figure 6**
Implantation heights of living sprouts on the parent trunk in Mixed Forest and Dry Evergreen Forest. The implantation heights are given in doubling classes of distance from the base of the trunk. N (sprouts) = 602 (MF) and 514 (DEF).

## Discussion

### Sprouting in trees

The formation of sprouts as observed in *Dicymbe* is very different from the more frequently observed occurrence of sprouts on broken, cut or otherwise damaged trees. In the tropics, sprouts are formed in response to tree damage (Putz & Brokaw 1989, Clark & Clark 1991), *e.g.*, as a result of hurricanes (Walker 1991, Bellingham *et al.* 1994, Vandermeer *et al.* 1995) or as the objective or consequence of forest management (Uhl *et al.* 1981, Hartshorn 1989, Khan & Tripathi 1989, M. Rijks *et al., in prep.*). There are many examples of coppicing from temperate forests. In these instances, sprouts are created as opportunistic organs that replace damaged organs of the parent (Jeník 1994). Their formation is limited to a short period following the removal of apical dominance of the tree or the organ that is being replaced. In *Dicymbe*, sprouting, although stimulated by damage, is a naturally occurring phenomenon that takes place during most of the life of the tree and thus is of a cumulative rather than instantaneous nature. In its cumulative nature it is comparable to root suckering (*e.g.*, in *Alnus, Populus* and *Ulmus*, Koop (1987); *Fagus grandifolia*, Jones & Raynal (1986); the shrub-form of *Dimorphandra conjugata* in the Guianas, Fanshawe (1952)).

Trunk suckering or coppicing in trees, which involves the formation of clonal modules that follow the architectural model of the parent on the trunk of the parent (Hallé *et al.* 1978, Jeník 1994), was described for *e.g., Alnus, Betulus, Salix, Ulmus* and *Tilia* in Europe (Koop 1987) and for *Nothofagus cunninghamii* in Tasmania (Read & Hill 1988). In *Fagus japonica* and *F. engleriana*, sprouting appears to be the principal means of reproduction, especially in areas with bamboo domination in the undergrowth (Ohkubo 1992, Peters 1992). In Guyana, *Dicymbe corymbosa*, which is absent

**Table 5**
**Comparison of size and number of *Dicymbe* sprouts and saplings in the study plots near Mabura Hill, Guyana. Drh is diameter at reference height, 50 cm for sprouts and 130 cm for saplings. Differences in size distributions were tested with Kolmogorov-Smirnov two-sample tests (only in the diameter range 2.5-20 cm). Test results for the sprout-sapling comparisons are on the bottom row; for between site comparisons in the right hand column.**

| | Dry Evergreen Forest | | Mixed Forest | | |
|---|---|---|---|---|---|
| | Median diameter (cm) | N (ha$^{-1}$) | Median diameter (cm) | N (ha$^{-1}$) | |
| **Diameter 1-20 cm drh** | | | | | |
| Sprouts | 2.5 | 284 | 2.0 | 274 | |
| Saplings | (>1.0)[1] | 528 | (>1.0)[1] | 560 | |
| **Diameter 2.5-20 cm drh** | | | | | |
| Sprouts | 3.6 | 142 | 3.5 | 103 | $p<0.05$ |
| Saplings | 4.5 | 170 | 4.2 | 171 | $p<0.05$ |
| | $p<0.01$ | | $p<0.05$ | | |

[1] **saplings between 1 and 2.5 cm dbh were only tallied, so no median could be calculated.**

in the Mabura area, also shows vigorous sprouting (Fanshawe 1954, Richards 1996, fig. 4.1), whereas we observed the frequent occurrence of small basal trunk sprouts in *Vouacapoua macropetala, Pentaclethra macroloba* and in one unidentified species. Other examples include *Trigonobalanus verticillata* (South East Asia), *Pithecellobium* sp. (Malaysia); *Cercidiphyllum* sp. (Japan; all cited by Corner 1990), *Castanopsis acuminatissima* (Java; Richards 1996), *Lobelia giberroa* (East Africa; Jeník 1994) and in *Persea indica* (La Gomera, M.J.A. Werger, *personal communication*). In general however, coppicing from roots or trunk in intact trees seems to be a rare mode of regeneration in trees, and certainly in the tropical rain forest.

## Factors affecting sprouting in Dicymbe

In the two *Dicymbe* populations, sprouting is a common phenomenon that occurs in more than two thirds of all trees above 10 cm dbh (Table 2). Parent size, crown damage and site contributed significantly to the total number and the size of the sprouts (Table 4), although well over 50% of the variation remained unexplained. This is probably partly due to the death and disappearance of sprouts, especially in older trees. If only the number of sprouts implanted within 4 m from the tree base or only the number of living sprouts within 4 m from the base were considered, first damage and then site lost their significance.

Parent size can be interpreted as an age parameter, which explains a positive relation between the size of the largest sprouts and parent size. Furthermore, with increasing age an increasing number of buds is expected to break dormancy and to develop as a sprout. It is not clear whether senescence of the parent tree stimulates the development of sprouts (as there are already sprouts on healthy, small sized trees), but if this is so, this should also contribute to a positive relation between size and sprout number.

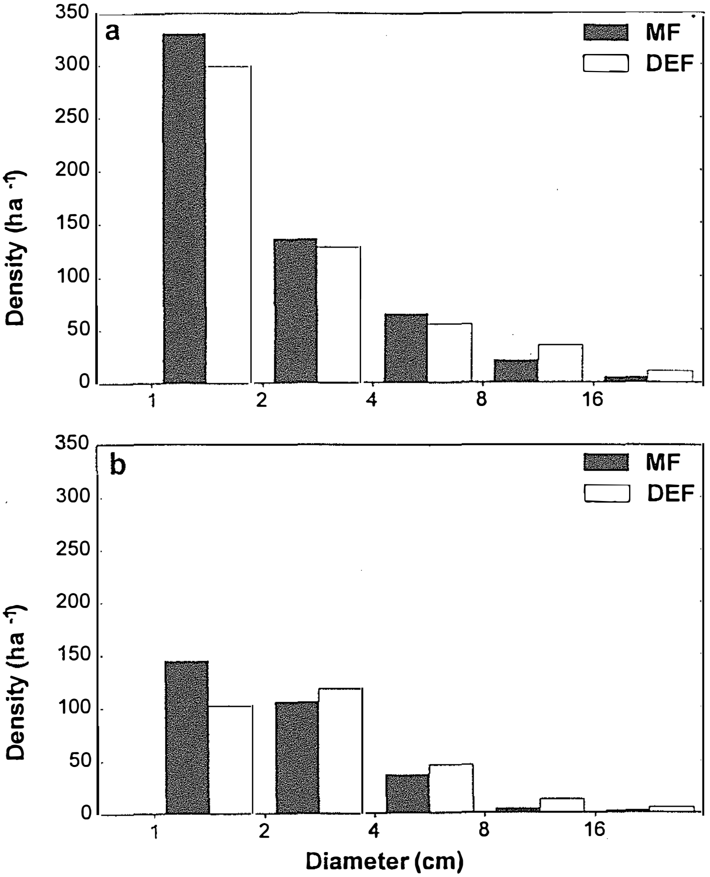

**Figure 7**
**Comparison of a. sprout and b. sapling size class distributions between 1 and 20 cm drh in two 1 ha plots in Mixed Forest and Dry Evergreen Forest.**

There seemed to be a maximum to the number of sprouts that is developed on the basal part of the bole (below 4 m), which is related to the parent size (Fig. 2).

Loss of the crown or part of it triggers the formation of reiterative sprouts (Tomlinson 1983), presumably through the loss of suppression by phyto-hormones that are produced by the dominant shoot. Such an effect of phyto-hormones on the formation of sprouts and root suckers was shown in experiments by Eliasson (1961), Sterret & Chapell (1967) and Schier (1981) on *Populus* and *Robinia.* The effect of crown damage on sprout numbers in *Dicymbe* is only significant when the sprouts above 4 m are included in the analysis. Similarly, damage stimulated sprouting in the root-suckering *Fagus grandifolia,* where sprouts are formed from root callus tissue that is formed on damaged roots (Jones & Raynal, 1986, 1988). Crown and stem damage are frequently cited to promote sprouting after the occurrence of hurricanes (Bellingham *et al.* 1994) or natural disturbance (Putz & Brokaw 1989). Unlike the higher sprouts, the formation of basal sprouts in *Dicymbe* did not seem to be limited to the occurrence of dam-

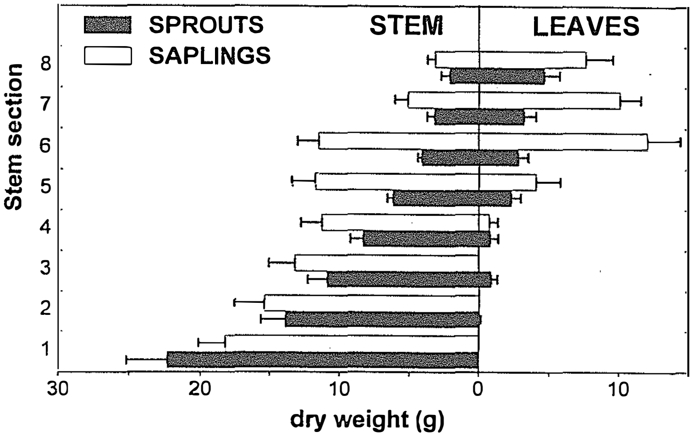

**Figure 8**
**Distribution of stem and leaves along the stem in *Dicymbe* saplings and sprouts from the MF site. Means ± 1 se dry weight are given per 25 cm stem section. The sections are numbered from 1 (stem base) to 8 (stem tip) on the abscissa. N=11 for both categories for each section.**

age, senescence or disease (*cf.* Koop 1987), but here it is apparently part of the natural growth strategy of the species in the service of future maintenance of the individual in the canopy. Damage did positively affect the size of sprouts, also the basal ones (Table 4).

Site had a different effect on total sprout number (*i.e.* including dead sprouts; in MF more than in DEF) than on size (in MF smaller than in DEF). Contrary to our expectations, in MF the sprouts were numerous but small, while in the DEF they were few but larger (Table 3, Fig. 4). The parent tree size class distribution showed a contrasting pattern, with the DEF population being characterised by many but relatively small trees and the MF population by fewer but relatively large trees. (Fig. 1). The population size distributions of the parents in both plots confirm the pattern found by ter Steege *et al.* (1993) for parent trees growing on white and brown sand soils at a site *c.* 10 km away from the study plots, although the maximum diameters reported by them are much higher. Therefore, site factors that contribute to the different patterns found among sprouts must be of a different nature than those that explain the differences in parent size distribution (see below).

### Parent tree size distribution and white sand forests

The differences in *Dicymbe* population and stand size distribution between the DEF and MF sites are representative for the differences in stand structure between forests growing on bleached white sands and surrounding, more mesic forests on other soil-types elsewhere in the world. Generally, white sand forests are characterised by a low stature, a high stocking of stems below 20 cm dbh and a scarcity of large trees (dbh>60 cm) when they are compared with nearby forests on different soils (Davis & Richards 1934, Klinge & Herrera 1983, Whitmore 1984, Coomes & Grubb 1996). In spite of

**Table 6**

**Comparison of above ground plant morphology and biomass allocation patterns between saplings and sprouts harvested from the Mixed Forest site near Mabura Hill, Guyana. N=11 for both groups. Tests were performed with Mann-Whitney unpaired ranks test; in column marked p: ***: p≤0.001; **: p≤0.01; ns: not significant.**

| | Sprouts | | Saplings | | p |
|---|---|---|---|---|---|
| | Mean ± se | | Mean ± se | | |
| Length (cm) | 182.1 | 4.7 | 184.0 | 4.7 | ns |
| Dbh (mm) | 6.2 | 0.3 | 6.3 | 0.4 | ns |
| Stem weight (g) | 69.9 | 6.8 | 88.7 | 10.1 | ns |
| Leaf weight (g) | 12.8 | 1.4 | 32.6 | 5.0 | ** |
| Total weight (g) | 82.7 | 6.5 | 121.3 | 13.8 | *** |
| No of leaves | 5.7 | 0.5 | 12.6 | 1.6 | ** |
| No of leaflets | 45.9 | 5.6 | 95.3 | 12.1 | ** |
| Leaf area ($cm^2$) | 1736 | 192 | 4934 | 711 | ** |
| SLA ($cm^2$ $g^{-1}$) | 136.4 | 4.5 | 153.5 | 6.5 | (0.053) |
| $LWR_{above}$ (%) | 16.8 | 2.4 | 26.4 | 2.3 | ** |
| $LAR_{above}$ ($cm^2$ $g^{-1}$) | 22.7 | 3.4 | 39.9 | 3.1 | ** |
| Weight-to-volume ratio in segment 6 (g $cm^{-3}$) | 0.56 | 0.03 | 1.48 | 0.15 | *** |

the generality of this trend throughout the world, no simple mechanism is identified yet that explains this difference (see Whitmore (1984) and Richards (1996) for a discussion). An attractive explanation such as low nutrient availability on white sands alone cannot be assumed to be responsible for the observed differences in this study, as differences in nutrient availability and internal nutrient cycles in the two study plots were shown to be very small compared with the surrounding Mixed Forest (Brouwer 1996, *cf.* Whitmore 1984, *cf.* Table 1a).

### Sprout size distribution

The observed variation in population structure of the sprouts between the sites may possibly be ascribed to differences in light availability. DEF forest, albeit dense in terms of stems, is rather light (Davis & Richards 1934, *cf.* Whitmore (1984) and Bruenig (1996) for Kerangas on Kalimantan and Coomes & Grubb (1996) for Caatinga in Venezuela). Data supporting this difference are unfortunately not available, but it is among other things apparent from the occurrence of heliophytic epiphytes at low strata in DEF (Davis & Richards 1933). With higher light availability, sprouts in the DEF may be capable of sustaining higher growth rates than sprouts in the MF, leading to a relatively high number of large sprouts. The site effect on sprout number was only significant when also dead sprouts were considered (Table 4), so in the MF more sprouts are produced, but many of these die. This explanation for the observation that the sprouts in the DEF forest are large does not explain why they are also few. Possibly the low sprout number at this site may be the consequence of an inhibitory effect of large sprouts through phyto-hormones.

There is not much support for the possibility that low sprout numbers at the DEF site are explained by competition between sprouts followed by mortality of the smaller ones. In the understorey, light is limiting to growth and competition is expected to be for this resource. The effect of individual sprouts on the light environment in the crown of other sprouts is limited in comparison to the effect of the parent tree. Size inequality, which is indicative for asymmetrical competition for light (Weiner 1990), was most pronounced in trees with many sprouts. However, this can equally well be explained by a combination of variation in growth due to locally varying crown light environments, and variation in sprout age. If inter-sprout competition would lead to size inequality followed by self thinning, larger numbers of small, dead sprouts would be expected at the DEF site. This was not the case (*cf.* Table 3), although it is not clear to what extent this observation is affected by differential disappearance rates of dead sprouts at both sites. Self-thinning was also not evident from a negative relationship between average sprout size and sprout number.

Size inequality and subsequent thinning among sprouts growing on stumps (rather than intact trees) have been ascribed to inter-sprout competition (Johnson 1975, Khan & Tripathi 1989, Retana *et al.* 1992, Villá *et al.* 1994). On stumps, sprouts are produced during a short period only and competition for light is more likely to occur due to higher light intensities in the crowns of the sprouts.

### Sprout and sapling strategies

There were significant differences between treelets produced by generative means (saplings) and treelets produced by vegetative means (sprouts). The number of saplings was larger at both sites, especially in the 1-2 (2.5) cm size class (Table 5, Fig. 7). Saplings from the MF site had a higher LWR (above ground) and more leaf area than sprouts of similar size (Table 6). Saplings need to support a root system and may therefore be expected to require a larger minimum leaf area ratio than sprouts of similar size and photosynthetic characteristics.

In absence of a developed root system, sprouts derive water and nutrients from the parent tree. Probably sprouts are therefore less vulnerable to periodic drought stress than saplings. It is unclear whether this dependence also exists for carbohydrates. Branches (Watson & Casper 1984, Sprugel *et al.* 1991) and developing ramets of many clonal herbaceous species (Marshall 1990) are shown to become functionally independent from the parent in terms of their carbon economy as soon as the leaves become functional. If, in analogy, sprouts also show this independence, sprouts with a negative carbon balance would not be supported. This could explain the high percentage of dead sprouts in comparison with saplings. This percentage was not quantified for saplings in this study, but observations on mortality of saplings of the same size indicate an annual mortality of less than 2%, and a much lower population of standing dead individuals (Chapter 8).

These observations point to a number of important differences between stem sprouts produced by *Dicymbe* and other trees, and ramets produced by clonal herbaceous species. In herbaceous species, ramets are positioned away from the parent, thus increasing the spatial distribution of the genet and exploiting potentially favourable sites. In trees, the ramets are produced in an environment that is already saturated with the leaves and roots of the parent, and therefore, the genet as a whole has no direct advantage of the production of ramets in terms of increased access to limiting resources. Such an advantage explains why herbaceous clonal species allocate carbohydrates from parent or sister ramets to the recovery of disadvantaged ramets (Marshall 1990), or even to develop and maintain ramets specialised in the uptake of water in light-deficient environments (Stuefer *et al.* 1996), whereas carbon deficits of declining *Dicymbe* sprouts are apparently not supplemented by the parent. In many herbaceous plants, ramets are soon after their production more or less equivalent in size and reproductive potential to the parent, and contribute to a multiplication of the original number of ramets. In contrast, sprouts in *Dicymbe* require many years to become equivalent to the parent in size and reproductive potential, and although often many sprouts are produced on a single parent, the number of vegetative progeny from one parent is restricted to effectively one. Only the most basal sprouts occasionally develop an independent root system through adventitious rooting, but most sprouts remain dependent on the parent root structures.

What is the function of sprouting in *Dicymbe*? *Dicymbe* certainly does not depend on sprouts alone for its regeneration. It produces large amounts of seedlings (Chapter 3) and the species is dominant in the seedling and sapling strata at the study sites (Chapter 8, Isaacs *et al.* 1996). During the study period it was observed that large sprouts that reached into the canopy carried flowers and thus contributed to the generative reproduction of the genet.

The formation of sprouts is probably an alternative way to produce new individuals with a different suite of constraints to growth and survival. Sprouts contribute, at most, to the perpetuation of the genet at the same locality, whereas saplings contribute to the regeneration and dispersal of the individual. Once the parent dies, sprouts have the advantage of a large initial size, a well developed root system and a favourable, central position in the newly formed gap. This gives them a competitive edge over other seedlings and saplings in the gap (*cf.* Chapter 2). Thus the probability of maintaining itself at the same site is enhanced in *Dicymbe* when compared to other species.

However, there are four potential disadvantages of sprouts compared to saplings: a disproportionately sized root system, an unsuitable crown light environment, a lower wood density and the gap formation process itself. First, although sprouts may inherit a large root system (Koop 1987), they may also have to sustain it. However, it is argued that plants consist of physiological sub-units that are little integrated among each other (Watson & Casper 1984). In that case it is unlikely that sprouts will have to provide for the carbon demand of the root system just after the disappearance of the parent. Second, as long as the parent is alive, the light environment in their crown is almost by definition darker than for saplings, although this is not apparent from a difference in SLA between saplings and sprouts (Table 6). Sprouts grow in the shade of the parent, whereas saplings only reach a similar size in relatively well-lit places. Higher mortality and lower growth rates under low light conditions may explain why, in larger size classes (more than 2.5 cm dbh), there are more large saplings than sprouts, in spite of larger amounts of small (1-2.5 cm dbh) sprouts (*cf.* Table 5). Third, although not measured directly, the sprouts seemed to have a lower wood density than saplings (Table 6). This might be attributed to wood formed during the rapid initial growth phase. A low wood density possibly increases the risk of disease or breakage, and during the study sprouts occasionally broke off as result of handling during the measurements. Fourth, when the parent tree falls, only those sprouts survive which are not hit by it, and which are implanted below the breakage point. Complete uprooting of the tree inevitably brings about death for all attached sprouts. In the field, it is frequently observed that *Dicymbe* trees gradually collapse or snap off at some distance above ground level. At present however it is not known whether snapping off in *Dicymbe* is more frequent than in other species and can be considered a strategy that promotes the survival of sprouts.

In conclusion, sprouts and saplings represent alternative pathways for *Dicymbe* to maintain itself in the community. The investments required for one sprout in terms of limiting resources (most likely phosphorus, Raaimakers (1994), the quantities of which in wood and green leaves are low to very low, Brouwer (1996)) are possibly not much different from the accumulated investments required for one sapling of the same size (a large number of flowers and seeds with a high nutrient content, Chapter 3). Saplings are more suitable for the occupation of new sites, sprouts increase the ability of an individual to retain its own position in the canopy. Successful regeneration by means of sprouts is readily observed in both forest types, as can be seen from the presence of a decaying parent trunk at the base of some trees, or from trees with an irregularly shaped trunk base with callus tissue on the place where the connection with the parent had been. In the DEF we distinguished 9 such trees (8% of all *Dicymbe* >10 cm dbh in the plot), and in the MF 7-8 trees (9-10%). It is an interesting matter whether the balance between generative and vegetative propagation is different in both forest types. If it is assumed that the population size distributions reliably mirror growth and mortality patterns at the two sites (Fig. 7), and that a buffering effect of the parent against the effects of periodic drought is more important on the more drought prone soil (in the DEF), then it seems likely that vegetative regeneration is quantitatively more important in the Dry Evergreen Forest than in the Mixed Forest. Although at present there are no data to quantify this claim, field observations do suggest that mature trees grown from sprouts are more common in Dry Evergreen Forest than in Mixed Forest.

## Acknowledgements

We thank Demerara Timbers Ltd. for logistic support in their concession, and Marinus Werger, René Boot, Hans ter Steege and Josef Stuefer for critically reading the manuscript. This study was financially supported by a grant of STIR (MHR) and WSO (EM) and was carried out as part of, and funded in part by, the Tropenbos Programme in Guyana.

chapter 5

# Delayed germination of *Chlorocardium rodiei* in the tropical rain forest of Guyana

*Roderick J. Zagt & David S. Hammond*

## Abstract

Survival analysis was used to study survival and germination of three seed cohorts of *Chlorocardium rodiei*, a very large-seeded species from the tropical rain forest in Guyana. Seed fall occurred over a period of six months in each year, and was variable in amount and phenology. Although the median time till appearance of leaves was one year, each of four germination stages that were distinguished could last more than 1.5 years, and germination was still continuing after 3 years. Interannual differences in survival functions were accounted for by differences in survival in the seed stage, but not in the rooted and leafy stages. Seeds had a higher survivorship than rooted and leafy individuals. Survivorship of seeds was negatively correlated with rainfall per three-month period, but rooting had no clear relation with the amount of rain.

Seeds which were dispersed late in the season had a higher success of rooting, which was related to a higher rate of rooting but not to a higher survival for late seeds compared to early seeds. There was no difference in shoot production rate between individuals that rooted in different periods, but individuals that rooted early had a higher survival than late rooters. This led to a higher success for early rooters when compared to late rooters. The data suggest that age (or correlates of age) was more important than rainfall in determining survival for these groups.

The possible causes and significance of the variability of germination behaviour in relation to the spreading of the risks of germination are discussed. A simple model based on the results of the study suggests that large variation in timing and rainfall leads to very limited variation in germination success.

## Introduction

The Greenheart (*Chlorocardium rodiei* (Schomb.) Rohwer, Richter & van der Werff (syn. *Ocotea rodiaei*, Lauraceae)), a tree from the tropical rain forest in Guyana, has attracted ecological interest ever since Davis & Richards (1934) called Greenheart-dominated forests 'one of the chief glories of (then) British Guiana'. The germination ecology of this large-seeded species has been discussed at various times (Fanshawe 1947, Richards 1952, ter Steege 1990, ter Steege *et al.* 1994, 1996), but one outstanding feature of its germination has received little attention: the unusually slow germination process. Fanshawe (1947) noted that the seeds germinated in the forest in four to six months, but that moist seeds will retain their viability for one or two years, and that the seeds 'continue to germinate' over a two to three month period. This signifies a the peculiar situation for a heavy-seeded rain forest species: it maintains a *de facto* seed bank on the forest floor. New seed cohorts supply this seed bank before the previous cohorts are depleted. Apart from being slow, the germination process is also very variable; *i.e.* some seeds germinate within a few months, while other seeds need more than a year to germinate.

A tentative general hypothesis that might be able to explain the protracted and variable germination period of *Chlorocardium* could be that germination rates and mortality risks vary greatly with the abiotic or biotic conditions met during germination. *Chlorocardium* seeds were shown to be vulnerable to drought (ter Steege *et al.* 1994) and predation by insects and rodents (Hammond *et al., unpublished manuscript*). Especially rodent germination was demonstrated to be local and concentrated to a short period of resource scarcity for rodents (see also Chapter 7). Variable germination may act as a risk-spreading mechanism which reduces the risk of loosing an entire seed cohort due to occasional drought or predation by rodents.

In this paper the evidence is considered for this hypothesis. It reports the results of a 3.5 year study of seed production and germination for *Chlorocardium* in tropical rain forest in Guyana. Specifically, the following questions were addressed: (1) What is the quantity and temporal pattern of seed production in *Chlorocardium*? (2) What is the timing of rooting, germination and death? (3) Are the phenological patterns of germination correlated with rain fall patterns? (4) Are there differences between cohorts from different years?

## Study site and natural history of the species

The study was conducted in the Tropenbos Ecological Reserve located *c.* 20 km south of Mabura Hill, Central Guyana (5°13' N 58°48' W). The climate is hot and humid with a yearly precipitation of *c.* 2700 mm in a bimodal pattern with maxima in May-July and December (Jetten 1994; ter Steege & Persaud 1991).

The study was conducted in a 2 ha plot. It was located in a large tract of undisturbed Evergreen Rain Forest on Haplic Ferralsol (brown loamy sand), classified as well-drained mixed forest (*sensu* ter Steege *et al.* 1993), also called the *Dicymbe altsonii* faciation of the *Eschweilera-Licania* association (Fanshawe 1952). The plot was considered representative for this forest type in the Reserve area in terms of soil, structure and density of the trees (Chapter 6, 8). The tree density in this plot was 397 trees ha$^{-1}$ (diameter at breast height (dbh) ≥10 cm) with an estimated basal area of 39.3 m$^2$ and a canopy at 30-40 m height. *Chlorocardium rodiei* is a co-dominant of the canopy layer with a density in the plot of 38 individuals dbh >10 cm per ha. The maximum observed dbh for *Chlorocardium* in the plot was 104 cm. The tree reaches maturity in a dbh traject of *c.* 21-31 cm (Chapter 8); the density of adult trees in the plot was 32 ha$^{-1}$ (1994). These densities are high for tropical trees but representative for *Chlorocardium* in this forest type (*e.g.*, Richards 1952; ter Steege 1990). Flowers can be found throughout the year but mainly in March-June (ter Steege 1990, ter Steege & Persaud 1991). During 1992-1995, 68-78% of the adults flowered per year.

The fruits take about one year to mature; the phenology of seed dispersal is reported in the results. After dispersal, the seeds remain protected by the woody exocarp (so they are actually fruits). They are large and heavy: size 7 × 5 × 4 cm; fresh weight 65.5 ± 22.3 g, (mean ± 1 SD; ter Steege 1990); dry weight 38.9 g (Hammond & Brown 1995); they are primarily dispersed by gravity while an unknown percentage is further dispersed by rodents (Hammond *et al., unpublished manuscript*) or displaced downhill (Fanshawe 1947). Post-dispersal seed predation is mainly due to Scolytid beetles (*Sternobothrus spp.*) and rodents (*Dasyprocta agouti* (=*D. leporina*) and *Myoprocta acouchy* (=*M. exilis*); Hammond & Brown 1993, ter Steege *et al.* 1996); attack is often not directly lethal.

## Methods

### Monitoring of seed fall and germination

A 2 ha plot (consisting of two square 1 ha subunits) was established and physically subdivided in 5 m × 5 m subplots (n=800). The total yearly seed production in the plot was determined each year from 1992-1994 at the end of the dispersal season (July-August) by measuring the number of freshly fallen seeds in the centre 1 m$^2$ of all 800 subplots of the study plot. This procedure gives a minimum estimate of seed production because an unknown number of seeds may have been predated and disintegrated between seed fall and census.

The timing of seed fall, -survival and -germination was studied in 33 25 m$^2$ sample plots from January 1992 until June 1995. These sample plots were a random sample of 5 m × 5 m subplots located in areas within the *Chlorocardium* seed shadow in the 2 ha study plot.

Seed fall was monitored weekly in the period mid-January till mid-June in 1992-1994. New seeds were marked with a numbered plastic or wooden stick in the ground next to the seed, which was replaced by a coloured tag once a stem developed. For analysis, seeds were grouped in ten 2-week dispersal cohorts (seeds dispersed after week 18 are lumped in group 10), and in three annual cohorts (1992-1994). This study was designed to monitor primary (barochorous) dispersal, and this is meant when the word dispersal is used in this paper. Secondary dispersal of seeds by rodents or other vectors into or out of the sample plots did possibly occur, but this is not reported here.

Survival and germination of tagged seeds were monitored 25 times in the study period, in 1992-1993 more frequently than in 1994-1995. The median inter-census period was 46.5 days (range 14-99 days). Monitoring of the cohorts started at the end of the dispersal period, meaning that early dispersed seeds remained unchecked for a period of up to five months. Due to a large number of seeds, in two of the sample plots survival and germination were censused in 2.5 m × 2.5 m subplots in stead of the entire sample plot.

### Definitions of germination stages and death

At each census, seeds were classified into one of six categories: 1. seed (seeds unchanged); 2. burst (woody exocarp burst open between the cotyledons); 3. root (radicle appearing); 4. germinant (stem appearing, but no leaves developed yet); 5. seedling (stem and leaves present); and 6. dead. Note that 'germination' and 'seedling' only refer to individuals with leaves, in this paper, and not to rooted individuals. The move from one stage to another is called transition in this paper. For sake of clarity, germination was considered to be progressive, *i.e.* once a certain stage was reached, the individual could not fall back to an earlier stage. In reality, germination in *Chlorocardium* is not that simple, and even individuals that were reported as a 'dead seedling' could be found 'rooting' months later. As long as the embryo is partly alive and some cotyledonary reserves are still present, lost roots and stems can be replaced. Because of these large regenerative capabilities, and the difficulty to verify whether the embryo was dead without damaging the seed, it was hard to be certain of the death of a seed or seedling. Therefore, individuals without sprout were considered to be dead once the cotyledons were completely exhausted or at any earlier moment that the embryo was apparently dead.

### Rainfall

Rainfall data were obtained from the Tropenbos Meteorological Station (using a tipping bucket connected to a data-logger; Jetten 1994) or, in absence of these data, from the Tropenbos Field Station (daily readings from a rainfall gauge). Both stations were located within 2 km from the study plot. These measurements stopped in April 1994. Rainfall is presented as 10-day sums of daily rainfall, averaged over 3-month intervals (see below). This procedure averaged away shorter dry seasons, such as the April dry season in 1993.

### Analysis

Total seed fall between years was compared with Friedman anova. The timing of seed fall between years, and the age of individuals at rooting was compared with Kruskal-Wallis anova. Final observed frequencies of rooting or germination were analysed using contingency tables.

Survival analysis (Pyke & Thomson 1986, Muenchow 1986, Armitage & Berry, 1987; see Schupp 1990 for an application to a tropical tree species) was used to study

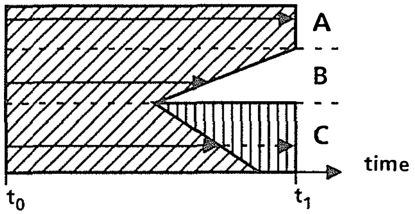

**Figure 1**
Scheme of the censoring of observations. Seeds are dispersed at $t_0$ and monitored till the end of the study at $t_1$. The dark area represents time spent in the seed stage, the light area is time spent in later stages. Individuals (represented by arrows) of group A do not die nor germinate by the end of the study period, so these observations are censored at $t_1$: their minimum survival is known, but not their realised survival. Group B are individuals which die as a seed. Their survival time is exactly known. Individuals in group C survive to germinate, after which they may or may not die. For analysis of seed survival, group B includes the complete observations, and groups A and C include incomplete, censored observations. For analysis of germination, group C includes the complete observations, and groups A and B the censored observations (because in neither case the moment of germination could be determined). The period of 'survival' is then the period between $t_0$ and the moment of death or censoring (given by arrows with drawn lines).

germination and survival rates and the phenology of germination. This technique estimates the distribution of survival times of populations of individuals. Individuals which are still alive (or 'lost') at the end of the observation period can be handled as censored observation, *i.e.* these observations only contain partial information (their minimum survival time). For 'survival', any time to a certain event can be used. In this study, time to rooting, time to germination and time to death were studied.

The idea of censoring was extended in order to compare survival times between germination stages. That is, censoring occurs not only when the end of the observation period is reached without reaching the terminal event, but also when an event occurs that precludes the occurrence of the terminal event (see Fig. 1 for explanation).

The rationale of censoring these individuals is that individuals moving from one stage to the next are exposed to different hazards than the ones which do not. Thus, death at a later stage contains no (or little) information about the risks in the previous stage. Similarly, individuals that die before they move to the next stage are censored, because through their death information is lost about the timing of this transition.

Three related functions were determined for each sample of survival times. In this study, time-intervals of three months (91.5 days) were used to describe these functions, encompassing the longest interval between censuses (except the last two). The survival function is the cumulative number of individuals surviving or remaining in the same stage up to the respective time interval. In this paper, this function is called transition function when dealing with transitions from one stage to the next. The hazard function is, for each interval, the number of deaths or transitions per day divided by the average number of individuals at risk. Hazard rates tend to be very variable when the number of survivors is small. The probability density function is the probability of death or transition per day, during a certain time interval multiplied by the probability of survival or stasis until that time interval. The hazard rate emphasises the risk of dying (transition) for individuals that have survived the previous periods, while the probability density function gives an idea, at population level, when most deaths (transitions) occur.

**Table 1**
***Chlorocardium* seed production in 1992-1994 in the 2 ha study area based on surveys of 800 1 $m^2$ sample plots, and in the 25 $m^2$ study plots. Surveys were done at the end of each seed dispersal period.**

| Annual cohort | Mean number of seeds ($m^{-2}$) | Maximum ($m^{-2}$) | Presence (%) | Total number of seeds | Of which production date known (%) |
|---|---|---|---|---|---|
| **Based on surveys of 1 $m^2$ plots[1]** | | | | | |
| 1992 | $0.42^a$ | 14 | 16.5 | 339[2] | |
| 1993 | $0.74^b$ | 30 | 23.7 | 594[2] | |
| 1994 | $0.28^a$ | 8 | 15.9 | 222[2] | |
| **Based on 25 $m^2$ sample plots** | | | | | |
| 1992 | $1.44^{xy}$ | 21.2 | | 1549[3] | 1373 (88.6) |
| 1993 | $1.14^x$ | 10.7 | | 1223[3] | 1143 (93.5) |
| 1994 | $0.50^y$ | 3.1 | | 538[3] | 522 (97.0) |

[1] N of seeds per plot differed per year: Friedman anova $\chi^2 = 60.2$; df=2; $p<0.001$; (letters give result of pair-wise Friedman anovas; means sharing the same letter were not different at $p \leq 0.05$).
[2] total on 800 $m^2$.
[3] total on 825 $m^2$.

Survival times were expressed in two different ways. First, the number of days between seed fall and death, transition or censorship was determined. Results expressed in this way gave information about the 'timing' of death or germination for individual seeds. Seeds with an unknown production date (see Table 1) were excluded from these calculations. Second, the number of days between January 1 of the year of dispersal and death, transition or censorship was determined. This measure refers to 'phenology', as it concerns the timing of germination and death in the population in relation to calendar time.

Comparisons between cohorts, dispersal periods and stages were done by performing a $\chi^2$ test on the sum of Mantel scores (Mantel 1967) of each group. Two-sample comparisons were done with the logrank test (*e.g.*, Pyke & Thompson 1986).

Individuals from all sample plots were pooled for analysis. For this analysis, the stage 'burst' was merged with 'seed' and 'germinant' with 'seedling'. From these data, the timing and phenology (as distinguished above) of death and transition from one stage to the next were determined for seeds, rooted individuals and germinated individuals, and compared between annual cohorts and dispersal cohorts. Not all statistics could be calculated for annual cohort 1994, due to the abbreviated study period. All analysis was done with the Statistica package (Statsoft Inc. 1993)

### Correlation with rainfall

The relation between the rainfall pattern and the phenology of germination and survival were studied with multiple regression analysis. The dependent variables were angular transformed hazard rates of death and rooting per three-month period (quarter);

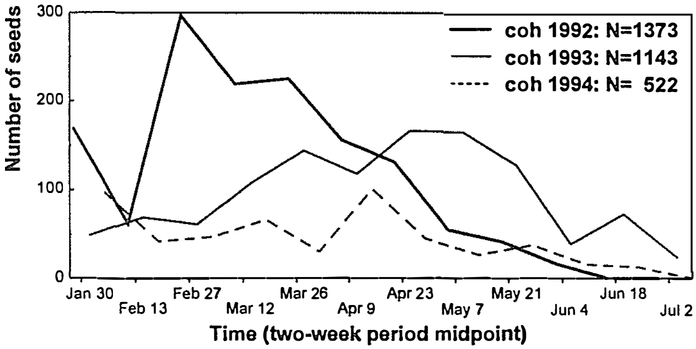

**Figure 2**
**Distribution of seed rain for the 1992-1994 cohorts of *Chlorocardium* near Mabura Hill, Guyana. Total number of seeds is given per 14-day period in 33 plots of 25 m$^2$. The median day of seed fall differed between years (Kruskal-Wallis anova $H_{2,3038}$=419; p<0.001).**

the independent variables were time (quarter), dispersal time, rainfall (average 10-day sum of rainfall per quarter) and the interaction between time and rainfall. Ten days were considered a reasonable period over which possible drought could affect germination. Hazard rates were only calculated for sample sizes of 10 or more. Due to the incomplete rain fall record, and the fact that many seeds from cohort 1994 were still germinating by the time censuses stopped, these relations were only studied for the 1992 and 1993 cohorts.

## Results

### Seed fall

The number of seeds in the 1 m$^2$ sample plots varied between years in the order 1993>1992=1994 (Table 1). The analysis with the data from the 33 sample plots of 25 m$^2$ gave the same results, except that 1992 is not different from either of the other years. The seed number in 1992 is highest due to a very high seed density in two of the plots. Seed production per 25 m$^2$ plot was correlated between all years (Spearman r = 0.84 or higher, p<0.001, n=33).

Seed fall spanned a period of *c.* 6 months (Fig. 2). The median day of seed fall was not the same between years. It was early in 1992 (median of seed production on February 28, period 4), late in 1993 (median on April 6, period 7) and without a clear peak in 1994 (median on March 8, period 5). This variation existed also at the level of sample plots (which had in most cases one tree dispersing into it): the rank order of the median date of seed production per plot with more than ten seeds in each year was every year different (Gamma correlation coefficient =0.26-0.55, p =0.07-0.45 for comparisons between years, n=11 sample plots).

**Table 2**

**The duration of the germination process in *Chlorocardium*. Median number of days between seed fall and arrival in each of four germination stages and median duration of these germination stages. See methods section for definition of stages. Minima are strongly determined by length of inter-census interval. Maxima exclude seeds that were still germinating by the end of the study.**

| | Seed - burst | Seed - root | Seed - germinant | Seed - leafy seedling |
|---|---|---|---|---|
| Median duration | 124 | 194 | 281 | 366 |
| Range | 16-813 | 38-859 | 100-1084 | 164-1105 |
| | Seed - burst | Burst - root | Root - germinant | Germinant - leafy seedling |
| Median duration | 124 | 77 | 99 | 90 |
| Range | 16-813 | 21-467 | 21-722 | 21-400 |

**Table 3**

**Observed final rooting and germination percentages for 1992-1994 cohorts of *Chlorocardium*. The data for 1994 constitute an underestimation as rooting and germination were still continuing by the end of the study period. Based on 641, 813, and 428 individuals (1992-1994). Rooting and germination percentages were significantly different between years ($\chi^2$ tests; *** $p \leq 0.001$), except in the hypothetical case that all remaining seeds and roots would germinate ($\chi^2_5 = 3.46$; $p=0.63$). Pairwise $\chi^2$ comparisons indicated that 1992 and 1993 were equal, but that these two differed from 1994, even if all remaining seeds and roots would germinate.**

| Annual cohort | Rooted (%) | Germinated (%) | Seeds remaining (%) | Roots remaining (%) |
|---|---|---|---|---|
| 1992 | 68.8 | 52.0 | 0.0 | 0.2 |
| 1993 | 67.5 | 50.0 | 0.5 | 1.1 |
| 1994 | 48.4 | 31.7 | 5.4 | 9.8 |
| $\chi^2_5$ | 55.8*** | 50.1*** | | |

### Stage lengths

The time spent by an individual in any given stage varied considerably (Table 2). Rooting may occur as early as a month after seed fall, and germination in two months, but most seeds took much longer to germinate. After about a year 50% of the future seedlings developed a leafy shoot; however, even after three years germination was not complete for all seeds in the 1992 cohort (Fig. 3).

### Survival in germination stages

Seeds, roots and seedlings had significantly different survival functions when data from all years were pooled (Fig. 4a). In two-by-two comparisons per year, seeds had higher survival rates than both roots and seedlings, and roots higher than seedlings (Log rank |Z| 1.88-8.62; df=1, all p<0.05) in 1992 and 1993. In 1994 the same ten-

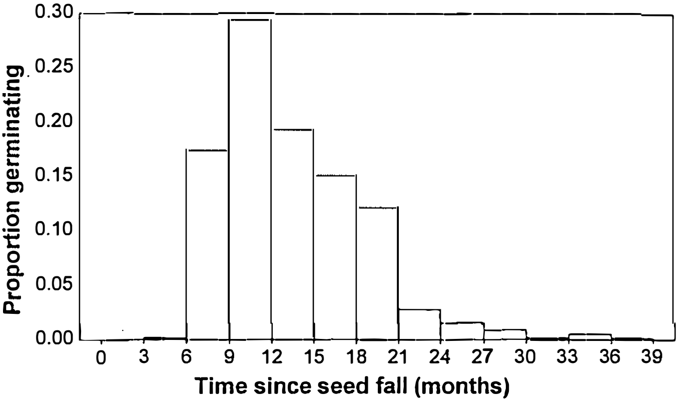

**Figure 3**

**The timing of germination (development of a stem) of the 1992-1993 annual cohorts in *Chlorocardium*. Cohort 1994 is omitted because many individuals were still germinating by the end of the study period. Note that cohort 1993 could not contribute to germination after 24 months because the monitoring stopped in June 1995. The total number of germinated seeds was 743.**

dencies were present, but only seeds and seedlings were statistically different. Therefore, the seed stage can be considered the stage with the lowest mortality risk.

The overall survival functions of the three annual cohorts were significantly different ($\chi^2$=49.62; df=2; p<0.001, n=1882), with half-lives (± 1SE) for 1992-1994 of 518 ± 12, 410 ± 9 and 372 ± 14 days, respectively. Survival of individuals in the seed stage was different between years, but survival of individuals in the root or seedling stage was not (Fig. 4c-d), so differences in overall survival between annual cohorts were entirely due to mortality during the seed stage. In Table 3 the number of individuals that eventually rooted and germinated in the study populations is given.

### Timing of death among dispersal cohorts

Multiple regression analysis indicated that calendar time, dispersal period and rainfall each explained significant proportions of the variation in the hazard function of individuals in the seed stage in both 1992 and 1993. The death risk increased with time (partial correlation coefficient of hazard rate with time after controlling for dispersal period and rain = 0.58 (1992, n=55) and 0.62 (1993, n=53), p<0.001). The dry season appears to be a risky season for seeds (Fig. 5). Six out of ten dispersal cohorts had a peak probability of dying during the dry season in the third quarter of 1992. In 1993 there was no clear peak, corresponding with a comparably less pronounced dry season in that year. In both years, the hazard function of death in a certain period was consistently negatively correlated to the amount of rain during that period (partial correlation coefficient after controlling for time and dispersal period -0.42, p<0.01 (1992) and -0.33, p<0.05 (1993); Fig. 6). Early dispersal cohorts had a higher risk of death than late dispersal cohorts (partial correlation coefficients -0.47, p<0.001 (1992) and -

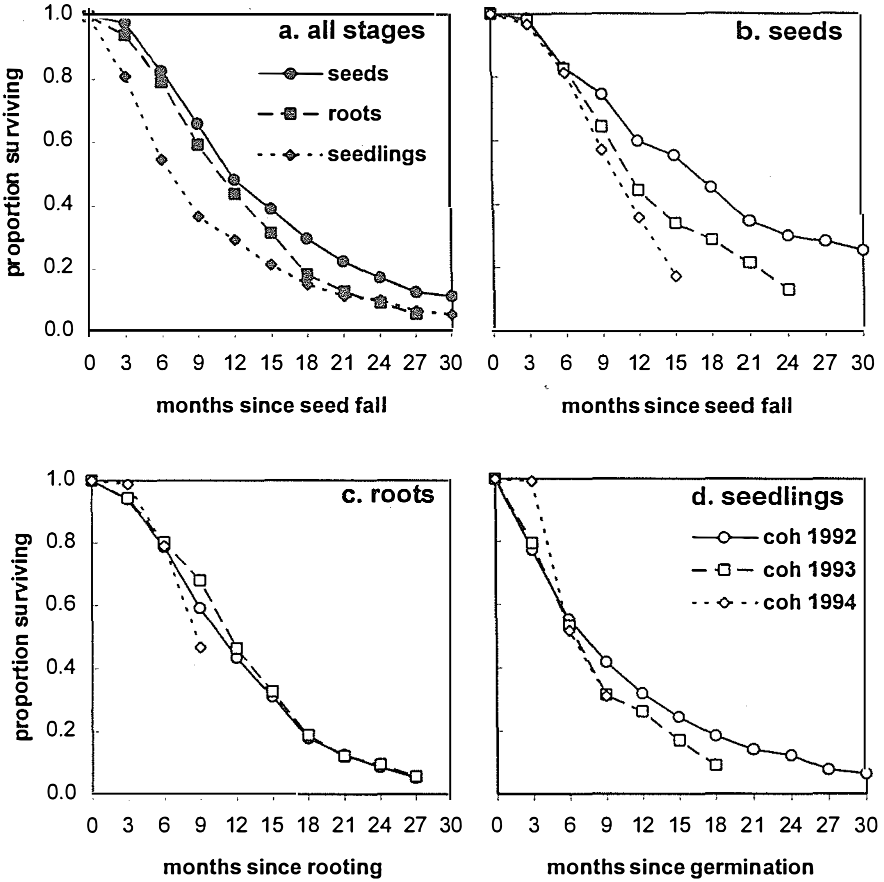

**Figure 4**

**4a. Survival of individuals in the seed, root and seedling stages in *Chlorocardium*. Cohorts of all years were pooled. Seeds, roots and seedlings had significantly different survival functions in pair-wise comparisons: $\chi^2$= 14.2-84.1; all $p<0.001$). 4b-d. Survival functions for (b) seeds, (c) roots and (d) seedlings for annual cohorts 1992-1994. Legend for 4b-d in 4d. The annual survival functions were different for seeds ($\chi^2$=14.2; df=2; $p<0.001$), but not for roots and seedlings ($\chi^2$= 2.49 resp. 2.97; df=2; $p>0.23$).**

0.63, $p<0.001$ (1993); $R^2$ for the regressions were 0.45 (1992) and 0.71 (1993), $p<0.001$).

### Timing of rooting among dispersal cohorts

The timing of root formation for the 1992-1993 cohorts is given in Fig. 5. Seven of ten dispersal cohorts in 1992 showed maximum rooting activity in the third quarter, before the first dry season; in 1993 four of ten cohorts had maximum rooting activity in the third quarter, and the remaining six in the fourth quarter. Synchronisation of rooting is suggested by a negative correlation between the median duration of the seed stage and average seed fall date: late cohorts root more rapidly than early cohorts. This

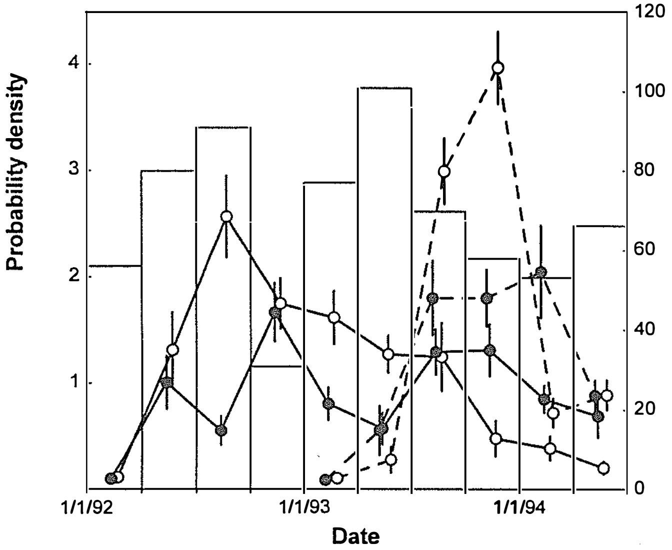

**Figure 5**
Mortality, rooting and rainfall in the 1992 (drawn lines) and 1993 (broken lines) cohorts in *Chlorocardium*. Mortality (closed symbols) and rooting (open symbols) are average (± 1SE) probability densities of n=10 dispersal cohorts per three month period (see methods for explanation). Rainfall (bars) is the average 10-day sum of daily rainfall per three month period.

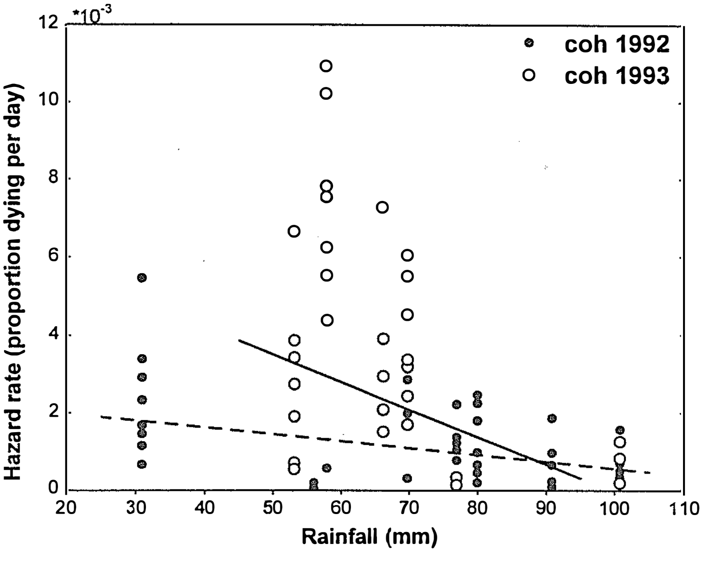

**Figure 6**
The relation between rainfall and the hazard rate (of death) as a seed in *Chlorocardium* in 1992 and 1993. See methods for explanation of hazard rate. Points represent hazard rates of death per dispersal cohort per three month period. Only periods with more than 10 remaining seeds were included. The regression lines give the relation between rainfall and hazard rate, uncorrected for dispersal period and time.

**Table 4**

**The rooting success per two-week dispersal cohort in 1992 and 1993. N is the number of seeds dispersed per dispersal cohort.**

| Average seed fall date | Rooting percentage | | | |
|---|---|---|---|---|
| | 1992 | n | 1993 | n |
| Jan 30 | 54 | 59 | 38 | 34 |
| Feb 13 | 87 | 30 | 39 | 51 |
| Feb 27 | 64 | 132 | 57 | 44 |
| Mar 12 | 65 | 104 | 57 | 76 |
| Mar 26 | 68 | 97 | 61 | 109 |
| Apr 9 | 71 | 88 | 78 | 91 |
| Apr 23 | 74 | 77 | 72 | 121 |
| May 7 | 82 | 33 | 74 | 105 |
| May 21 | 81 | 16 | 80 | 84 |
| >May 28 | 100 | 5 | 81 | 98 |

correlation is just a tendency for cohort 1992 (Spearman r=-0.56, p=0.09), but clear for cohort 1993 and 1994 (r=-0.95, p<0.001; resp. r=-0.87, p<0.01; Fig. 7). There was no correlation between average seed fall date and median rooting date (Spearman r - 0.26-0.41, p=0.24-0.99), and the median date of rooting was reached at about the same day for all dispersal cohorts in each year.

The relation of rooting 'hazard' with rainfall is not clear cut. For the 1992 cohort, rooting of seeds from different dispersal cohorts was not correlated to rainfall (partial correlation coefficient after controlling for time and dispersal period =0.15, p=0.27, n=55). In 1993 rainfall was negatively correlated with rooting 'hazard' (partial correlation coefficient = -0.44; p<0.01, n=53).

These differences between dispersal cohorts in the phenology of rooting led to differences in survival between dispersal cohorts during the seed stage (Table 4). The success of rooting was highest in late dispersal cohorts. This was mainly due to rapid rooting, and much less to a lower death risk. The survival functions of seeds were even indistinguishable between dispersal cohorts in 1992 ($\chi^2$=12.1, p=0.147), although they were different in 1993 ($\chi^2$=22.7, p<0.01). The transition function from seed to root however was different between dispersal cohorts in each year (1992: $\chi^2$=31.2, p<0.001; $\chi^2$=73.6, p<0.001), in such a way that survival was negatively correlated with median time till rooting (Spearman r=-0.71, p<0.05 (1992) and r=-0.94, p<0.001 (1993); in 1994 rooting was not completed by the end of the study: r=-0.65, p<0.05) (Table 4).

### The fate of rooted individuals

Based on above, rooted individuals of the 1992-1993 cohorts of *Chlorocardium* could be classified in three categories: an early group, rooting during the rainy season in the third quarter of the year; a middle group, rooting during the long dry season in

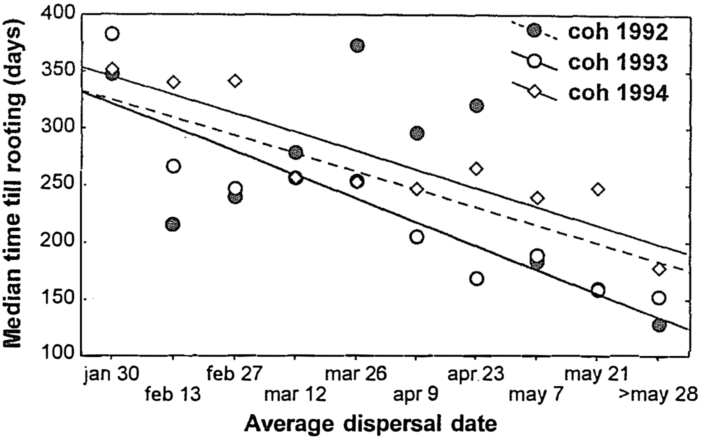

**Figure 7**

**Median duration of the seed stage per dispersal period for *Chlorocardium* seeds of the 1992-1994 cohorts. There was a significant negative correlation between average dispersal date and median time till root formation in 1993 and 1994, but not in 1992.**

the fourth quarter, and a late group, rooting after that (Table 5). Differences in the timing of rooting did not lead to differences in germination behaviour in 1992 or 1993 (Fig. 8). However, the survival functions were different between these groups. Survival was significantly longer in the early group than in the middle and late groups in both years.

It is unresolved whether survival of rooted individuals depended on the climatic conditions in the period 1992-1993. The hazard rate (of death) peaks in the long dry season of 1993 for all three rooting groups of cohort 1992. If survival is really due to climatic conditions, then it would be expected that individuals belonging to different annual cohorts that rooted in the same period would have similar survival functions. A comparison between the survival functions of individuals from cohorts 1992 and 1993 which rooted in the period May-September 1993, was not conclusive, possibly due to a lack of individuals in the 1992 group ($|Z|=1.61$, $p=0.053$, $n=38$ (1992) and 221 (1993). However, mortality in the early group of cohort 1992 during the more pronounced dry season in 1992 is not high. Comparisons between the early, middle and late groups of cohorts 1992 and 1993, that is, individuals of equal age, show that these have a very similar survival functions (*cf.* Fig. 8, Logrank tests $|Z|=0.06-1.43$, $p=0.08-0.48$). These results suggest that mortality at this stage is not or only to a limited extent affected by climatic conditions, but more by the age of the individuals at the moment of rooting. This effect is not caused by slow rooters having a slow germination and hence a high risk of mortality: the length of the seed and the root stages are weakly negatively correlated (Spearman $r=-0.25$ (1992) and $-0.23$ (1993), $p<0.001$). Therefore, the longer the rooting process takes, the lower the probability of survival during the root stage.

**Table 5**

**Survival and germination of rooted *Chlorocardium* individuals which rooted in different periods. In total 386 (513) individuals of the 1992 (1993) cohort were observed rooting; 19 (11) of them rooted later than Sep 30, 1993 (1994) and are not considered in this table. The number of successful germinations was different between rooting groups ($\chi^2_{11}=22.7$; $p<0.05$); for cohort 1992 separately this was not the case ($\chi^2_5=6.8$; $p=0.23$); but for cohort 1993 it was ($\chi^2_5=15.7$; $p<0.01$). Groups that share the same letter in the last column had no significant difference in germination in 2 × 2 contingency tables at $p<0.05$. The mean age of the individuals at rooting was different in either cohort (Kruskal-Wallis anova $H_{2,363}=282.6$, $p<0.001$ (1992); $H_{2,478}=278.5$, $p<0.001$ (1993)).**

| Group (cohort) | Rooted before | Mean age at rooting (days) | n | Dying as a root (%) | Germinating (%) |
|---|---|---|---|---|---|
| Early (1992) | Sep 30, 1992 | 140 | 205 | 22 | $78^{ac}$ |
| Middle (1992) | Dec 31, 1992 | 238 | 70 | 33 | $67^{abd}$ |
| Late (1992) | Sep 30, 1993 | 412 | 92 | 35 | $64^{d}$ |
| Early (1993) | Sep 30, 1993 | 121 | 221 | 25 | $79^{c}$ |
| Middle (1993) | Dec 31, 1993 | 190 | 230 | 32 | $68^{b}$ |
| Late (1993) | Sep 30, 1994 | 383 | 51 | 41 | $53^{d}$ |

## Discussion

### Delayed germination in primary rain forest species

This study showed that, among seeds of tropical primary species, *Chlorocardium* has a relatively prolonged germination. In comparative studies of germination behaviour in Neotropical and Malayan tropical forest ecosystems, Garwood (1983) and Ng (1978) reported maximum delays of germination of >370 and 1106 days (158 weeks), respectively. Seeds of *Bertholletia excelsa* are reported to take 12 to 18 months to germinate (Mori & Prance 1990). The large-seeded climax species *Ormosia coutinhoi* in Guyana has a hard seed-coat which, if it is not damaged, may delay germination up to 2 years (*personal observation* R.J. Zagt). *Aleurites* spp. are large-seeded, but are taken up in the soil seed bank and may remain there for > 2 year (Grubb 1996). Other studies, such as Raich & Gong (1990) for Malaya, Hopkins & Graham (1987) for Queensland, Australia, and Thompson *et al.* (1995) for Ghana report much shorter maximum seed longevities for primary species. Foster (1986) listed delayed germination as one of the possible correlates of large seededness. Not all large seeds show delayed germination though: *e.g.*, *Mora* species in Guyana (seed fresh weight >100 g) germinate within two weeks after dehiscence (ter Steege 1994a).

*Chlorocardium* differs in two important aspects from many other species with delayed germination: the high variability in time to germination and the long duration of the germination process itself, from emergence of the radicle to expansion of the first leaves. Garwood (1983) gives standard deviations of rooting which are generally below 40 days, even in species with very much delayed germination, whereas rooting and germination in *Chlorocardium* have standard deviations of 133-148 days. The longest ger-

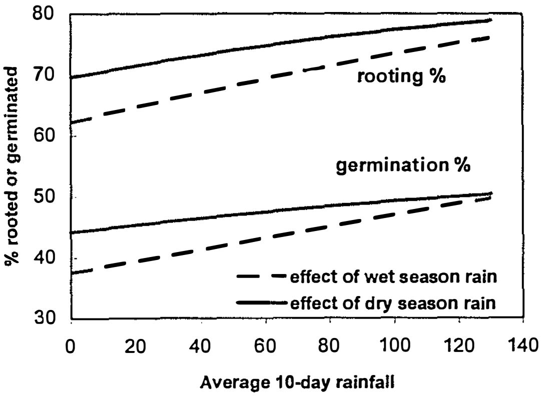

**Figure 9**
Results of simulations of the effect of variation in rainfall in quarters 3 (wet season, broken line) or 4 (dry season, drawn line) on rooting and germination of *Chlorocardium* seeds. Rainfall in all remaining quarters followed the observed pattern of 1992-1994. See text for further details.

about the development of the embryo at the moment of dispersal, and whether further development occurs after that. The large variation in seed size (ter Steege 1990), and, hence, volume-to-surface area ratio, and differences in breakdown rate of the woody exocarp both potentially contribute to differences in the rate at which imbibition of the seed takes place.

No data exist that show to what extent the woody exocarp acts as a barrier to imbibition in *Chlorocardium.* If physical dormancy is imposed by an impenetrable seed coat which is gradually breaking down (Baskin & Baskin 1989), then the 'hazard' of rooting should be increasing with time. This was the case. Increasing permeability of the exocarp might be caused by decay or by an increasing number of exit-holes of Scolytid beetles. However, in this study, seeds that burst open during the fall from the tree, and hence had no barrier to imbibition, did not show accelerated rooting in comparison to undamaged individuals (logrank $|Z|=1.42$, $p>0.05$). The same result was obtained in an experiment involving controlled cotyledon excision (D.S. Hammond, *unpublished results*).

### The effect of rain on survival and rooting

Germination and survival of tropical tree seeds are often affected by rainfall. Many species on Barro Colorado Island (BCI, Panama) lay dormant until the arrival of the rainy season (Garwood 1983). Irregular rains in the dry season resulted in untimely germination of *Hybanthus prunifolius* on BCI (Augspurger 1979). Schupp (1990) reported early germination and subsequent mortality to drought of *Faramea occidentalis* due to dry-season rains. The climate at Mabura Hill has a less pronounced seasonal character, but although variability was the general trend, patterns in germination and survival of *Chlorocardium* were present as a result of exogenous factors. Periods with little rainfall caused increased mortality for ungerminated seeds. This was especially clear in 1992, when the long dry season was more pronounced than in 1993. This result is in agreement with the finding of ter Steege *et al.* (1994) that large gap environments were detrimental for *Chlorocardium* seeds. Mortality in gaps was presumably due to low humidity and high insolation, as the effect disappeared when the seeds were

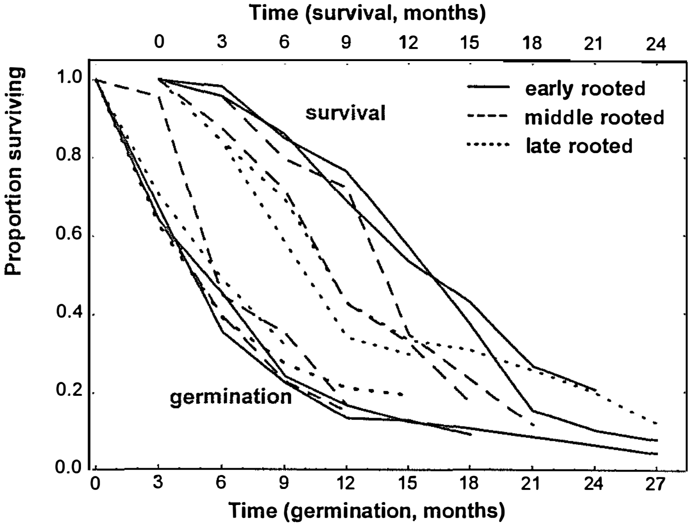

**Figure 8**

Transition and survival functions for individuals rooted in different periods. Early rooting groups rooted in the third quarter of the year of dispersal, middle groups during the fourth quarter and late groups in the next year. No distinction is made between cohorts 1992 and 1993, as there were no significant differences between any of the transition functions, nor between survival functions within a rooting group. The lower X-axis is for the germination functions, the upper X-axis for the survival functions. The timing of germination was not different between rooting groups: $\chi^2$=3.3, df=2, p=0.19 (1992); $\chi^2$=3.7, df=2, p=0.16 (1993). None of two-by-two comparisons between groups was different by logrank test: |Z| =0.1-1.6; p=0.06-0.47. The survival functions were different between rooting groups: $\chi^2$=19.4, df=2, p<0.001 (1992), $\chi^2$=15.7, df=2, p<0.001 (1993). Logrank tests for two-by-two comparisons |Z| > 2.1, p<0.02 for early group with either later group, in both years; |Z| <1.0, p>0.17 for comparison of middle and late groups in both years.

mination period as reported by Ng (1978) is 833 days (119 weeks) for *Anisophyllea griffithii*, which is still shorter than that of *Chlorocardium* (Table 2). No reference was found in the literature about slow germination once it has started, probably because it is a rare occurrence.

## Causes for variability in the timing of germination

Considering its ability to start germination after one month, a real dormancy period seems to be absent in *Chlorocardium*. Variability in the timing of seed germination has been ascribed to a continuous variability in seed morphological and physiological traits (intraspecific cryptic heteromorphism, Vázquez-Yanes & Orozco-Segovia 1984), leading to different degrees of dormancy between individual seeds (Ng 1978). Such variability may be due to a long dispersal period, variation in seed size, variable permeability of the fruit-wall for water, or differences in the maturity of the embryo at the moment of dispersal (Vázquez-Yanes & Orozco-Segovia 1984; P.-M. Forget, *pers. comm.*). Variation in dispersal period is large in *Chlorocardium* (Fig. 2), and this correlates with differences in the timing of root formation (Table 4). Nothing is known buried, or in understorey conditions. Similar responses were reported for the large-seeded *Gustavia superba* (Sork 1985). In the primary forest where the present study was conducted, such large gaps were not present, but dry seasons provided low humidity conditions. However, the unfavourable conditions of the dry season did not stop germination activity completely.

The impact of rainfall on rooting (none in 1992, negative in 1993) was not clear. Because of the imbibition requirement of the seed, a positive correlation with rainfall was expected (Augspurger 1979, Mayer & Poljakoff-Mayber 1982, Garwood 1983). Three factors may have contributed to the absence of a clear response to rainfall. Rainfall expressed on a three-month basis may not be suitable to describe the phenology of rooting. In addition, differential breakdown of the physical barrier to imbibition, and variation in moisture patterns at microsite level jointly blur a direct relation with rainfall (Blain & Kellman 1991). Lastly, the 1993 dry season may not have been severe enough to affect rooting. This is possible if negative effects of drought only occur below a certain threshold. This pattern agrees with the maternal investment germination syndrome, described by Angevine & Chabot (1979). This term applies to species with large seed reserves that supply the seedling with sufficient reserves to overtide periods of low resource availability. Dormancy in these species would be sufficient only to pass through an immediate climatic stress, *i.e.*, the negative effects of drought would only become apparent below a certain threshold.

In the period November 1994-May 1995 the rainfall was far below normal in the study area. No rainfall data are available to test this, but it could have contributed to the lower success of 1994 cohort (Table 3, Fig. 4b), and to the tendency ($p<0.10$) for the median time till rooting to be higher than for the other two cohorts (Fig. 7).

Seed-cohorts that were dispersed late in the season rooted on average more rapidly (Fig. 7), and had, at least partly for this reason, a higher rooting success (Table 4). The difference in rooting speed may be explained by assuming that suitable rooting conditions only occurred after the last seeds were dispersed, in the rainy season, and early cohorts had to wait for these conditions to occur. In absence of a clear response to rainfall other factors may explain the suitability of this period for rooting (such as low vapour pressure deficits during the rainy season, Foster 1986; Jetten 1994). An alternative explanation could be that early seeds were dispersed with an underdeveloped embryo (*cf.* Vázquez-Yanes & Orozco-Segovia 1984, Baskin & Baskin 1989) and required more time to mature after dispersal than late cohorts.

### Production of a leafy seedling

Germination speed was not affected by the timing of rooting (before, during or after the dry season), but survival was (Fig. 8). This suggests that germination proceeds independently of external factors and of the history of the seed. Survival was more related to the age of a rooting individual than to the climatic conditions during the root stage (Table 5). This may be due to a longer exposure time of seeds of late rooting individuals to insect predators and diseases (*cf.* Hammond *et al., unpublished manuscript.*).

### Risk spreading or not?

Selection will favour environmental cueing mechanisms that tend to decrease the probability of encountering unsuitable conditions after germination (Angevine & Chabot 1979). Alternatively, variation in the timing of germination could operate as a risk-spreading mechanism (Harper 1977), if the following conditions apply: (1) survival is strongly dependent on external conditions, such as climate or predation; (2) unacceptable conditions for growth and survival occur frequently; (3) environmental cues for these conditions are unreliable; and (4) there is a stage in the germination process which is less vulnerable than other stages. The result of the risk-spreading mechanism should be that variation in germination success is small and little dependent of external conditions.

Three conditions for risk-spreading applied, the other one hardly. Condition 1 is partly met. Survival of *Chlorocardium* seeds was dependent on rainfall, but although the dry season represents a period of high mortality, many seeds do survive this season. Predation does occur, but most of it is sublethal (Hammond *et al., unpublished manuscript.*).

Condition 2 and 3 apply for rainfall. There is considerable variation in the timing and extent of the 'normal' rainfall cycle in Guyana. In a 115-year record of monthly rainfall from Georgetown (*c.* 200 km to the north of the study site), inferred 10-day rainfall averages over quarters 3 and 4 were less than 35 mm in 19.1% and 8.7% of all years. Correlations between rainfall in March (month with maximum seed fall) and total rain in quarter 3 or 4 (when most rooting occurs), or rainfall in these months with rainfall 6 months later (when median germination is occurs, Table 2) all explain less than 7% of total variation. Long dry spells occur occasionally and unpredictably (Richards 1934, ter Steege 1994a). Periods with 3 or more consecutive months of less than 50 mm rain occurred in 12.2% of all years.

The fourth condition also applies, as seeds were shown to have lower hazard rates than seedlings and roots (Fig. 4a). However, in contrast to roots, rainfall was negatively correlated with seed survival, so seeds are not immune to unpredictable mortality. It is possible that there are other risks, which did not occur during the study period.

To test the effects of possible risk-spreading, a simple numerical model was constructed. The multiple regression equations relating time, dispersal period and rainfall to the 'hazards' of death and rooting in 1992 (see results, *cf.* fig 7) were used to estimate rooting success. On the basis of seed rain distribution over different dispersal cohorts and rainfall per quarter, survival and distribution of rooted individuals over the three root groups after 10 quarters could be calculated. With Table 5 the germination success was then determined.

Scenarios based on the rainfall data for 1992-1994, but with all seed dispersal concentrated in one single two-week period revealed hardly any effect of the timing of seed rain on germination percentages (44.5-46.7%; simulation with real seed rain data of 1992-1994 gave 46.0, 46.2 and 45.8%, compare with Table 3). The effect of varying rainfall in quarters 3 (wet season) or 4 (dry season) on cohorts with a rectangular seed rain distribution (100 seeds per dispersal cohort) is given in Fig. 9. An increase in rain from 30 to 100 mm (close to the 10 and 90% percentiles of rainfall in these quarters in 115 years) in these seasons is projected to cause a moderate increase in germination percentage of 7-16%.

In conclusion, some of the conditions for risk spreading apply, but not very strongly. The effect of variability found in the germination process of *Chlorocardium* does certainly contribute to a seedling production which is little dependent on large variations in the timing of seed rain, and in the amount of rainfall during the rooting process.

## Acknowledgements

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## chapter 6

# Distribution and demography in relation to light and size for seedlings of three Guyanese tropical rain forest species

*Roderick J. Zagt, José-Luis Machado & Peter B. Reich*

## Abstract

Seedling growth and survival are critical determinants of the composition of tropical rain forests. Although a large number of experimental studies have been carried out, large scale field studies remain remarkably scarce. In this paper, we study the distribution, growth and survival of the canopy species *Dicymbe altsonii*, *Chlorocardium rodiei* and the understorey species *Duguetia neglecta* under field conditions in the rain forest in Guyana. We asked whether these species differed in shade tolerance, and whether they responded predictably in terms of distribution, growth and survival to the variation in light in the forest. We monitored growth and survival of 3699 seedlings (<1.6 m) over a period of three years in 38 plots of 25 $m^2$ within a 2 ha forest area where naturally established, multi-aged cohorts of these species occurred. *Chlorocardium* (≥0.65 m) was monitored over the full 2 ha area. The plots were heterogeneous in light environment, seedling density and other factors that may affect growth and survival. We used plant canopy analysers to compare the distribution of light environments in the crown of a subsample of seedlings with the distribution of light environments in the plot. We hypothesised that seedlings of these species occupied different parts of the light gradient in the plot, and that there was a negative relation between the ability to survive in low light and growth rate in high light. Further, we hypothesised that realised growth depended on seedling size.

The results show that 75% of 882 sampling stations had a canopy openness below 1%, and that seedlings of all three species were generally growing in the same or slightly lower light environments than an unbiased reference sample. The species were not differently distributed over the light gradient in the plot. The height growth rates of all species were low, but responded significantly though weakly (all $R^2<0.12$) to variation in light availability. We did not find a trade-off between high light growth and low light survival. *Dicymbe* grew fastest over the entire light gradient, but had also a very high low light survivorship. *Chlorocardium*, which was expected to be more shade tolerant, had a high seedling mortality in the shade and a low growth rate. Seedling size explained as much variation in height and leaf growth as light availability. We distinguished between the effects of seedling height, leaf density (leaf number per unit stem length) and rank (relative height compared to neighbours). Leaf density and rank generally had a strong positive effect on growth, while the effect of absolute height was limited. A high leaf density depressed leaf growth. Few factors were related to survival: a modest increase in light and a large size were positively related to survival. Fast growing seedlings had a higher probability of survival than slow growing seedlings. The long-lived cotyledons of *Chlorocardium* appeared to enable this species to maintain low or even negative height and leaf growth rates for a long time, but this was not correlated with increased survivorship.

We conclude that in field conditions, seedling growth is related to species identity, light and seedling size, but that these factors explain a limited proportion of the variation. Differences in size, caused by differences in species characteristics, growth history and chance may be an important mechanism by which slowly growing species maintain themselves in the community.

## Introduction

The notion that tree seedling demography is crucial for the development of pattern and diversity of forests is an old idea which has produced attractive concepts such as cyclic regeneration (Aubréville 1938), distance dependent survival (Janzen 1970, Connell 1971) and gap partitioning theory (Hartshorn 1978, Denslow 1980, Orians 1982). It also has left field workers with the discouraging task to measure and interpret the roller coaster dynamics of seedling communities. Tropical tree seedlings defy many a sampling scheme with their enormous density (Liew & Wong 1973), high diversity (Li 1991), astronomic mortality rates (Howe *et al.* 1985), irregular production (Chan & Appanah 1980) and vanishing dispersal habits (Forget 1990). Progress has been made, but it is not strange that many studies of tree demography in the tropics all but ignore the seedling stage.

Recently, the importance of seedling demography for determining forest composition was explicitly demonstrated in temperate forest communities in North America. A simulation model of forest dynamics successfully predicted differences in forest composition based on empirical field data of inter and intraspecific differences in seedling growth and survival (Pacala *et al.* 1993, 1994, Kobe *et al.* 1995, Kobe 1996). Even though tropical forest communities may be far more diverse and complex than temperate communities, and successful simulation of canopy composition in the tropics is a distant goal, this is an encouraging result that underscores the significance of seedling demography. At the same time it reaffirms that the proper management of the tropical rain forest for the production of forest commodities or for conservation purposes requires knowledge about the factors governing seedling and sapling demography.

Experimental work has emphasised the response of tropical seedlings to variation in availability of light (*e.g.*, Popma & Bongers 1988, Osunkoya *et al.* 1993, Chazdon *et al.* 1996), water (*e.g.*, Burslem 1996) and nutrients (Huante *et al.* 1995, Burslem 1996, Gunatilleke *et al.* 1996, Veenendaal *et al.* 1996), and interspecific differences in these responses (*e.g.*, Raaimakers 1994, Ter Steege 1994a, Ashton 1995, Boot 1996). Another parameter that has attracted much attention is the distance between seedlings and conspecific adults (Augspurger 1983a, Connell *et al.* 1984, Hammond & Brown (*in press*). These experiments have provided a clear insight in the relation between the biotic and abiotic environment and plant responses for different (functional groups of) species (Whitmore 1996).

Together with the hands-on experience gathered by foresters (Whitmore 1996), the experimental approach has fostered a view that tree species segregate over a gradient of shade tolerance. The contrast pioneer-climax species is nearly proverbial (*cf.* Swaine & Whitmore 1988), but also within the group of climax species a trade-off is postulated between survival in the understorey versus growth in gaps. Shade tolerant species survive well and grow slowly in the shaded understorey, but show a low response to conditions of improved illumination. Shade intolerant species tend to have a lower survival in the understorey, but respond strongly to increased light (Hartshorn 1980, Hubbell 1992, Kitajima 1994, Kobe *et al.* 1995). According to this view, the competitive hierarchy between species depends on the prevalent light climate, and may, in principle, show reversals in species ranking (Latham 1992, Grubb 1996, Whitmore 1996).

The great value of this view is that it offers a general framework for understanding gap succession at a community level over a long time period, and indeed the earlier mentioned model that predicted canopy composition in North American forests was based on this trade-off. However, this trade-off, although at the basis of plant strategy, may not always lead to a clear ranking of relative seedling performance in the field, leading to a predictable succession of species in gaps.

Success in the field depends on the performance of individuals rather than species, in the context of determined (fixed) foci of regeneration (gaps). Apart from the well known effects of internal gap heterogeneity (Brandani *et al.* 1988, Nuñez-Farfan & Dirzo 1988), this paves the way for extra sources of variation in seedling performance due to differences in their size and ontogenetic stage at the moment of gap formation, and in the identity of the competitive neighbourhood between seedlings. In most experimental studies, the response of isolated, even-aged and even-sized seedlings has been studied. In the field however, seedlings rarely grow in an environment where neighbours are even-sized, even-aged and not interfering. Several authors have pointed out that a large size and a high rank in the local size hierarchy may be of advantage in determining the relative performance of seedlings in the understorey and in gaps (Brown & Whitmore 1992, Boot 1996, see also Chapter 2; *cf.* Gerry & Wilson 1995). A similar conclusion is reached if one-sided competition for light that characterises competition in crowded, mono-specific and single-aged stands is applicable to natural multi-aged, multi-species communities (Weiner 1990, *cf.* Kohyama 1992a). This suggests that local size hierarchies potentially override the effect of species-specific plant characteristics on growth and survival in seedling communities, although there are other studies that indicate that eventually differences in growth rate overwhelm differences in initial size (Weiner & Thomas 1986). Grubb (1996) pointed out that the ontogenetic phase of individuals is an important determinant of shade tolerance, and that species may change rank order of shade tolerance during their ontogenetic development.

Hence, the question arises: is there a negative relation between low light survival and high light growth in seedlings in tropical communities, and does this lead to variation in the success of species in terms of growth and survival between microsites? Does differential performance of species in low *vs.* high light environments show up in the spatial distribution of seedlings over the light gradient in the forest, with shade-tolerant species over-represented at low light sites and fast growing species at better illuminated sites? Which is the effect of seedling size, its position in the local size hierarchy of seedlings and (small) differences in resource availability within a patch on its growth and survival? Do these factors disrupt this expected distribution pattern? It may be that the ecological consequence of the trade-off between low light survival and high light growth (*i.e.* a clear and predictable succession pattern) is considerably affected by the effects of size and small-scale environmental heterogeneity. In that case this trade-off may still explain long-term and wide-range community patterns, but that there may be a large variation at the level of single gaps. This would allow more species to coexist at the same time, and succession would proceed more slowly to 'climax' stages. Small differences in size may already be established by differences in growth and survival in the understorey (Boot 1994, Osunkoya 1994).

The issue of predictability of seedling growth and competition at patch level is relevant for silvicultural aspects of forest management and for the understanding of species coexistence in the rain forest. Silvicultural management aims at the manipulation of the forest in pursuit of an economically or ecologically favourable species composition (Lamprecht 1989). The main management tool is manipulation of the forest canopy, which allows control over the gap size frequency and the light environment of the forest or of specific desired trees, and thus species composition (Denslow 1980, Brown & Whitmore 1992, ter Steege *et al.* 1996). All silvicultural manipulations require that the response of the community is predictable to a certain extent. Furthermore, the mechanisms that are responsible for maintenance of species richness are still unresolved. An important issue of controversy is whether species are different (niche-differentiated) or not (Hubbell & Foster 1986b, Chapter 2). The implication of species being niche-differentiated is that the development of the species composition in a given small area of forest is predictable, given the conditions at that site. The importance of niche-differentiation is often emphasised in relation to species-specific responses to gap light environments (Hartshorn 1978, Denslow 1980).

Unfortunately, many years of tropical seedling research have produced a disappointingly small number of studies in which these issues are examined in the natural, unmanipulated seedling populations which are needed to provide a field test of the experimentally obtained results, at least where it concerns the group of late-successional species. Long-term (max. 17 y) growth and/or survival of tree seedlings were studied in Queensland (Connell *et al.* 17 y), Panama (Brokaw 1985, 6 y; Welden *et al.* 1991, 4 y), De Steven (1994, 5 y), Costa Rica (Clark & Clark 1992, 6 y; Li 1991, 1996, 7 y), French Guyana (Puig & Fabre, 1997, 8 y) and Sabah (Whitmore & Brown 1996, 6 y), a list that could be extended with shorter studies.

In this paper, we address the general question whether seedling distribution and performance (growth and mortality) of three late successional species: *Dicymbe altsonii*, *Chlorocardium rodiei* (two small gap specialists) and *Duguetia neglecta* (a true understorey species) relate predictably to light availability, seedling size and species-specific light requirements in understorey and small gap environments in the tropical rain forest in Guyana, South America. Large areas in central Guyana are co-dominated by *Chlorocardium* and *Dicymbe*. *Dicymbe* appears to be the superior competitor in this area, given its abundance and growth performance in large (logging) gaps and adult growth rates. *Chlorocardium* seedlings grow very slowly (ter Steege *et al.* 1994) and its seedlings are reputed to survive a long time in the understorey (Clarke 1956, Boot 1994), possibly supported by the large cotyledons which are retained for more than a year. *Duguetia* is able to complete its life cycle in the understorey and performs poorly in logging gaps (ter Steege *et al.* 1996). *Chlorocardium* is a sought after hardwood, and there is considerable economic interest in the ecological characteristics that permit the species to successfully regenerate in undisturbed and logged-over forest.

We monitored multi-aged seedling populations of these species over a range of light climates during a four year demographic study. We proposed to address the following objectives and test the associated hypotheses:

1 Seedling distribution and light environments.
a The distribution of species is not random with regard to the distribution of light, rather it will be skewed towards higher light micro-environments where survival is expected to be higher.
b Different species will have different distributions based on differential mortality in low light environments in accordance with their hypothesised shade tolerance (in order of increasing shade tolerance: *Dicymbe*, *Chlorocardium*, *Duguetia*.
2 Seedling growth and survival in relation to light.
a The response to variation in light availability in terms of growth will vary between species, with the 'most shade-tolerant' species showing the least response.
b The response to variation in light availability in terms of survival will be inversely related to the species' growth response to light.
3 Seedling growth and survival will be related to absolute and relative (compared to neighbours) plant size.
4 Large cotyledons will reduce the effect of low light and small size on *Chlorocardium*.
5 Within species, fast growing seedlings will have a higher survival probability than slow growing seedlings. (Kobe *et al.* 1995, Walters & Reich 1996).

At the same time, the study provided information about a number of other factors that potentially affect seedling growth and survival in the field: local seedling density and distance to the nearest conspecific adult (*cf.* Janzen 1970, Connell 1971), herbivory and fungal attack.

This study describes distribution and demography of a large population of seedlings in a large area with robust light measurements. By not choosing an experimental approach but taking these questions into the field and study naturally occurring seedling populations, we probably lost some sensitivity that is required to find differences between species or responses to specific factors. However, thanks to this approach we were able to determine whether processes and factors that were previously shown to be 'significant' were also 'meaningful' in a field situation where many factors simultaneously act upon the seedlings.

## Methods

### Study site and species description

The study was conducted between 1991 and 1995 in the 1200 ha Ecological Reserve of the Tropenbos-Guyana Programme, *c.* 20 km south of Mabura Hill, central Guyana (5°13' N, 58°48' W). Average rainfall and temperature in the area are 2700 mm and 27°C, respectively (Jetten 1994). Rainfall follows a bimodal pattern with maxima in May-July and in December (Jetten 1994). The study area is located in a logging concession, in which large undisturbed tracts of forest lie alternated with patches of logged-over though recovering forest. The soil types in the area belong to one of two major groups: a group of clayey Plinthosols and a group of sandy and loamy soils of various types (Jetten 1994, van Kekem *et al.* 1997). The vegetation of the area is classified as Evergreen Rain Forest (Mixed Forest) and Dry Evergreen Forest (ter Steege *et al.* 1993, 1996). The distribution of species and forest types is strongly determined by soil type (Davis & Richards 1934, Fanshawe 1952, ter Steege *et al.* 1993, Jetten 1994). The resultant communities are frequently dominated by one or a few species.

Three species were selected for this study, which were common in the study plots and represented a range of non-pioneer regeneration strategies (Table 1).

*Dicymbe altsonii* Sandw. (Caesalpiniaceae, Clump Wallaba) is a large canopy tree that can be classified as a gap dependent species. It is a relatively fast growing species during all phases of its life-cycle. The seedlings are produced in large biennial crops (Chapter 3) that persist in the understorey. The species is distributed in a small area in central Guyana and north-western Brazil (Cowan & Lindeman 1989). In the study area, *Dicymbe* occurs exclusively on sandy and loamy soils, over a broad hydrological gradient (ter Steege *et al.* 1993). It is dominant or co-dominant in a number of forest types (Fanshawe 1952, ter Steege *et al.* 1993, Jetten 1994).

*Chlorocardium rodiei* (Schomb.) Rohwer, Richter & v.d. Werff. (Lauraceae, Greenheart) is also a large canopy tree of outstanding commercial significance. It is classified as a gap-dependent species (ter Steege *et al.* 1994). The growth of seedlings and adults is very slow. Large individuals are often dispersed in clumps, locally called 'reefs'. The species is nearly endemic to Guyana (ter Steege 1990), and occurs on brown loamy sands and laterite, usually on gentle hill slopes. It is considered a dominant in *Eschweilera-Licania* forest (Fanshawe 1952, ter Steege *et al.* 1993).

*Duguetia neglecta* Sandw. (Annonaceae, Yarri yarri) is a very abundant understorey tree that rarely exceeds 10 cm in diameter (at breast height, dbh). It can be classified as a shade tolerant species. Little ecological information is available about this species. Usually only a small percentage of all individuals is reproducing. It is most likely bird dispersed, and although its seedlings are not rare, they are much less common than the two previous species. The species occurs in the same forest types as *Chlorocardium*, and is distributed in Guyana and Surinam.

### Plot outline

The study was conducted in a 2 ha plot, which was located in a large tract of undisturbed Evergreen Rain Forest on Haplic Ferralsol (brown loamy sand). The plot consisted of two adjacent 1 ha plots and was considered representative for this forest type in the Reserve area in terms of soil, structure and density of the trees. The forest was relatively open (tree density for both plots 359 and 453 trees ≥10 cm diameter at breast height (dbh) per ha; basal area 36.0 and 41.3 $m^2$) with a canopy at 30-40 m height. The most abundant tree species were *Dicymbe altsonii* (69.0 trees/ha; 44.0% BA), *Chlorocardium rodiei* (38.0; 20.9%) and *Eschweilera sagotiana* (including a few *E. decolorans*, 44.0; 9.3%) in the canopy layer, *Oxandra asbecki* (62.5; 2.5%) and

**Table 1**

**Comparison of plant and life history characters of the three study species. Based on Chapters 3 and 5, Hammond & Brown (1995), H. ter Steege, *personal communication*, and R.J. Zagt *unpublished data*, which refer to the situation in the study plot.**

| | *Dicymbe altsonii* | *Chlorocardium rodiei* | *Duguetia neglecta* |
|---|---|---|---|
| Distribution | central Guyana | central Guyana | Guyana, Surinam |
| Regeneration strategy | gap dependent | gap dependent | shade tolerant |
| Seed dry weight (mean, g) | 5.7 - 8.5 | 38.9 - 41.6 | 0.3 |
| Fruiting | biannual | annual | annual? |
| Seed crop in plot ($ha^{-1}$) | 40 000[1] | 5 000 | ? |
| Dispersal mechanism | dehiscion | gravity/ (mammals) | birds? |
| Germination | direct | delayed | direct? |
| Seedling height [2] (m) | 0.35 | 0.40 | 0.05 |
| Branching type | orthotropic | plagiotropic | plagiotropic |
| Leaf form | compound, alternate[3] | simple, opposite | simple, alternate |
| DBH at maturity (m) | 0.25 | 0.21 | 0.02? |
| Maximum height (m) | 35 - 40 | 35 - 40 | 20 |
| Maximum DBH (m) | 1.50 | 1.20 | 0.15 |
| Adult density ($ha^{-1}$) [4] | 58.0 (48.4) | 31.5 (16.6) | 67.5 (68.6) [5] |
| Adult dbh growth rate (mean, cm $y^{-1}$) | 0.43 | 0.14 | 0.05 |

[1] **in a fruiting year.**
[2] **with fully expanded first leaves.**
[3] **except first pair, which is opposite.**
[4] **in the 2 ha study plot; between brackets average density in *c.* 10 ha including and surrounding the study plot.**
[5] ***Duguetia* ≥4 cm.**

*Maburea trinervis* (32.0; 1.8%) in the subcanopy layer and *Duguetia neglecta* (1.0; <0.1%) in the understorey layer. The composition of the study plots resembles the 'well-drained mixed forest' (ter Steege *et al.* 1993) and the *Eschweilera-Licania* and *Eschweilera-Dicymbe* associations (Fanshawe 1952).

The plots were subdivided by a 5 m by 5 m grid. Each 5 m by 5 m cell was classified as recent gap (apparent age less than 1 years), gap in advanced stage of regrowth (canopy height less than 15 m) or mature forest (canopy height more than 15 m) in July 1991. A predetermined number of seedling sample plots (grid cells) were randomly selected from each of these classes. Eight were positioned in gaps (that represented 7% of all classified cells in 1991), 10 in regrowth (15%) and 20 in mature forest (78%), equally distributed over both 1 ha plots. The total number of seedling sample plots was 38 (4.75% of the plot area). The stratification reflected the situation at the time of the start of the study in 1991, but was soon disturbed by the formation of a gap.

## Seedling demography

### *Sampling scheme and measurements*

All individuals less than 1.60 m height from the base of the plant (called 'seedling' throughout this paper) of the three study species in the seedling sample plots were labelled between October-December 1991. For *Chlorocardium* in a height range of 0.65-1.60 m the study area was extended to the entire study area (*i.e.* 2 ha). Subsequent enumerations started in October 1992, 1993 and 1994 and extended over the next four months. New *Chlorocardium* cohorts (sample plots), new *Chlorocardium* recruits in the ≥0.65 m height class (remaining area), and new *Duguetia* cohorts were added yearly to the study population. *Dicymbe* produced seedling cohorts in 1991 and 1993; however, only the 1991 cohort was included in the study, beginning with the enumeration of 1992, when they were about 1.5 year old.

### *Measurements of the seedlings*

At each enumeration, the following data were obtained for all seedlings:

1. Stem length, measured from base till the highest top meristem;
2. Leaf density, obtained as the quotient of leaf number and stem length (in N of leaves per decimetre; *cf.* Ashton 1990). We used leaf density as a rapidly determined approximation of 'leafiness' of a plant, and considered it more indicative of the morphological component of growth (usually represented by leaf area ratio (LAR) or leaf weight ratio) than leaf number. LAR has frequently been shown to be a close correlate of RGR under low light conditions (*e.g.*, Popma & Bongers 1988, Cornelissen *et al.* 1996, Kitajima 1996). However, leaf area per leaf varies within and between seedlings of the same species, and between species, and the same leaf density may actually have a different meaning for plants of different heights due to differences in, *e.g.*, respiratory costs and light harvesting capacity. Therefore, the meaning of leaf density should be interpreted with care and is not suitable for between-species comparisons. For *Dicymbe* compound leaves were counted as one leaf.
3. Individual Dawkins crown illumination index (Dawkins & Field 1978, Clark & Clark 1992; Table 2) was determined as a visual measure of light availability. Although the index provides only a very crude approximation of the light climate of a seedling (Chapter 2), it was demonstrated to correlate well with light measures derived from hemispherical photography (Clark *et al.* 1996). Moreover, it is a method that is rapid, easy to employ and feasible to use on individual seedlings. We used only the last recorded Dawkins crown illumination index for analysis.
4. Presence of cotyledons in *Chlorocardium*, which retains its cotyledons for a period of up to 4 years; recorded as present during at least one measurement or absent;
5. Presence of fungi or herbivory on stem, cotyledons or leaves; recorded present if more than 10% of the total leaf area was damaged;
6. Evidence of traumatic reduction in height, caused by *e.g.* breakage through branch fall, and
7. Age class; germinated during the study period ('1') or germinated before ('0').

**Table 2**
**Dawkins' crown illumination index (adapted from Dawkins and Field 1978).**

| Dawkins score | Meaning |
|---|---|
| 1 | no direct lateral or overhead light; |
| 2l (low) | some direct lateral light, no overhead light |
| 2m (middle) | between 2l and 2h |
| 2h (high) | much direct lateral light, no overhead light, *e.g.*, in the area bordering a gap |
| 3,4,5 | various amounts of direct overhead light (distinction not relevant for seedlings) |

8 Death was supposed to have occurred at the enumeration that it was recorded. If a seedling was scored 'not found' for two or more consecutive enumerations, it was supposed to have died at the first enumeration that it was not found.

In each seedling sampling plot the seedlings were ordered from the tallest to the smallest, based on seedling heights at the first measurement. Thus a rank number was assigned from 1 to N (the number of seedlings in the plot). The rank number is independent of individuals larger than 1.60 m height, and individuals belonging to other species. Nevertheless, because *Dicymbe* and *Chlorocardium* seedlings were taller than most recently germinated seedlings of other species, and they were by far the most common species, their assigned rank number was hardly affected by the presence of other species. *Duguetia* seedlings were much smaller, and therefore their position in the size hierarchy was probably overestimated. Ranks were expressed as a percentage of the highest rank number present per subplot, which was angular transformed before analysis. This procedure was followed to obtain a normally distributed variable for rank that did not depend on seedling density. A rank number was not determined in the extended sample for *Chlorocardium* outside the seedling sample plots. The variables rank, stem length and leaf density are together called size parameters or 'plant size' throughout this paper.

### *Measurement of the plot environment*

Each 5 m × 5 m subplot in the study area (n=800) was described by the following variables:

1 Forest structure, whereby a distinction was made between gap (canopy opening created during the study period or just before, *i.e.* less than 4 years old at the end of the study period); building phase (canopy opening in various stages of regrowth; canopy less than 15 m high); mature forest (canopy height more than 15 m) and a category of border situations between the previous categories. This was done twice, in 1991 and in 1994.

2 Dawkins crown index in the middle of the subplot at 1.8 m, in 1992 and 1994 (Table 2). This is a plot level score, as opposed to Dawkins scores determined for each seedling.

3 Canopy openness determined with a plant canopy analyser in April 1995, after the last enumeration (see below: *Index of light availability*). The canopy openness was determined at the corners of each subplot. The openness value for a plot was obtained by simple averaging of the values for the four corners.
4 Local basal area, the total tree basal area in a neighbourhood of nine 5 × 5 m subplots centred around the subplot, in two size classes: for trees between 10 and 20 cm dbh (sub-canopy trees) and for trees over 20 cm dbh (trees in the canopy). Most canopy trees have a crown radius between 5 and 10 m, so this parameter gives a measure of the amount of biomass above a subplot.
5 Distance to the nearest adult (for definition of adult see Table 1) of the three study species.
6 Elevation relative to the lowest point in the 2 ha plot.
7 Total seedling density per subplot in 1994, when the number of seedlings not belonging to the study species was counted. This parameter was determined in the seedling sample plots only.

The seedlings in the two 1 ha plots that together constituted the study plot were enumerated separately as a part of a larger measuring scheme. The associated time lapse between the seedling measurements may have affected the way in which subjective measures (such as the Dawkins crown index) were assigned to the plants. For this reason, and in order to accommodate possible differences between the plots in characteristics that were not captured by the parameters that are described above (*e.g.*, soil characteristics), we included a (dummy) variable for site and its interactions with the size and light parameters in the analyses that follow.

We expected parameters that described the light environment directly (Dawkins crown illumination scores, canopy openness) or indirectly (local basal area; forest structure) at the level of the subplot, to show a high degree of multicolinearity. Therefore, principal components analysis (PCA) was performed to extract one single variable that described the gap-understorey gradient (*cf.* Philippi 1993). For each categorical variable we created a set of dummy variables, and all 800 subplots were assigned a score for all variables. Orthogonal principal components were extracted that maximised the variances of the normalised variable scores (varimax rotation). The scores of each subplot on the axis describing the first principal factor (called PCA1 in the analysis) was used for further analysis.

### *Index of light availability*

Canopy openness, an index of diffuse radiation availability (Hanan & Begue 1995, J.L. Machado & P.B. Reich *in prep.*), was estimated at the growth point of individual seedlings (*Duguetia*: 122, *Dicymbe*: 229 and *Chlorocardium*: 321), at two heights from the ground (0.65 and 1.3 m) for every 5 × 5 m grid point in the 2 ha plot (total of 882 grid points), and in the centre of each seedling sample plot (total of 38 midpoints) with paired LAI-2000 plant canopy analysers (LiCor Inc., Lincoln, NB, USA) in April of 1995. All canopy openness measurements (top of seedlings, grid points and above canopy) were taken during one hour after pre-dawn and one hour before dusk during days when the sky was uniformly overcast, with one LAI-2000 unit while the paired unit was placed at the top of the roof (7 m high) of the field station (< 2 km away) in a clearing of approximately 2500 $m^2$ in size to record above canopy readings. The hemispherical sensor measuring canopy openness of seedlings and grid points was provided with a 360 degrees field of view by asking the operator to position below the hemispherical sensor before every measurement.

## Analysis

### *Seedling distribution over a light gradient*

The frequency distribution of canopy openness above the seedlings where this was individually measured was compared with the unbiased frequency distribution of canopy openness at the 5 m × 5 m grid points (for *Chlorocardium* ≥0.65 m tall) or at the centre and corners of the seedling sample plots. The distribution of canopy openness of the reference samples at the 5 m × 5 m grid points and in the seedling sample plots were not different each other (see: *Results. Comparison of canopy openness between seedlings and an unbiased sample*). The canopy openness of the reference sample was determined at 0.65 cm height, as this was closest to the average height of the seedlings. The canopy openness of the seedlings and the unbiased sample were compared with Mann-Whitney unpaired rank tests. The seedlings were divided in young seedlings and old seedlings, in order to test whether a change in distribution occurred. Old seedlings germinated before the beginning of the study (1991), and young seedlings during the study period. The *Duguetia* sample only contained old seedlings.

### *Differences in growth and survival between species*

We tested whether species responded differently to variation in light availability with linear regression. The sample consisted of growth rates of the seedlings with individually measured canopy openness, and the independent variables were canopy openness, two dummy variables representing the three species, site, and the two-way interactions. The samples were too small to include the other measured variables in this regression model. Differences in survivorship between species were assessed by determining survivorship at the last measurement (after 3 years) for those seedlings that had germinated before the study period, did not suffer traumatic damage, grew under low light conditions (Dawkins index 1), and were suppressed (defined as having a growth rate between -2 and 2 cm $y^{-1}$, see below for calculation of growth rates). For these seedlings the probability was highest that survival was determined by resource limitation rather than damage and age dependent mortality factors (such as herbivory and fungi). We tested the difference in survival between the species with a $\chi^2$ test.

### *Regression analysis of growth and survival per species*

The effects of plant- and environmental parameters on seedling growth and survival are presented by several regression equations. For each species multiple linear regression models relating height and leaf growth to all measured seedling and environmental variables were set up for the entire seedling population. The effect of seedling and environmental characteristics on two and three-year seedling survival was studied with backwards stepwise logistic regression.

Seedlings that were present in at least two enumerations were used to calculate height and leaf growth rates. Excluded were therefore: seedlings that died after one enumeration, and seedlings that germinated after the third enumeration. Furthermore, seedlings that suffered reductions in height of more than 10 cm without a record of trauma were excluded, as well as seedlings with very inconsistent growth pattern, *e.g.,* a large increase followed by a large decrease, and seedlings evidently growing as a result of retranslocation of resources from cotyledons to stem (often with *Chlorocardium* under low-light conditions). These were recently germinated seedlings with not fully expanded leaves and not lignified stem that were growing at a high rate.

As the vast majority of seedlings were found under very low light conditions, height and leaf growth rates were low. The influence of measuring errors was therefore large, resulting in large year-to-year fluctuations in measured growth. There was no correlation in measured growth rates between subsequent years, although such correlation might be expected if growth depends on the availability of resources. The lack of correlation is further caused by discontinuous growth, with a large height increase and many new leaves in one year and no growth in the next year. Because of this and the fact that most environmental variables were measured only once during the study period, we obtained linear growth rates (in cm or number of leaves per year) as the regression coefficient of the linear regression of height or leaf number against time, rather than calculating yearly growth rates. These regression coefficients were used as the dependent variables in the multiple regressions described below. Exponential growth rates were also calculated from regression on natural log-transformed heights and leaf numbers, but they are not reported. The results in the analyses were similar, but the distribution of residual errors in the regressions was not often not normal.

All parameters that were described above, as well as first measured height and first measured leaf density were used as independent factors for regression analysis. Species, age class, presence of cotyledons, the last recorded Dawkins crown index (Table 2), site, presence of herbivory and presence of fungi were entered in the regressions as dummy variables. Because some seedlings died after growing 2 or 3 years, death was entered as an additional dummy variable. Some second order interactions were studied, mainly between the dummies for age, cotyledons, death and the main continuous variables. Seedling height and leaf growth rates were added as extra independent variables in logistic regression of survival.

The regressions were performed for each species separately, because the species differed in a number of ways, and some variables (such as leaf density) can not be compared between species.

For the multiple linear regressions on height and leaf growth, stepwise backwards procedures were used to eliminate variables that did not significantly (F-test; criterion: $p \leq 0.05$) decrease the residual variation. The fit of the resulting models is given by $R^2$, the proportion of explained variance. The importance of each independent factor is indicated by the partial correlation coefficient (P*r*), which gives the correlation with the response variable after correcting for the effect of the remaining variables in the regression. If a second order interaction proved significant, then the two main effects were both retained in the model, irrespective of their significance. For groups of variables (such as the dummy variables for Dawkins index), we calculated *Pr* as the square root of the ratio of the increase in $R^2$ caused by the variables and the residual variance of the model that excludes the parameters under consideration.

We studied the relation between plant and environmental variables and survival with logistic regression, *i.e.*, the dependent variable was the logit of the probability of survival. Logistic regression was performed on the same set of seedlings as multiple regression, implying that all seedlings included in the analysis survived at least one year. The regressions were done twice: for seedlings that were present at the first enumeration, 3 year survivorship was determined, whereas for these and for seedlings first measured at the second enumeration a separate analysis was performed over 2 year survivorship. The results for 2 year survivorship should be interpreted with caution, because this includes seedling survival over enumeration 1-3 as well as enumeration 2-4, so that differing weather conditions over these periods may have formed an additional source of variation. Moreover, for *Dicymbe* all seedlings that germinated in 1991 could only be present in the sample for 2 year survivorship. The parameter coefficients were estimated by a quasi-newton procedure that minimised the negative log likelihood function of the model. The fit of the model to the data was evaluated by comparing the log likelihood of the model including the variables with the model containing only the intercept. The difference in log likelihood was tested as $-0.5 \times \chi^2$, with df. equal to the number of estimated parameters. Variables were eliminated with a backwards stepwise procedure. The importance of each variable was evaluated by testing the difference in likelihood between models with and without the variable as $\chi^2$, as described above. The effect of each factor is reported as its fitted coefficient.

For *Chlorocardium* two sets of regression were done each time: one with all seedlings ≥0.65 m in the entire plot, and one for seedling sample plots. A regression was first performed on all seedlings (excluding rank and seedling density, which were only determined in the seedling sample plots). Then, for the much fewer *Chlorocardium* seedlings in the sample plots a new stepwise backward procedure was followed, beginning with the earlier obtained model to which rank, density and their interactions were added, as well as age, which was not relevant in the larger sample. Other factors and interactions than these were not considered. Variables that were not normally distributed were transformed before regression. Linear height growth rates were natural (log x + 1) transformed and signed. The effect of size on growth was always explicitly modelled in the regressions. Variables that were redundant (*i.e.* the value of which could be explained by the other independent variables in the regression) were omitted. The number of leaves and leaf density were strongly correlated and had similar effects; for clarity only leaf density was used in the regressions. Rank and initial seedling height were virtually identical within sample plots; over the entire dataset they were correlated but not identical (r=-0.84). All regression analysis was done with the Statistica package (Statsoft Inc. 1993).

We addressed hypothesis 3 (importance of light availability *vs.* plant size) by testing whether plant size (height, leaf density and/or rank) significantly improved the fit of the above models. We then nominally compared the importance of size *vs.* light by comparing their joint partial correlation coefficients with the joint *Pr* of the light variables. We repeated this analysis for seedlings growing in deep shade (canopy openness <0.8%) in order to see whether the relative importance of size and light was different under these conditions. All other potential correlates of seedling growth and survival: the distance to the nearest adult, seedling density, presence of cotyledons and the relation between growth on survival were tested directly in the regression analysis.

## Results

### The study populations

The number of seedlings per sample plot varied between species (Table 3). *Dicymbe* dominated the sample plots in abundance (present in all sample plots with a high density) and size (Fig. 1). *Duguetia* was not abundant, but evenly distributed over all sample plots, but one. Most individuals were very small. *Chlorocardium* was abundant, but had a limited distribution within the plot. The number of seedlings varied widely between plots. The total number of seedlings that was recorded in the sample plots was high (1125), but at most 625 were simultaneously present. *Chlorocardium* is unique among the study species in possessing a seed bank (Chapter 5), and if seeds would be added, the maximum number per sampling plot was over 300. In the extended sample (seedlings ≥0.65 m height), *Chlorocardium* was present in nearly 50% of all subplots, usually with only a few individuals. High mortality rates limited the sample of seedlings for which height and leaf growth rates could be determined, especially in *Chlorocardium.* Small seedlings were under-represented in this sample.

The number of seedlings (0-1.3 m) belonging to other species was measured in the 38 seedling sample plots in 1994. The relation between the fraction of these other species per sample plot (y) and the total seedling density (x) was $y=0.84-0.002 \times x$ ($F_{35,1}=19.1$; $p<0.001$, $R^2=0.35$). The study species were a minority in 60% of the sample plots, but never represented less than 15% of the total number of individuals per plot.

On average the seedlings grew slowly, with *Dicymbe* recording the highest growth rate (Table 4). Of a total of 3699 seedlings with measured growth, 56% had an average yearly height growth rate between 0 and 5 cm, and just 9% grew more than 10 cm per year (Fig. 2). Another 19% showed reduction in height as a result of damage, die-back or measuring error (defined as height reduction without recorded damage; 13%). A total of 488 (13%) seedlings had recorded stem breakage, and although a minority recovered, some of them showed a severe negative growth rate. These seedlings with recorded damage were excluded from the regression analysis for growth and survival. The yearly increase in leaf number was well below one, and for *Chlorocardium* there was, on average, even a net leaf loss. The correlation between height growth and leaf growth was positive, significant but weak for all three species (Table 4).

**Table 3**

**The number of seedlings in the 38 5 m × 5 m seedling sampling plots and in the 2 ha study plot (*Chlorocardium* ≥0.65 m high) near Mabura Hill, Guyana. The total is the total number of individuals labelled in the entire study period. Presence is the fraction (%) of plots where the species was found. The median and range give the situation for 1993. The actual number of seedlings used for analysis is less, including only seedlings for which growth rates could be calculated (present during at least two enumerations).**

| | | N of seedlings | | | |
|---|---|---|---|---|---|
| Species | Area ($m^2$) | Total | Median (range) per plot | | Presence (%) |
| *Dicymbe* | 950 | 2 808 | 49.5 | (9-147) | 100 |
| *Duguetia* | 950 | 193 | 4.0 | (0-16) | 97 |
| *Chlorocardium*: | | | | | |
| sample plots | 950 | 1 125 | 3.0 | (0-158) | 79 |
| height ≥0.65 m | 20 000 | 1 295 | 1.0 | (0-17) | 43 |

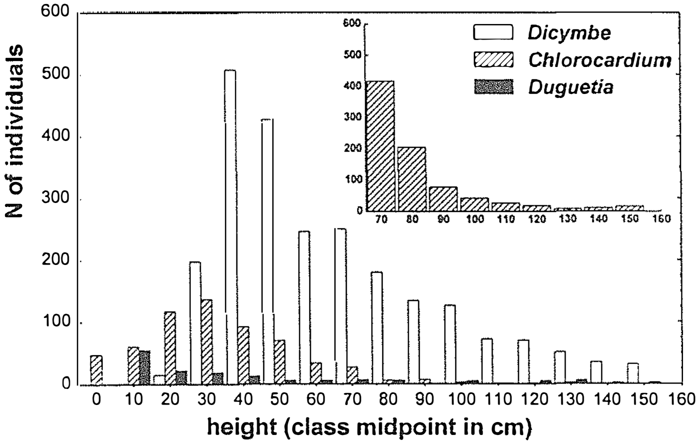

**Figure 1**

**Height distribution in 1993 of the seedlings belonging to the study species in 38 5 m × 5 m seedling sample plots in the 2 ha study plot near Mabura Hill, Guyana. Inset: height distribution of *Chlorocardium* seedlings ≥0.65 m height in the 2 ha plot, on the same scale.**

Yearly survival rates were very high in *Dicymbe* and *Duguetia* that established before the beginning of the study, whereas survival for seedling cohorts that established during the study period was lower (Table 5). *Chlorocardium* had a low survival, and after 3 years less than half of the original populations remained. The percentage survivorship of the sub-sample of suppressed seedlings seems to be high in comparison with 'real' 3 year survival because these seedlings survived at least one year in which growth rate was determined (see below).

**Table 4**

Average annual growth rates for seedlings of three species in the demographic plots in tropical rain forest near Mabura Hill, Guyana. Growth rates are regression coefficients of seedling height or leaf number against time, with 2-4 observations per seedling. Seedlings with recorded stem breakage were excluded. Letters indicate significantly different means ($p \leq 0.05$) as determined by non-parametric one-way anova. Correlation is Pearson correlation coefficient between height and leaf growth (performed on log-transformed data). Significant correlation coefficients are indicated with asterisks: **$p \leq 0.01$; ***$p \leq 0.001$. In the last column is the percentage seedlings that had a positive height growth and a stable or increasing number of leaves.

| | height growth | | leaf growth | | | |
|---|---|---|---|---|---|---|
| Species | average ± SE (cm $yr^{-1}$) | N | average ± SE (N $yr^{-1}$) | N | correlation | % growing individuals |
| *Dicymbe* | 4.43 ± 0.12b | 2123 | 0.14 ± 0.02y | 2121 | 0.42*** | 58.4 |
| *Chlorocardium* | 2.41 ± 0.14a | 943 | -0.22 ± 0.10x | 941 | 0.16*** | 39.7 |
| *Duguetia* | 1.68 ± 0.26a | 132 | 0.88 ± 0.30z | 110 | 0.24** | 51.8 |

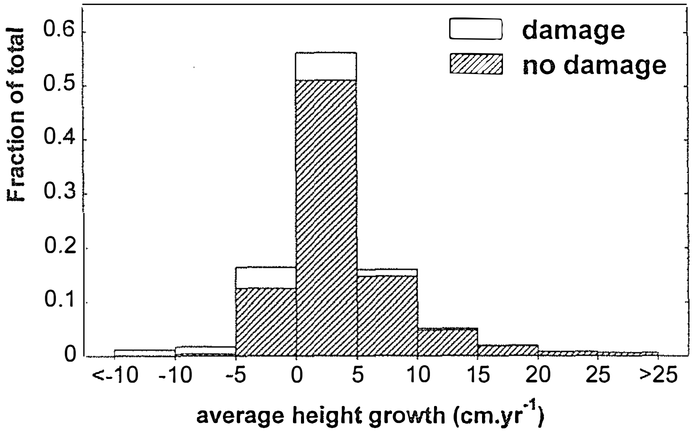

**Figure 2**

The distribution of mean annual growth rates for seedlings of three species in the demographic plots in tropical rain forest near Mabura Hill, Guyana. Growth rates are regression coefficients of seedling height against time, with 2-4 observations per seedling. Seedlings with recorded stem breakage are indicated separately. N=3699 seedlings.

## Seedling distribution and light environments

### *Stand structure and light environment*

About 6% of all subplots was classified as gap in 1994, 16% as building phase, 72% as mature forest, with an additional 6% of subplots being classified on the border between these types. Compared to 1991, 2.7% of mature forest sites changed into gap, corresponding with a forest turnover rate of *c.* 1% per year.

The distribution of canopy openness in the study plot was strongly skewed to the left (Fig. 3). About 70% of all 5 by 5 m grid points in both the 2 ha study plot and the

**Table 5**

**Yearly and three-yearly survivorship of seedlings in 38 5 m × 5 m seedling sample plots in the rain forest near Mabura Hill, Guyana. Average 1-yr survival (± SE) is the average of 3 one year intervals (2 for new cohorts of *Dicymbe* and *Duguetia*), based on seedlings present at the beginning of each interval (sample size >100 for all species except *Duguetia*, new cohorts: 20-34, and subsamples for *Chlorocardium* sample plots: 28 and *Duguetia*: 47). The 3-yr survival is the percentage of seedlings surviving since the beginning of the study. This is independent of the dynamics of new cohorts. New cohorts are seedlings germinated during the study period, old cohorts germinated before (before 1991).**

| | Average 1 year survivorship (%) | | 3 year survivorship (%) | |
|---|---|---|---|---|
| Species | New cohorts | Old cohorts | Old cohorts | Subsample[2] |
| *Dicymbe* | 85.8 ± 0.5 | 93.5 ± 2.0 | 81.7 | 84.6 |
| *Duguetia* | 68.9 ± 1.2 | 93.5 ± 2.6 | 81.6 | 95.7 |
| *Chlorocardium*: | | | | |
| sample plots | 52.6 ± 17.5 | 66.5 ± 5.1 | 24.8 | 57.1 |
| plot[1] | - | 78.6 ± 3.3 | 52.3 | 74.0 |

[1] **height ≥0.65 m, based on 2 ha.**

[2] **sub-sample consisting of suppressed individuals of old cohorts with Dawkins index 1 (see methods for further explanation).**

38 seedling sample plots had a canopy openness of less than 1%. There was a small but consistent difference of about 0.25% (confidence interval 0.20-0.30%) between the readings at 0.65 and 1.30 m height. Points with high canopy openness were very rare and only 1-1.5% of all grid points had greater than 10% canopy openness. The distribution of canopy openness in the seedling sample plots was not different from canopy openness above the grid points in the entire study plot (geometric means for sample plots and entire plot 0.62 and 0.67%, respectively; Mann-Whitney unpaired ranks test: Z=-1.30, p>0.05). The canopy openness above the grid-points was different between the two 1 ha plots (geometric means 0.53 and 0.87%, Z=-7.8, p<0.001)

There were clear differences in the light environment between subplots that were classified in 1994 as gap, building phase, mature forest and edge situation respectively (Fig. 4), although a large range of light environments was found in each of these types.

### *Comparison of canopy openness between seedlings and an unbiased sample*

We compared the frequency distribution of canopy openness above the seedlings with the unbiased sample of canopy openness at the 5 m x 5 m grid (*Chlorocardium* ≥0.65 m) or the sample plot corners and midpoints (remaining seedlings). Our hypothesis that the seedlings had a higher average canopy openness than the unbiased sample could not be demonstrated for any of the species, even when we considered only cohorts that established previous to our study (Table 6). The average crown light environment of *Chlorocardium* ≥0.65 m in the 2 ha plot was lower than expected from the unbiased sample. Similarly, all seedlings growing in the sample plots had a lower average canopy openness than expected from the unbiased sample, but these differenc-

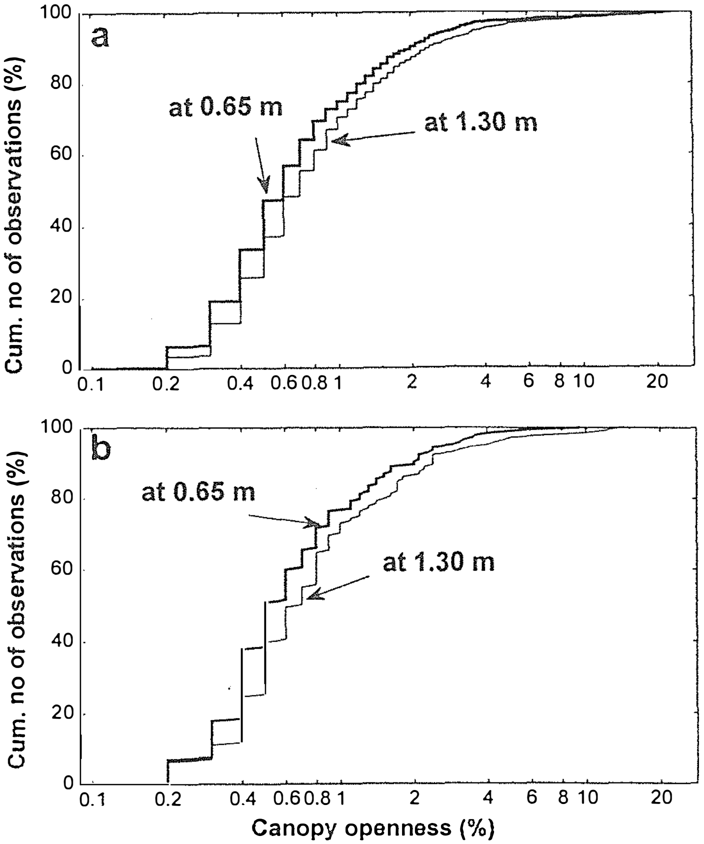

**Figure 3**
**Cumulative frequency distribution of measured canopy openness at two heights on (a) a 5 m × 5 m grid in the 2 ha study plot (N=882 sample stations) and (b) on the corner and midpoints of the seedling sample plots (N=190), in a rain forest near Mabura Hill, Guyana.**

es were not significant. There were also no difference in mean canopy openness among the species (Kruskal-Wallis anova $H_{2,672}$ =1.2, p=0.56).

### Seedling growth and survival in relation to light: inter-specific differences

Height growth rate of seedlings of all three species was significantly positively related to canopy openness (Table 7, Fig. 5). Not surprisingly, other sources of variation in growth rate were large, and canopy openness explained just 5-11% of the variation in growth (Table 7). The response to light was not significantly different between species, although *Dicymbe* had a higher base growth rate (intercept) than the other two species. The response to light was not dependent on site (effect of the interaction site × canopy openness on the full model: $F_{1,517}$=0.4, p=0.52).

Survival of suppressed seedlings in low light conditions (Dawkins index 1) was significantly different between species ($\chi^2_5$=21.1, p<0.001 for seedlings in sample plots; $\chi^2_5$=22.5, p<0.001 if *Duguetia* and *Dicymbe* are compared with *Chlorocardium* ≥0.65

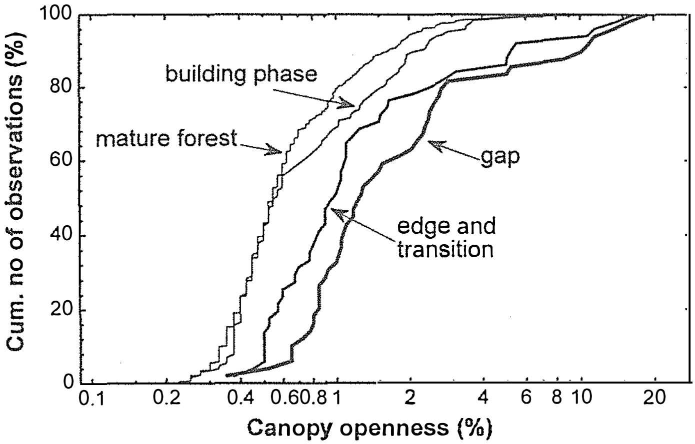

**Figure 4**
Cumulative frequency distribution of measured canopy openness at 0.65 m in 5 m × 5 m subplots grouped by forest stage determined in 1994. See text for definition of forest stages.

**Table 6**
Mean canopy openness measured with paired plant canopy analysers for the seedling sample and an unbiased sample at 0.65 m height. Age groups were tested separately to reveal possible age effects. Asterisks indicate a significant difference between seedlings and the reference tested with Mann Whitney U tests; ** $p \leq 0.01$; no asterisk, $p \geq 0.05$. Distribution sensitive Kolmogorov-Smirnov tests did not yield different results and are not reported. Geometric means of openness are reported because the data were approximately log-normal distributed. All seedling samples were from 38 5 m × 5 m sample plots, except *Chlorocardium* ≥0.65 m, which were sampled in the entire 2 ha study plot.

| Species | Germinated | Seedling sample | | Unbiased reference sample | |
|---|---|---|---|---|---|
| | | N | Openness (%) | N | Openness (%) |
| *Dicymbe* | before 1991 | 80 | 0.53 | 190 | 0.62 |
| *Dicymbe* | after 1991 | 149 | 0.58 | 190 | 0.62 |
| *Chlorocardium* ≥0.65 m | before 1991 | 243 | 0.55** | 882 | 0.68 |
| *Chlorocardium* | before 1991 | 37 | 0.58 | 190 | 0.62 |
| *Chlorocardium* | after 1991 | 42 | 0.58 | 190 | 0.62 |
| *Duguetia* | before 1991 | 64 | 0.50 | 190 | 0.62 |

m). Pairwise comparison indicated that each species differed from both other species ($\chi^2_1 > 4.1$, $p < 0.05$ in all cases). Survivorship increased in the order *Chlorocardium* < *Dicymbe* < *Duguetia*.

## Growth and survival in relation to seedling size, cotyledons and other factors

### *Regression analysis of growth and survival*

The relation between height and leaf growth and variables for plant and environmental characteristics was studied with backwards stepwise regression. For *Dicymbe*,

**Table 7**

**Fitted coefficients for the regression ln height growth = $c + b \cdot X$, where $c = c_1 + c_2 \cdot [D] + c_3 \cdot [C]$, and $b = b_1 \cdot X + b_2 \cdot [D] \cdot X + b_3 \cdot [C] \cdot X$. X= ln canopy openness, [D] is a dummy for *Dicymbe*, [C] is a dummy for *Chlorocardium*, $b_i$ and $c_i$ are fitted coefficients. [C] and [D] have the value 1 if an individual belongs to *Dicymbe* and *Chlorocardium*, respectively, and 0 if it does not. Different letters behind a coefficient refer to inter-specific comparisons. Stars denote the probability of the coefficients being zero: * $p \leq 0.05$; ***$p \leq 0.001$. The results show that *Dicymbe* has a significantly higher intercept than *Chlorocardium* and *Duguetia*, but that the slopes of the response to light are not statistically different between species.**

| | fitted coefficients | | | | N | $R^2$ |
|---|---|---|---|---|---|---|
| | c | | b | | | |
| *Dicymbe* | 1.76*** | a | 0.54*** | x | 210 | 0.11 |
| *Chlorocardium* | 0.98*** | b | 0.34*** | x | 255 | 0.05 |
| *Duguetia* | 1.06*** | b | 0.44* | x | 58 | 0.07 |

the number of variables that explained significant proportions of the observed variation in growth rate was large, and the coefficient of determination was relatively high (Table 8 and 9). For *Duguetia* and especially *Chlorocardium* the coefficient of determination was much lower and fewer factors were found to significantly contribute to variation in growth. Partial correlation coefficients were generally low.

### *Height growth*

Non-understorey light levels (Dawkins index >21, Table 2) stimulated growth in all species, although the relation between light and growth was not very strong (Table 8). Independent of the individual Dawkins scores, light at the scale of sample plots (PCA1) stimulated growth in *Dicymbe* and *Duguetia* (negative scores on PCA1 correlate with high light availability). PCA1 was not significant in *Chlorocardium*, which is surprising as the spatial scale of the *Chlorocardium* sample, and therefore the variation in PCA1, is larger than for the other species.

Height growth was related to plant size, expressed in one or more of the three variables initial stem length, initial leaf density and rank (Fig. 6a, 7a). Initial stem length was negatively related to growth in all three species, although not significantly in *Chlorocardium* in sample plots. A high initial leaf density correlated positively with growth in *Dicymbe* and *Duguetia*, but in *Chlorocardium* ≥0.65 m height this effect was only clear if leaf density was larger than 1 (Fig. 7a). In individuals from the sample plots leaf density did not correlate with height growth. Rank was the factor having the highest partial correlation coefficient with height growth in *Dicymbe* and *Chlorocardium*, but was uncorrelated to growth rate in *Duguetia*: independent of absolute plant size and absolute light availability, the relative vertical position of a seedling in the seedling bank was important, and the higher the position in the local size hierarchy, the higher seedling growth. In *Chlorocardium* the seedlings' rank was significantly less important in young seedlings.

The joint partial correlation between plant size and height growth was in most cases

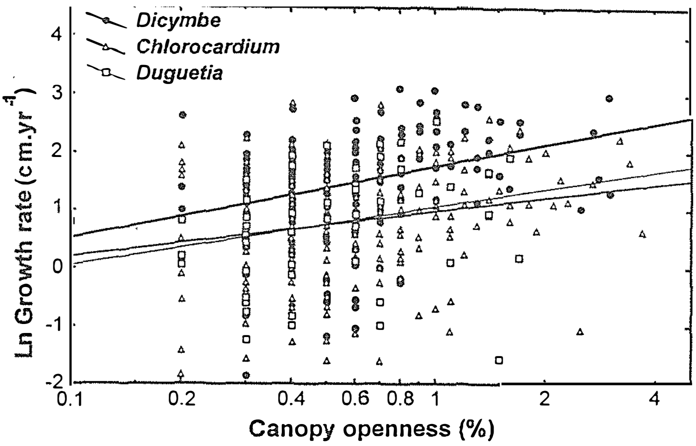

**Figure 5**
**The relation between growth and canopy openness for a sample of seedlings of three species of rain forest tree near Mabura Hill, Guyana. Absolute growth rates were (ln x +1) transformed. See table 7 for regression equations.**

as large as or larger than the joint partial correlation between light and height growth: in all three regressions where both were retained in the model, size had a larger *Pr* than light (Table 10). In *Dicymbe*, the effect of light was only marginally reduced by excluding high-light sample plots from this analysis (Table 10), although the relative importance of seedling size for height growth seemed to be increased compared to light in these deep understorey sites. Light lost its correlation with height growth for *Chlorocardium* in these sites.

Age correlated with growth in *Dicymbe* and *Chlorocardium* (sample plots). Young seedlings were hardly present in *Chlorocardium* ≥0.65 m and in *Duguetia*. For *Chlorocardium* the presence of cotyledons was correlated with a high growth rate.

Other environmental factors that explained growth in at least one species were seedling density in the sample plot, and distance to the nearest parent. Both were positively correlated with *Dicymbe* growth. Elevation significantly affected growth in *Chlorocardium*. The lower a subplot was situated on the height gradient in the plot, the higher the growth of *Chlorocardium*. The effect was weak. The effects of leaf density, rank and light (Dawkins index of PCA1) were different between the two sites for *Dicymbe* and *Duguetia* (only light), but not for *Chlorocardium*, even though there was no interaction site × canopy openness in the seedling sample (see above).

Seedlings that died during the study period grew more slowly than surviving seedlings, in *Dicymbe* and *Chlorocardium* (Table 8). Thus, death was preceded by a period of slow growth, or, death was more likely to occur in slowly growing individuals (see below). Two mortality factors, attack by fungi and herbivores, were not found to be affecting height growth rates in the seedlings, except for herbivory in *Dicymbe*. It is instructive to compare the regression results for *Chlorocardium* with and without knowl-

**Table 8**

Factors affecting height growth in seedlings of three species in the tropical rain forest near Mabura Hill, Guyana. The partial correlation coefficients are given of variables retained in the model by stepwise backwards multiple regression. The level of significance (by an F-test) of the variables is given by asterisks: *$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$; no asterisk: not significant. Fate known and unknown, respectively, indicate whether eventual death of the seedling was included in the regression or not (*Chlorocardium*). The effect of excluding death as an explanatory factor in the regression was very small for *Dicymbe* and *Duguetia*.

| Variable | *Dicymbe* | *Chlorocardium* (sample plots) | | *Chlorocardium* (height ≥0.65m) | | *Duguetia* |
|---|---|---|---|---|---|---|
| | | fate unknown | fate known | fate unknown | fate known | |
| N of observations | 2119 | 201 | | 732 | | 101 |
| Age | 0.19*** | 0.29*** | 0.32*** | | | |
| Initial height | -0.24*** | | | -0.07 | -0.08* | -0.30** |
| Initial leaf density | 0.09*** | | | -0.06 | -0.06 | 0.45*** |
| Leaf density square | -0.07*** | | | 0.12*** | 0.12*** | |
| Rank | -0.33*** | -0.19** | -0.19** | | | |
| Presence of cotyledons | | 0.09 | -0.06 | 0.19*** | 0.11** | |
| Death | -0.13*** | | -0.10 | | -0.10** | |
| Dawkins index | 0.12*** | | | 0.16*** | 0.17*** | 0.31* |
| PCA1 | -0.12*** | | | | | -0.28** |
| Site | 0.01 | | | -0.08* | -0.08* | -0.10 |
| Seedling density | 0.14*** | | | | | |
| Nearest adult | 0.12*** | | | | | |
| Herbivory | -0.06* | | | | | |
| Elevation | 0.07** | | | -0.08* | -0.07* | |
| Site * Leaf density | 0.08*** | | | | | |
| Site * Rank | -0.06** | | | | | |
| Site * Dawkins Index | 0.13*** | | | | | |
| Site * PCA1 | | | | | | 0.24* |
| Death * Cotyledons | | | 0.18* | | 0.13*** | |
| F | 71.5*** | 10.4*** | 7.7*** | 10.8*** | 10.0*** | 6.3*** |
| $R^2$ | 0.41 | 0.14 | 0.17 | 0.12 | 0.13 | 0.35 |

edge of eventual survival of the seedling. The positive effect of cotyledons on growth (in seedlings ≥0.65 m height) was large if the eventual fate of the seedling was omitted from the regression model. However, if fate is known, its partial correlation coefficient was lower, and instead the interaction between death and presence of cotyledons was positively correlated to growth. Thus, in *Chlorocardium*, imminent death was negatively correlated with growth rate, except in seedlings with cotyledons present, where this

**Table 9**

**Factors affecting leaf growth in seedlings of three species in the tropical rain forest near Mabura Hill, Guyana. The partial correlation coefficients of variables retained in the model by stepwise backwards multiple regression are given. The level of significance (by an F-test) of the variables is given by asterisks: *p≤0.05, **p≤0.01, ***p≤0.001; no asterisk: not significant. Fate known and unknown, respectively, indicate whether eventual death of the seedling was included in the regression or not (*Chlorocardium*). The effect of excluding death as an explanatory factor in the regression was very small for *Dicymbe* and *Duguetia*.**

| Variable | *Dicymbe* | *Chlorocardium* (sample plots) | | *Chlorocardium* (height ≥0.65m) | | *Duguetia* |
|---|---|---|---|---|---|---|
| | | fate unknown | fate known | fate unknown | fate known | |
| N of observations | 2119 | 201 | | 732 | | 101 |
| Initial height | -0.27*** | | | | | |
| Initial leaf density | -0.26*** | -0.08 | -0.02 | -0.09* | -0.02 | -0.07 |
| Leaf density square | | | | 0.09* | | |
| Rank | -0.25*** | | | | | |
| Presence of cotyledons | | 0.16* | 0.12 | 0.11** | 0.15*** | |
| Death | -0.11*** | | 0.14 | | 0.03 | |
| Dawkins index | 0.10*** | 0.25** | 0.20* | 0.25*** | 0.23*** | 0.33* |
| PCA1 | -0.12*** | | | | | |
| Site | -0.11*** | | | | | 0.16 |
| Seedling density | 0.13*** | | | | | |
| Nearest adult | 0.13*** | | | | | |
| Herbivory | -0.08*** | | | | | |
| Fungi | -0.06*** | | | | | |
| Elevation | -0.06** | -0.27*** | -0.24*** | -0.11** | -0.14*** | |
| Site * Dawkins index | 0.13*** | | | | | |
| Site * PCA1 | 0.06** | | | | | |
| Site * Leaf density | | | | | | -0.22* |
| Leaf density * Cotyledons | | -0.25*** | -0.15* | -0.16*** | -0.20*** | |
| Death * Leaf density | | | -0.28*** | | -0.16*** | |
| F | 39.8*** | 10.3*** | 12.1*** | 10.4*** | 17.3*** | 5.5*** |
| $R^2$ | 0.24 | 0.27 | 0.36 | 0.11 | 0.18 | 0.26 |

effect was compensated. In *Dicymbe* and *Duguetia* the difference between regression equations with and without inclusion of eventual fate was very small.

### *Leaf growth*

The growth of the number of leaves showed some very different patterns compared to height growth (Table 9, Figs 6b and 7b). The $R^2$ values were lower, except in

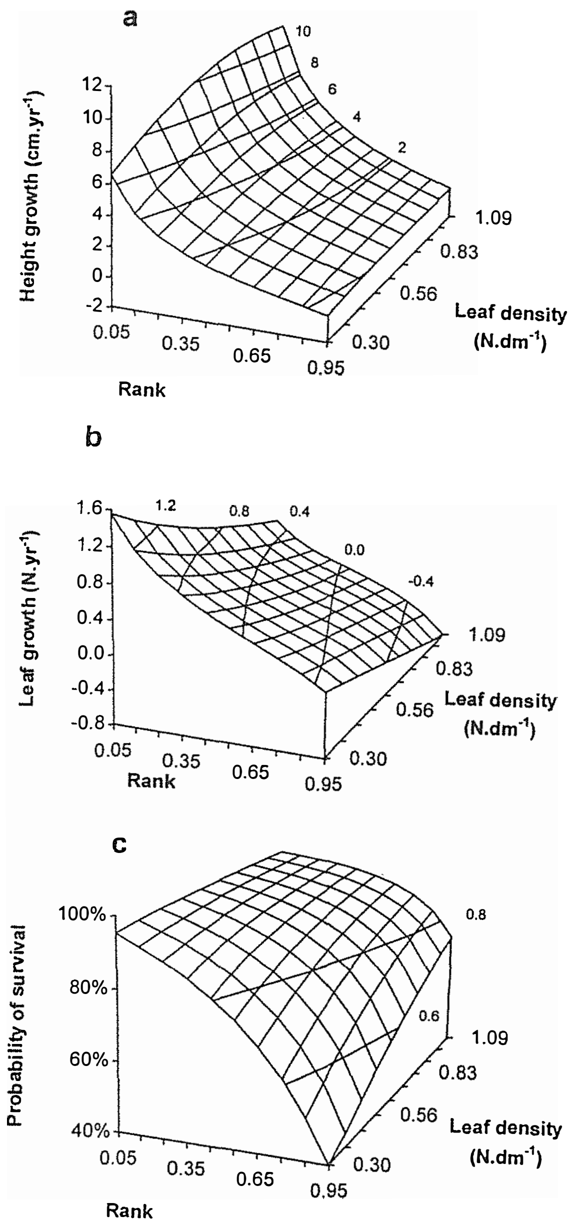

**Figure 6**
The independent effects of initial position in the size hierarchy (rank) and initial leaf density on the predicted height growth (a), leaf growth (b) and 3 y survival probability (c) of *Dicymbe* seedlings, as determined by the regressions from tables 8-10. Illustrated ranges of rank and leaf density represent the central 90% observed in the study populations. Rank is expressed relatively to the lowest observed rank per subplot, from highest (value 0.05) to lowest (0.95). The values are the predicted values from regression analysis, for hypothetical surviving (in a and b) seedlings that germinated before 1991, had Dawkins crown illumination score 2I, an initial height of 0.55 m, no herbivore or fungal damage, and average scores for all other variables. The axes give back-transformed values of the variables.

*Chlorocardium* (see below). Size had a higher P*r* than light only for *Chlorocardium*, whereas in both other species P*r* was similar. An important difference between height growth and leaf growth was the negative, not positive effect of leaf density on leaf growth. In *Chlorocardium* this effect was mainly present in presence of cotyledons, and only few combinations of variables resulted in positive leaf growth. Seedling age was not related to leaf growth in any of the species.

Other variables had comparable effects on leaf growth as on height growth. Height

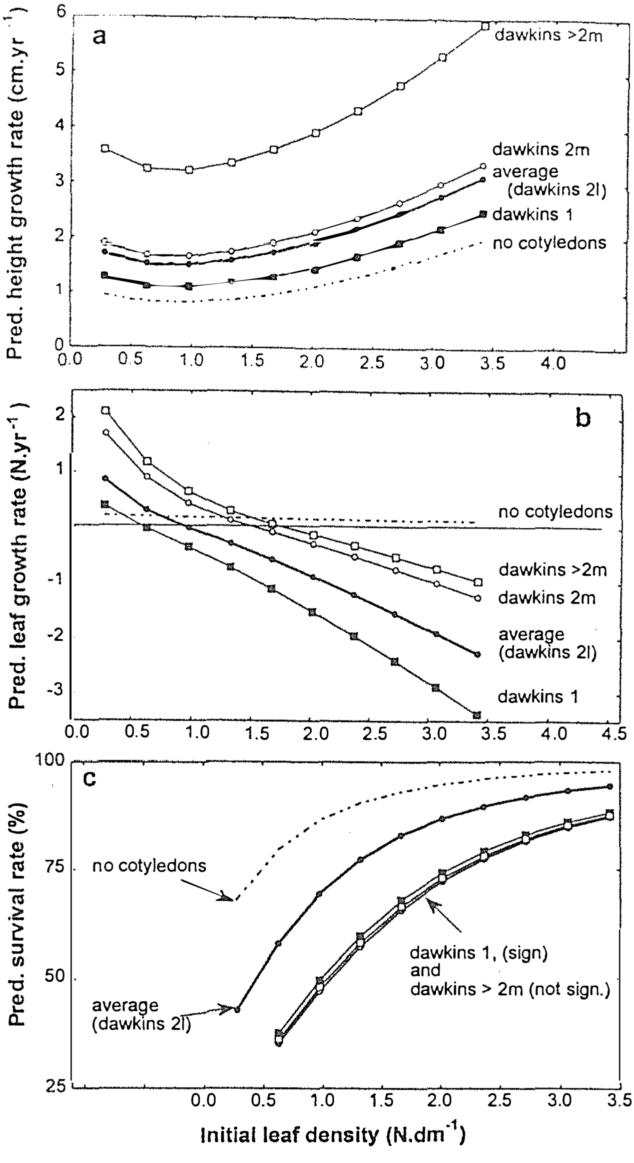

**Figure 7**
The independent effect of initial leaf density on the predicted height growth (a), leaf growth (b) and 3 year survival probability (c) of *Chlorocardium* seedlings (≥0.65 m height), as determined by the regressions from tables 8-10. Illustrated range of leaf density represents the central 90% observed in the study populations. The fat line marked 'average' describes the predicted response of hypothetical seedlings which are surviving (in a and b), germinated before 1991, had Dawkins crown index 2l, an initial height of 0.75 m, cotyledons present, no herbivore or fungal damage, and average scores for all other variables. The other lines represent responses of hypothetical seedlings differing from the former in a single character, which is indicated next to the line. In 7c, the effect of Dawkins classes 2m and >2m is not different from class 1. The axes give back-transformed values of the variables.

**Table 10**

**Comparison of the effects of light (Dawkins index, PCA1) and size (height, leaf density and rank), including all their interactions on height and leaf growth in seedlings of three species in tropical rain forest near Mabura Hill, Guyana. The effects are expressed as the proportional increase in explained variance between regressions with and without all light *cq.* size parameters (*cf.* partial regression coefficient, see Methods). The contribution of size and light could be positive or negative (see Tables 8 and 9). For the species with the largest sample sizes, a similar analysis was made for seedlings growing in very dark sample plots (canopy openness ≤0.8%). Regressions including the effect of imminent death (Tables 8 and 9) were taken as the basis for these comparisons. The level of significance (by an F-test) of the variables is given by asterisks: *p≤0.05, **p≤0.01, ***p≤0.001; no asterisk: not significant. - in *Chlorocardium*: height and size parameters were not significant in the original regressions.**

| | Correlation with height growth of | | Correlation with leaf growth of | |
|---|---|---|---|---|
| Species | Light | Size | Light | Size |
| **All sample plots** | | | | |
| *Dicymbe* | 0.37*** | 0.45*** | 0.35*** | 0.33*** |
| *Chlorocardium* (sample plots) | - | - | 0.20* | 0.51* |
| *Chlorocardium* (≥0.65 m) | 0.17*** | 0.20*** | 0.23*** | 0.31*** |
| *Duguetia* | 0.47*** | 0.48*** | 0.33* | 0.29* |
| **Sample plots with canopy openness ≤0.8%** | | | | |
| *Dicymbe* | 0.30*** | 0.48*** | 0.28*** | 0.41*** |
| *Chlorocardium* (≥0.65 m) | 0.12 | 0.18** | 0.29*** | 0.36*** |

and rank were only significant in *Dicymbe*, with similar effects as in the case of height growth. The presence of cotyledons increased leaf growth in *Chlorocardium*, but its effect was reduced at higher leaf density (Fig. 7b). Imminent death was associated with reduced or negative leaf growth rates over at least a year in advance of actual death in *Dicymbe*. This points to a long period of declining vitality. In *Chlorocardium*, death was positively but not significantly correlated with leaf growth, but this was offset by a strong negative interaction with leaf density. Hence, leaf dynamics as observed in *Chlorocardium* is determined to a considerable extend by dying seedlings losing all their leaves. Site significantly affected the response of leaf growth in *Dicymbe* and *Duguetia* to light. The correlations of light and size with leaf growth were not much affected by the length of de light gradient that was studied: in deep understorey with a low canopy openness they were about the same as for the entire population (Table 10; *Dicymbe* and *Chlorocardium* ≥0.65 m).

### *Survival*

Very few factors were correlated with 2 year or 3 year seedling survival, as determined by logistic regression. The main factors were rank and initial leaf density (Table 11; fig 6c, 7c), although leaf density did not correlate with 2 year survival in *Chlorocardium*. Survival was not correlated with any parameter describing light availability in *Dicymbe*, but in *Chlorocardium*, some light parameters were weakly correlated with survival. In isolation of the other factors, the effect of the Dawkins index was sig-

**Table 11**

**The effect of plant and site factors on the probability of survival in seedlings of three species in tropical rain forest near Mabura Hill, Guyana. The coefficients obtained with stepwise backward logistic regressions are shown. A negative coefficient means an increased, a positive coefficient a decreased probability of survival. Asterisks give the probability of being different from zero, determined with t-tests: *p≤0.05; **p≤0.01; ***p≤0.001; no asterisk: p>0.05. $\chi^2$ is -2*difference in log likelihood between the model with all factors and the model with the intercept only; df is the number of estimated coefficients. For *Duguetia* there were no models that were significantly better than the model with the intercept alone.**

| Variable | *Dicymbe* | | *Chlorocardium* (sample plots) | | *Chlorocardium* (height≥0.65m) | |
|---|---|---|---|---|---|---|
| survivorship over | 3 years | 2 years | 3 years | 2 years | 3 years | 2 years |
| N of observations | 1098 | 1803 | 100 | 175 | 445 | 601 |
| Intercept | -2.85*** | -2.01*** | -2.04 | -2.56*** | 0.70 | -0.06 |
| Initial leaf density | -3.23*** | -5.91*** | -2.10* | | -2.52*** | -2.30*** |
| Presence of cotyledons | | | 2.25*** | 1.17** | 1.03*** | 0.88*** |
| Rank | 3.08*** | 3.23*** | | 3.18** | 2.07** | |
| Dawkins 2l | | | | -1.22** | -0.83** | -0.30 |
| Dawkins 2m | | | | 0.31 | 0.11 | -2.36* |
| Dawkins >2m | | | | --- 1) | 0.06 | -1.31 |
| Seedling density | | -0.00*** | | | | |
| Fungi | | 0.75*** | | | | |
| $\chi^2$ | 94.3*** | 209.2*** | 43.0*** | 39.5*** | 105.6*** | 91.3*** |

[1] there were no seedlings with this light class.

**Table 12**

**The effects of light expressed as individual Dawkins indices (represented by dummy variables) on 2 year and 3 year survivorship of seedlings in the study plot, determined with logistic regression in which size variables are excluded. $\chi^2$ is the difference in negative log likelihood between the model including all light effects and the model with only the constant, at df=3. Dawkins index gives the effect of the separate Dawkins dummy variables as compared to Dawkins index 1, tested with t-tests. A negative coefficient is to be interpreted as an increased probability of survival. Asterisks give the level of significance: * p≤0.05; **p≤0.01; ***p≤0.001; no asterisk: p>0.05. Refer to Table 2 for explanation of the Dawkins index.**

| Species | Survivorship over: | Dawkins index | | | $\chi^2$ |
|---|---|---|---|---|---|
| | | 2l | 2m | >2m | |
| *Dicymbe* | 2 yr | -0.74*** | - 1) | -0.39 | 17.6*** |
| | 3 yr | -0.84*** | -1.64* | -0.14 | 21.1*** |
| *Chlorocardium* | 2 yr | -1.18*** | 0.78 | - 1) | 16.2*** |
| sample plots | 3 yr | -1.18** | -0.43 | - 1) | 6.6* |
| *Chlorocardium* | 2 yr | -0.74*** | -2.59* | -1.70 | 24.0*** |
| ≥0.65 m | 3 yr | -1.17*** | -0.25 | -0.67 | 20.1*** |

[1] No reliable estimate possible

nificant for both species in all cases, but this was entirely attributable to the effect of the variable describing a low lateral illumination (Dawkins index 21; Table 12). Fungi were observed to significantly decrease the 2-year probability of survival in *Dicymbe.* This is due to the presence of just germinated seedlings in this sample. A high seedling density increased the probability of survival for these seedlings, although the effect was quantitatively not important. The presence of cotyledons in *Chlorocardium* decreased the probability of survival. We could not develop satisfactory models for mortality of *Duguetia*, of which only 8 individuals were observed to die. Mortality patterns were not different between site.

### The relation between growth and survival

In recent models of forest dynamics (SORTIE, Pacala *et al.* 1993, Kobe *et al.* 1995), seedling survival is explicitly modelled as a function of recent growth history. Growth is modelled as a function of light availability and thus light indirectly affects mortality in that model. We tested this for *Dicymbe* and *Chlorocardium* by adding seedling height and leaf growth rates to the models describing mortality (Table 13). For both groups of *Dicymbe* seedlings a higher height and leaf growth rate significantly increased the probability of survival, with leaf growth rate showing a higher level of significance. In *Chlorocardium* height growth was not important for the probability of survival, but leaf growth was. The effects of rank remained largely unchanged after adding growth rates, and the effect of leaf density became stronger in all cases. For *Chlorocardium* in the seedling sample plots, leaf density correlated with survival if growth rates were present in the model (effect of addition of leaf density to the model: $\chi^2= 8.9$, $p<0.01$; unlike Table 11).

It is very hard to distinguish cause and consequence with this approach. An effect of growth rate on survival probability could be expected as we demonstrated above that eventual death explained a significant proportion of variance in regressions of height and leaf growth, especially in *Chlorocardium.* We reduced this effect by repeating the analysis for individuals which were not evidently losing leaves during the study period. This hardly affected the results for *Dicymbe*, although leaf growth seemed to have a stronger effect on survival than height growth. In contrast, in healthy *Chlorocardium* seedlings height and leaf growth rates were not significantly correlated with survival (Table 13).

## Discussion

### Seedling distribution and light environments

Overall, seedlings of each species grew in equal or darker environments than expected by chance (Table 6), and there were no inter-specific differences in light environment. This contradicts our hypothesis that seedlings are distributed in lighter environments, due to a higher mortality at darker sites, and that they are segregating over the light gradient as a result of differences in shade tolerance. However, our observations are in agreement with results reported by Clark *et al.* (1993, 1996), who found that 1-3 m high seedlings of 5 shade tolerant species at La Selva, Costa Rica, were distributed

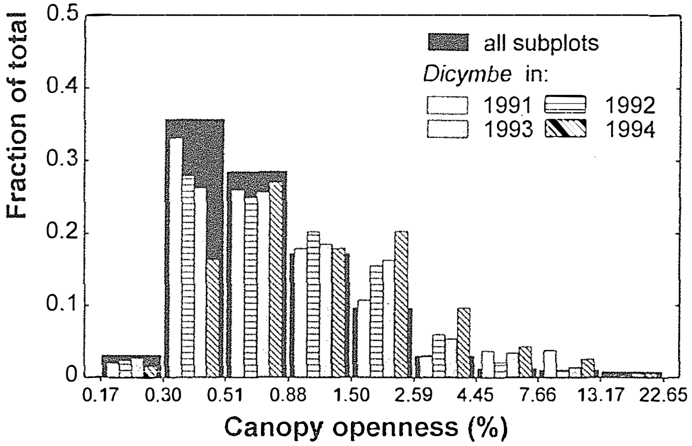

**Figure 8**
**Frequency distribution of the average canopy openness for individuals of the 1991 *Dicymbe* seedling cohort (narrow bars) and an unbiased sample at 0.65 m height (wide bars in the background). Natural log transformed canopy openness is expressed in classes of equal width. The unbiased sample was calculated from the average of four openness measurements taken at the corners of 5 m × 5 m subplots in the study plot (n=800). The seedlings were measured in the centre of 1 $m^2$ samples in the centre of the subplots in July 1991, July 1992, August 1993 and July 1994. All seedlings in one subplot were assigned the same light value as the subplot. In all years the openness above the seedlings was significantly higher than above the unbiased sample (Mann-Whitney unpaired ranks test, $p \leq 0.001$ in all cases).**

in significantly darker microsites than expected by chance. The shade tolerant *Dicorynia guianensis* was also found to 'prefer' darker microsites within a gap in a study in French Guiana (van der Meer 1995). The results of logistic regression of survival suggest that in *Chlorocardium* and *Dicymbe* survival depended on light, both directly (*Chlorocardium*, Table 11), and indirectly through the effect of light on growth (which was positively correlated with the probability of survival; Tables 8 and 12). We consider four explanations for this unexpected result.

First, the unbiased sample was measured at 0.65 m height, whereas most seedlings were shorter (*cf.* Fig. 1), and therefore in a slightly darker light environment. However, this can not explain the significantly darker average crown illumination for the population of *Chlorocardium* $\leq$0.65 m.

Second, the unbiased sample may be representative for the light environment in the plot, but it is not necessarily the appropriate sample for testing the distribution of seedling cohorts. We illustrate this by calculating the distribution of crown illumination scores of one single-aged *Dicymbe* cohort over 3 consecutive years, using the average openness of the sample plot determined in 1995. For this we used *Dicymbe* seedlings which germinated in July 1991 and whose number was measured in the central 1 $m^2$ of every 25 $m^2$ subplot in the entire study area between 1991 and 1994 (four measurements in 800 subplots). This sample was not fully comparable with the previous

**Table 13**

**The effects of height and leaf growth on the probability of two and three year survival. Height and leaf growth were added to the models described in Table 11 and their joint effect was measured in terms of increase in log-likelihood of the model. This was tested as $\chi^2$ (see Methods). The level of significance is indicated by asterisks: *** $p \leq 0.001$; ** $p \leq 0.01$; * $p \leq 0.05$; no asterisk: $p > 0.05$.**

| | *Dicymbe* | | *Chlorocardium* (sample plots) | | *Chlorocardium* (height ≥0.65m) | |
|---|---|---|---|---|---|---|
| survivorship over | 3 yr | 2 yr | 3 yr | 2 yr | 3 yr | 2 yr |
| N | 1098 | 1803 | 100 | 173 | 445 | 601 |
| Effect of height growth | -0.30* | -0.26* | 0.24 | 0.22 | 0.17 | 0.10 |
| Effect of leaf growth | -1.25*** | -0.88*** | -1.48** | -0.48* | -1.60*** | -1.27*** |
| $\chi^2$ of increase | 45.1*** | 37.3*** | 14.4*** | 16.5*** | 70.3*** | 59.2*** |
| **Only seedlings with leaf growth ≥0** | | | | | | |
| N | 700 | 1174 | 49 | 90 | 224 | 297 |
| Effect of height growth | -0.39* | -0.25 | 0.58 | 0.04 | -0.03 | 0.05 |
| Effect of leaf growth | -1.16* | -1.38** | -1.07 | -0.07 | -1.00* | -0.64 |
| $\chi^2$ of increase | 18.1*** | 26.2*** | 2.1 | 0.0 | 4.9 | 2.0 |

seedling populations, because these cohorts were unmarked, light was not individually measured but taken as the average openness value for the subplot, and the actual light measurements took place at the end of the study. However, these data show a clear trend towards a distribution that was biased to brighter areas in 1994 when compared with 1991 (Fig. 8). This is independent of trends caused by growth from darker to lighter vertical light environments. At all four measurements the seedlings were significantly in brighter areas than expected from the unbiased sample (unlike Table 6).

Clark *et al.* (1996), in the above mentioned study, explained this result by a decline in illumination of the microsites in which their seedlings established. Rich *et al.* (1993) have shown that photosynthetic photon flux density (PPFD) declined in gaps over a one year period, but not in the understorey, so the mechanism suggested by Clark *et al.* (1996) is expected only for seedlings that establish in gaps, and not (or less) for shade tolerant species that establish throughout the forest understorey. Furthermore, our seedlings were much smaller and, hence, probably younger than the seedlings in the Clark *et al.* (1996) study, so a possible decline of the light environment over the lifetime of the seedlings is expected to be less in our study.

A fourth possibility is that seedling shade tolerance does not change for several years at low light levels, assuming that the light compensation point for young seedlings is lower than for older individuals with a larger respiratory structure (as manifested by a reduction in Leaf Area Ratio, among others). Original seedling distributions remain conserved until the seedlings become more light demanding. However, a small but significant (indirect) light-dependence of survival among these seedlings seems to be present, and comparison of old and young seedling distributions did not indicate a decreasing shade tolerance (Table 6). Grubb (1996) suggested that species differ in the rate at which their light requirement changes with increasing size. This could not be demonstrated in our data, probably because we only studied a very small height range of seedlings. We have no information about size-related trends in LAR or SLA for these seedlings.

In any case, we argue that the multi-aged nature of our sample populations contributed to the apparent absence of a preference for brighter microsites, and that the distribution of a seedling population over the light gradient just after germination would provide a better null-hypothesis for testing and interpreting the seedling light environment than an unbiased but contemporaneous light sample. The former acknowledges the dynamic nature of rain forest seed shadows and, depending on the age of the seedlings, might be more informative about the light environment in which the seedlings establish and grow up.

### Light dependence of growth and survival

#### *High light growth versus low light survival*

There was no obvious relation between high light growth and low light survival in these three species. *Dicymbe* was the fastest growing species in all light environments (Fig. 5), and its survival even in very low light conditions was not lower than in the understorey species *Duguetia*, and higher than in *Chlorocardium* (Table 5). This infers that in these species, over the size range studied, there was not a clear-cut trade-off between high light growth and low light survival, counter to results by Hubbell (1992), Kitajima (1994) or Kobe *et al.* (1995). There was no reversal in species ranking of performance in any light climate, as would be suggested by a model of shifting competitive hierarchy (*e.g.*, Latham 1992). Grubb (1996) pointed out that this relation may actually be more complex, as the ecological tolerance of seedlings to shade may not only differ between species, but also between stages of development, for example as a result of differences between investment in stem and leaves. Over the size range studied here evidence of such a change in ranking could not be found, but there are indications that in low light (Dawkins index 1), saplings of *Dicymbe* (dbh >1 cm) have lower growth rates than similar sized *Chlorocardium*, while at higher light levels (Dawkins index >21) this is reversed (Chapter 8). Thus, a switch-over in relative growth performance may occur, but not in seedlings.

It should be stressed that the variation in growth response to light was so large, that it is difficult to make a simple quantification of 'the' response of a species to light. This suggests that a species-specific trade-off between high light growth and low light survival and a resource gradient alone are not sufficient to permit coexistence of these three species. In particular, we showed that plant size, and hence the result of previous growth and survival, had a strong impact on a seedlings ranking in the growth hierarchy in a patch. In these seedlings, the effect of variation in size was not weaker than the effect of variation in light (Table 10). Leaf density or total leaf area, related to absolute growth rate (Table 8) and rank, a measure for competitive ability, provide poorly growing individuals with a means to maintain a higher absolute growth rate than individuals with a higher potential relative growth rate (Boot 1994). In this way some individuals will be able to reach maturity in some gaps, at some moments in the forest cycle. The importance of seedling size stresses that competition and succession in gaps occur at the individual level rather than at the species level.

### *Light and growth*

The growth and survival of the three species were related to the availability of light, independent of how light availability was expressed: individually determined canopy openness (Fig. 5), individual Dawkins indices (Table 8 and 9) or light availability at subplot level as given by the PCA score. In general, however, these correlations were not high. For *Chlorocardium* in the sample plots, we did not even find a correlation between height growth and the Dawkins crown index. The short range of light availability that we observed (Fig. 3) probably limited the variation in response of the seedlings to light. Besides that, a range of other factors affecting growth responses obscured the effects of light. Still, the results of this study confirm that small variations in canopy openness lead to differences in growth, and *Dicymbe* even responded significantly to differences in canopy openness below *c.* 0.8% (Table 10).

The relation between light and growth differed somewhat between the two plots that made up the study area. The effect of plot on the light responsiveness to height and leaf growth in *Dicymbe* and *Duguetia* might be a consequence of the subjective way of determining the Dawkins index. The two sites were measured with a time lag of 2-3 months, and it is possible that the assignment of the Dawkins index to plants was unconsciously scaled to the range of light environments that was present in the plots (the plots differed slightly in light climate). This view is supported by the difference in results between objective and subjective light measurements. There was no site effect if light was expressed as canopy openness, determined with the plant canopy analyser, but there was a site effect for the Dawkins index.

Experimental studies of seedling growth in manipulated light environments (*e.g.*, Popma & Bongers 1988, Osunkoya *et al.* 1993, Veenendaal *et al.* 1996) and in the field (Augspurger 1984, De Steven & Putz 1984, Howe 1990, Molofsky & Fisher 1993, Ashton *et al.* 1995) invariably show a strong response of height and leaf growth to light, although the response may be complex (Ashton 1995). Clear differences in growth over a short light gradient like the one we measured in this study were demonstrated by Osunkoya *et al.* (1993) and Boot (1996). By design, experiments use seedlings of similar initial size, and therefore differences in growth performance between species are regulated only by their morphological and physiological behaviour. Naturally established seedlings, however, do not always clearly show a relation between light availability and growth. In our study, the relation between growth and light was weak (Fig. 5), and several factors were more strongly correlated with growth than light (Table 8 and 9). Similarly, in seedlings of seven climax species studied in La Selva, Costa Rica, only 3, 3 and 1 species responded significantly to variation in, respectively, the diffuse site factor, Dawkins crown illumination index and number of overtopping crowns (Clark & Clark 1992; Clark *et al.* 1993; size <1 cm dbh). On Barro Colorado Island (BCI), Panama, growth of saplings between 1 and 4 cm dbh was higher in low canopy (<10m) sites than in high canopy sites in 66 of 115 tested species, but for the remaining species this was not the case. In *Dicorynia guianensis* in French Guiana, height growth was positively correlated to the direct site factor for seedlings that established after gap opening, but not for seedlings that established prior to gap opening (van der Meer 1995). Generally, however, seedlings growth rates in the field respond significantly to variation in individually measured crown illumination (Pearcy 1983, Oberbauer *et al.* 1988, 1993; Washitani & Tang 1991 for temperate species) or to light availability determined at patch-level (*e.g.*, Hartshorn 1978, Uhl *et al.* 1988, Alvarez-Buylla & Martinez-Ramos 1992, Brown & Whitmore 1992, ter Steege 1994c, Whitmore & Brown 1996, Hladik & Mitja 1996). King (1994) and Pacala *et al.* (1993, temperate species), with smaller sample sizes and a larger light range, found much stronger relation between species height and radial growth rates, respectively, and diffuse light, than we did ($R^2$ were 0.44-0.75, and 0.23-0.78).

### *Light and survival*

Survival was weakly related to light in *Chlorocardium*, but not in *Dicymbe* (Table 11). The light effect was demonstrated through the effects of rank and leaf density, and also through the effects of previous growth on survival. If these factors were omitted from the model, it appeared that a slight increase in light availability from Dawkins index 1 to 21 was favourable for the probability of survival, but further increases to gap light environments were not (Table 12). It is possible that the relative rarity of high Dawkins scores contributed to this apparent lack of effect.

We cannot compare the absence of a direct light effect in our study with other studies, as these rarely take the effects of leaf density or rank into account. Our secondary observation that only a slight increase in light availability increases survival parallels the results obtained in a field experiment involving survival of transplanted seedlings of 6 species over a gradient of photosynthetically active radiation (PAR) in Queensland (Osunkoya *et al.* 1992). Seedling survival increased over a gradient from 0.5 to 2% PAR, after which no further increase was noticed up to the maximum of 10% PAR. The authors suggested that any increase of light availability above the light compensation point would correlate with growth rather than survival. In uneven-aged cohorts of 3 Dipterocarp species at Danum, Sabah, 77 month survival increased over a gradient of canopy openness of 6-10%, while at a further increase to 26% survival stabilised or even decreased slightly (Whitmore & Brown 1996). It is not clear to what extent observed trends of herbivory over the same light gradient contributed to this reduction in survival. Finally, in an experimental approach involving 6 Guyanese climax species (among which *Dicymbe* and *Chlorocardium*) grown in shade cabinets over a light gradient from 0-4% PAR, 1 year survival was 90% or more for all species at 4% PAR, so a further increase in light would not lead to further increase of survival at this time scale (Boot 1996). Grubb *et al.* (1996), in a greenhouse study, found increased mortality in 10 European shrub species only at 0.3% of full daylight, whereas mortality at 1.6% was not different compared to higher light intensities.

## The significance of plant size for seedling growth

### *Growth*

Our hypothesis that seedling growth and survival will be related to absolute and relative plant size was strongly supported by the data. Seedling growth responded strongly to variation in size, expressed as stem length, leaf density and rank (Table 8-10). This is an important result, because as a rule, seedlings are surrounded by neighbours of a different size. The effects of these three size parameters varied somewhat between species, and also between height and leaf growth. In experimental studies in controlled environments, plant size responds predictably in terms of allometry and (species-specific) allocation patterns to different levels of light availability (Popma & Bongers 1988, Osunkoya *et al.* 1993, Kitajima 1994). Under these conditions, seedlings adjust their architecture in such a way that quantum harvesting is maximised, leading to a strong relation between plant height, light availability and growth. Uncontrolled leaf losses (herbivory, physical damage), and variable light environments caused by seasonal (Rich *et al.* 1993) and forest dynamics, theoretically require continuous reallocation of resources in order to maximise light interception. It is hard to conceive that light limited seedlings can achieve this rapidly, and therefore the relation between height and light interception or even light availability and light interception is weak, and a measure of leaf area or leaf number (such as leaf density) is required as an additional parameter explaining growth.

### *Leaf density*

Leaf density is interpreted as a measure for the relative amount of assimilating tissue in the plant. Initial leaf density was positively correlated to height growth, other factors being equal (not in *Chlorocardium* in sampling plots). In contrast, the relation between leaf growth and initial leaf density was consistently negative for all species, in *Chlorocardium* generally in interaction with other factors (Table 9). Thus a high leaf density stimulated height growth, but depressed leaf growth. This was not caused by the choice for absolute leaf growth instead of relative leaf growth, which could lead to a bias if leaf loss in leaf-rich plants is higher than in leaf-poor plants because they have more leaves to lose. The relation between relative leaf growth rate and leaf density remained negative (data not shown). Imminent death contributed to the observed relation, especially in *Chlorocardium*, but also in surviving seedlings a high initial leaf density was not favourable for further leaf growth. The observed effect was also conservative if we limited the sample to groups of comparable ontogenetic stage. We ran a number of checks on this relationship by choosing subsets of 1. Old *Dicymbe* >1 m tall (with generally high leaf density; partial correlation coefficient -0.18), 2. Small *Dicymbe* between 0.30 and 0.40 m tall (-0.18), that germinated in 1991 (-0.13); that were measured from the first enumeration (-0.23); but this did not affect the results. None of the possible mechanisms listed below is fully satisfactory. First, for individual plants and for a short period, but not as a long-term mechanism at population level, it can be imagined that production of a new internode with a new leaf leads to increased self-shading and the replacement of older leaves with a negative carbon-balance. Second, a reduced leaf growth in leafy individuals might be expected if the plants are adjusting from a light-limited allocation pattern towards a water or nutrient-limited allocation pattern, allocating more resources to the roots. However, such an effect is mainly expected in plants that experienced a recent sudden increase in light availability, and not many plants are expected to be in such a situation. In all species there was a non-significant tendency for an interaction effect between light and leaf density. A significant interaction between the two has been found in a field experiment in which growth of *Chlorocardium* was monitored over a light gradient between 0.5 and 8% (Chapter 7). In this experiment positive leaf growth was possible under low light at low leaf density (such as in the present study) or under high light (>4%) at high leaf density (>5), but not in intermediate situations (such as in the majority of our seedlings). It could be that normal development under shaded conditions in these seedlings leads to an incompatibility between light environment and morphology (leaf density). This could only be advantageous if this morphology gives seedlings a disproportional benefit from conditions created by gap formation. The cost of such a strategy would be a negative growth rate in understorey conditions. For individual seedlings that is a gamble, but for the population it need not be if recruitment is limited by the number of gap occurrences rather than by the number of well-established seedlings.

### *Seedling height and rank*

The relation between growth and initial stem length was complex. Generally, a taller plant has a higher Stem Weight Ratio (SWR) than a shorter plant (Walters *et al.* 1993, Boot 1994). The stem is a respiring organ, which may explain the negative relation between stem length and growth. However, independent of their size, highly ranked individuals grew faster than shorter individuals growing in the same sample plot. This implies that the growth of an individual depended on the size of neighbouring plants, as suggested by Kohyama (1992a). Plants can not register the presence of neighbours, but they can register changes in the quantity and quality of light resulting from the presence of neighbours. A tall seedling is more likely to have one or more leaves positioned above surrounding seedlings than a short seedling, and may thus experience a higher total quantum load than a seedling of a lower rank with the same value of the light parameter at its growth point. (Another potential effect of neighbours, the reduction of mechanical load caused by wind, is not likely to affect the allocation of resources very much in this forest). Furthermore, our main light parameter, the Dawkins crown illumination index, possesses only limited resolution, so the rank parameter may provide additional resolution to it. If this is the case, this may also explain the curious site-dependent effect of rank on height growth. If the Dawkins index was assigned in a slightly different way in one plot than the other, this might cause the 'scaling factor' rank to assume a different value in both plots. However, a similar effect did not occur for leaf growth.

Short seedlings may experience a lower Red/Far-Red (R/FR) ratio than tall seedlings because red light is harvested by surrounding, taller neighbours. Plants growing at a red-deficient regime often show increased rates of stem elongation (Smith 1982) and are thus expected, contrary to the results of the regression, to show a faster height growth than plants from less red-deficient environments, other factors being equal.

There is evidence that *Chlorocardium* (ter Steege *et al.* 1994, Boot 1996) and *Dicymbe* (R.J. Zagt, *unpublished results*) have a longer epicotyl resp. hypocotyl under low light conditions. It was not clear whether this is due to a low R/FR ratio, or low light itself. However, the length of all other stem internodes, and therefore continued growth, was independent of light availability or quality in *Chlorocardium* (ter Steege *et al.* 1994). Similarly, no effect of R/FR ratio on the growth of woody climax species was demonstrated by Kitajima (1994), so on the base of these data an effect of light quality on seedling growth as a consequence of shading by neighbours is not expected. The effect of neighbours on the availability of water and nutrients is probably minor in the low light conditions found in most of the study plot.

The effect of rank was clear for *Dicymbe* and for *Chlorocardium* height growth, but not for *Chlorocardium* leaf growth and *Duguetia*. For the latter species the variation in height (Fig. 1) and rank in the study population was probably too small to be important.

### *Comparison with other studies*

In literature, seedling size is often a dependent variable, not an independent variable as used here. Seedling height, leaf number and leaf area are generally positively related to the availability of light (ter Steege *et al.* 1994, Boot 1996 for examples involving the study species). In the heterogeneous cohorts studied here, simple correlations between individual canopy openness and initial height or initial leaf number were absent (r=-0.12-0.25, p>0.05 for all 6 correlations) or weak (sample plot openness instead of individual openness: r=-0.10-0.19, 3 out of 6 correlations significant). Therefore, differences in (initial) leaf density between the individuals in this study are not mainly determined by differences in light availability, but probably also to a considerable extent by leaf dynamics caused by herbivory or physical damage, and to differences in age.

In natural seedling populations studied to date, the relation between initial height and linear growth rate is usually positive, not negative as in the present study (Hartshorn 1978, Uhl *et al.* 1988 (pooled species), Clark & Clark 1992, Brown & Whitmore 1992, Whitmore & Brown 1996; Cao 1994, temperate species). For 7 of 12 seedling populations of pooled species in Queensland, height was negatively correlated with growth, in 4 of them significantly (Connell *et al.*, 1984). Five out of six Dipterocarp species studied by Still (1996) showed a negative relation between height and percentual growth rate. Height growth of transplanted *Virola surinamensis* seedlings was more affected by canopy openness than by size in the first year of growth, but more by size than by canopy openness in the second year (Howe 1990). The effects of height on growth are particularly clear in gaps, but not always in understorey conditions (Brown & Whitmore 1992). In all these studies, height was the only size parameter considered, and it should probably therefore not be considered as a correlate of the amount of respiring tissue in the plant, as we suggested above, but as a correlate of LAR. We tested this by repeating the regressions of Table 8 with stem length as the only size parameter, leaving out leaf density and rank. We expected that the effect of stem length would become positive or less negative. The partial correlation coefficients for initial height in these regressions were 0.08 (*Dicymbe*), 0.04 (not significant; *Chlorocardium*) and -0.21 (*Duguetia*). Indeed, for *Dicymbe* growth was positively related to height; in the remaining two species this relation became less negative or less strong if other size parameters were removed.

The relation between height growth and leaf area was studied by Oberbauer (1988, 1993) and Canham (1988, temperate species). In 3 out of 4 studied species at La Selva, Costa Rica, leaf area was strongly positively correlated with total leaf area (Oberbauer 1988, 1993), while height growth of *Acer saccharum*, but not *Fagus grandifolia*, was positively correlated with posterior crown radius and density (Canham 1988). The result that seedling relative growth rate (RGR) in intraspecific comparisons conducted in shade houses is usually negatively correlated with leaf area ratio (LAR; Popma & Bongers 1988, Kitajima 1994, 1996) is only seemingly in contradiction with these field results. In these experiments, initial plant sizes are about equal, and RGR and LAR respond jointly to increased light availability. Thus, LAR reflects adjustments towards the light climate, with relatively more biomass and area being allocated to leaves in light-limited conditions. In the forest understorey, such an adjustment is hampered by allogenic leaf losses and the limited carbon resources available for replacement of lost leaf tissue. Indeed, in natural populations of *Chlorocardium*, as well as *Mora gonggrijpii*, positive relations were present between light availability and LAR as well as leaf number (ter Steege *et al.* 1994, ter Steege 1994c). In comparisons between equally high seedlings with various amounts of (residual) leaf area in approximately homogeneous understorey conditions, we expect a positive relation between (initial) LAR and (continued) growth, similar to the relation we demonstrated for leaf density and height growth. A positive relation between LAR and RGR is also shown in interspecific comparisons under equal light conditions (more in low light than in high light) in experimental conditions (Walters *et al.* 1993, Kitajima 1994, Cornelissen *et al.* 1996).

The effects of initial size differences between seedlings on their performance were clear, but not everlasting. Size differences develop as a result of different growth histories (*e.g.*, a different age), but also as a result of dynamics of the biotic and abiotic environment. Size advantages may be lost as a result of branchfall, (interspecific) growth differences, leaf loss due to herbivores, disease, differential changes in crown light etc. As light availability increases above the levels encountered in this study, differences in potential growth rate also increase and the relevance of the initial size structure in seedling communities may be lower (Boot 1996). This loss of significance of size for growth was demonstrated in a study at Danum, Sabah, where 40 months after removal of the canopy three Dipterocarp species had amplified initial differences in height in all gaps studied (but not in the understorey). Interspecific differences in growth rate further contributed to the observed differences, except in the largest gap (Brown & Whitmore 1992). Remarkably, by 77 months all relation with initial size (or, by implication, size at 40 months) was lost in 3 out of 5 gaps (Whitmore & Brown, 1996). From the evidence given, interspecific differences in herbivore pressure contributed greatly to the loss of the importance of initial size.

### *The relation between plant size and survival*

Larger plants had an increased probability of survival (Table 11). Initial height did not affect survival, but a high rank in the size hierarchy and a high initial leaf density increased the probability of survival. As only seedlings surviving at least one year were used for this analysis, the analysis of Table 11 does not fully involve the much higher mortality rates observed for just germinated seedlings of the study species (Chapters 3, 5).

A positive relation between size (seedling height) and seedling survival is frequently demonstrated in field studies (Hartshorn 1972, Welden *et al.* 1991, Brown & Whitmore 1992, Clark & Clark 1992, De Steven 1994, Still 1996). Survival of *Cecropia obtusifolia* depended on height and on the number of leaves of the seedling (Alvarez-Buylla & Martinez-Ramos 1992), whereas survivorship of seedlings of *Dipteryx panamensis* at La Selva was positively related to the number of leaves at the start of the measuring period, and also to leaf size (Clark & Clark 1985). Apart from possible ontogenetic trends reflecting lignification and investments in defence against pathogens and predators, a combination of factors may contribute to this trend. Larger seedlings have an advantage of scale compared with smaller seedlings. Size makes seedlings less vulnerable to damage caused by small falling debris, and to loss of, in absolute sense, small amounts of leaves or branches (Grubb 1996), even though the probability of damage may increase (De Steven 1994). A negative relation between seedling size and mortality ascribed to physical factors was found for *Pentaclethra macroloba* (Hartshorn 1972) and 6 other climax species (Clark & Clark 1991) at La Selva (Costa Rica). Furthermore, a large size and a high survival are both manifestations of a high growth rate, and slowly growing, small, suppressed seedlings have a high probability of death (Kobe *et al.* 1995, Still 1996, Kobe & Coates 1997, *cf.* Weiner 1990). This could explain why rank rather than seedling height affected survival probability (rank was more strongly correlated to seedling height growth than height in *Dicymbe* and *Chlorocardium*; Table 8). Kobe *et al.* (1995) found only this indirect (via growth) effect of size on survival. In our seedlings however, the effect of the three size parameters was hardly affected by including previous seedling growth rates in the analysis.

## **Other correlates of growth and survival**

### *The significance of cotyledons for* Chlorocardium

The presence of long-lived cotyledons had several contradictory effects on the growth and survival of *Chlorocardium.* They improved height growth (Table 8). This implies that part of the height growth in *Chlorocardium* is due to retranslocation of resources from the cotyledons to the stem over a long period. This is consistent with *Chlorocardium* seedlings which grew up in total darkness (0% light) having a height of *c.* 2 m after 2 years (Boot 1996 and *pers. comm.*). ter Steege *et al.* (1994) and Boot (1994) showed that *Chlorocardium* in low light conditions have a negative carbon balance. Supposedly, these seedlings only survive for some time thanks to large cotyledonary reserves. The shoot that is produced after germination is very small considering the size of the seed (Table 1), but after accidental loss of the shoot a new one is readily formed at the base or on top of the surviving part of the shoot (Chapter 5). This is observed after damage in healthy seedlings, and even after death of declining shoots (*personal observation* R.J. Zagt). In the model this evident from the positive relation between imminent death and height growth in seedlings with their cotyledons present (Table 8).

The positive effect of cotyledons on leaf growth is offset by the result that in seedlings with cotyledons leaf density had a much stronger negative correlation with leaf growth than in seedlings without cotyledons. This is a logical result if possession of cotyledons enables seedlings to survive a longer period of negative leaf growth than seedlings without. If they do not, they would die quickly and not contribute to the calculation of leaf growth. This mechanism, if it would work like this, did not lead to a higher survivorship of seedlings with cotyledons (cotyledons actually decreased the probability of survival, Table 11).

The decreased survival probability for seedlings with cotyledons points at another aspect of cotyledons: they form a food resource for insects, fungi and small rodents and thus provide access to mortality agents that might kill the plant. There is one fungus observed to attack only the cotyledons of *Chlorocardium* (ter Steege *et al.* 1996; Hammond *et al., in prep.*), and some insect seed predators eventually switch to attack the seedling (Hammond *et al., in prep.*). A positive effect of cotyledons on survival of *Chlorocardium* seedlings was reported by ter Steege *et al.* (1994), for seedlings that were probably still in the stage of cotyledonary growth.

These results show that *Chlorocardium* has a distinctly different growth strategy than both other species. The seed reserves are not immediately invested in a large seedling, but are gradually translocated to subsidise a carbon deficient shoot (*cf.* Kitajima 1996). Plants with an apparently positive carbon balance, such those growing in logging gaps, may retain their cotyledons for a very long time (>5 y, R.J. Zagt, unpublished results).The possible advantage of this strategy is that seedling survival in the understorey is to a certain extent independent of the performance of the shoot. This is also suggested by further analysis of the 2 y survivorship data from Table 13, where it was shown that in 297 healthy seedlings (with a non-negative leaf growth), growth rates were not significant in explaining survival. However, for those seedlings among these without cotyledons, growth rates were, albeit barely, correlated with higher survival ($\chi^2$=6.2, p=0.044, n=219). In seedlings still in possession of cotyledons, survival was independent of their growth performance ($\chi^2$=2.0, p=0.37, n=78). (The same pattern was not present if also leaf-losing seedlings were permitted in the model.) Nevertheless, the performance of *Chlorocardium* shoots in the field was generally very poor (low height growth and a net loss of leaves (Table 5), low RGR, Boot (1996), ter Steege *et al.* (1994), high vulnerability to leaf herbivores and fungi, low saturated photosynthesis rate, Raaimakers *et al.* (1995)). This sharply contrasts with the unexpectedly high survival of *Chlorocardium* seedlings growing in a greenhouse in total darkness, (2 year survival was >90%: Boot (1996) and *personal communication*). Possibly survival of seedlings in the field would be even lower without the support of cotyledons.

### *Ontogenetic effects*

Ontogenetic effects of growth were explicitly represented by two variables: the presence of cotyledons (discussed above) and age, and implicitly by the size parameters, which were discussed above. In *Dicymbe*, seedlings less than 4 years old grew faster than older seedlings. This effect is possibly explained by growth in the stage that the stems were green and no or few resources were averted for lignification of the stem. In *Chlorocardium*, the only effect of age was a reduction of the effect of seedling rank, which is possible if growth is dependent on cotyledonary reserves rather than external factors. There were no effects of age on leaf growth, nor on survival. Possible effects of age on survival, as evident in Table 5 were probably not detected as we limited our analysis of survival to individuals with measured growth, *i.e.* mortality occurred at earliest in the second year of measurement, excluding the phase of high mortality typical of young seedlings. For this reason an effect of age on growth in *Duguetia* could not be established, because there were only very few young seedlings that survived one year.

### *The relation between growth and mortality*

A low growth rate (suppression) decreased the probability of survival for *Chlorocardium* and *Dicymbe* (Table 13), especially a low leaf growth rate. This confirms our hypothesis that fast growing seedlings have an increased survival probability compared to slow growing individuals. However, only for *Dicymbe* healthy seedlings without signs of decreasing vitality (a negative leaf growth rate), showed this relation, whereas for *Chlorocardium* growth rate was not related to survival in 'vital' seedlings. Mortality of suppressed individuals is a consequence of asymmetric competition in crowded stands, which is thought to regulate stand structure and population dynamics in forests (Weiner 1990, Kohyama 1992a, Kobe *et al.* 1995). In natural seedling populations an elevated mortality rate for suppressed seedlings was observed for three *Shorea* species in Sabah, but not a group of three related *Shorea* species with heavier wood (Still 1996). A relation between growth rate and subsequent probability of survival was also reported for north-temperate tree species by Kobe *et al.* (1995), Kobe & Coates (1997), and by Walters & Reich (1996) who explained inter-specific differences in survival by growth.

We also observed a reciprocal relation between imminent death and growth in *Dicymbe* and *Chlorocardium* (Table 8, 9). Considering the above, for *Dicymbe* this effect is best interpreted as a consequence of the effect of growth on mortality, whereas in *Chlorocardium* this seems not to be the case. An effect of imminent death on growth, independent from suppression, can be expected if mortality is preceded by a long period of slow growth, *e.g.*, as a result of disease or repeated attacks of mortality agents. It can be imagined that *Chlorocardium* seedlings (having cotyledons) but not *Dicymbe* show such a long period of decline before they die.

Hence, the effects of some plant characteristics on the patterns of seedling growth and survival appear to be very complicated. For example, a high leaf density is positive for height growth, negative for leaf growth, whereas survival is both positively (directly and through the effect on height growth) and negatively (through the effect on leaf growth) affected by a high leaf density.

### *Remaining variables*

Direct mortality agents, such as fungi or herbivores, had little effect on growth or survival (Table 8, 9, 10). Fungi affected 2-year survivorship but not 3-y survivorship (Table 11). This is an indirect age effect attributable to the seedlings from the 1991 cohort (for which 3 year survivorship is not known). Young *Dicymbe* seedlings are vulnerable to fungal infection on the stem (Chapter 3), but after the stem lignifies few seedlings show evidence of fungal attack. Fungi were a main cause of death in seedlings at BCI, Panama (Augspurger 1984).

Clear effects of herbivores on growth and survival that are reported in the literature often concern herbivory of seeds or cotyledons (Sork 1987, Osunkoya *et al.* 1992, Itoh *et al.* 1995, Hart 1995). The same was shown for *Chlorocardium* (Hammond *et al., in prep.*). An effect of herbivory of leaves or shoot apici on seedling performance (in gaps) was implied for Dipterocarps at Danum, Sabah (Whitmore & Brown 1996) and for *Faramea occidentalis* at BCI, Panama (Schupp 1988a). On the other hand, negative effects of artificial defoliation on growth in three Chinese subtropical species were not evident below 50-75% defoliation (Cornelissen 1993), whereas Coley (1983) found a significant relationship between leaf grazing rate and growth for only 3% of 41 species in gaps at BCI, Panama. However, all seedlings were in gaps in this study, and differences in illumination may have obscured the effects of herbivory. Similarly, effects of artificial defoliation on mortality in naturally germinated *Shorea* seedlings in Malaysia were not evident at a defoliation rate of 25% (Becker 1983). This is in contrast with very small losses of leaf area causing large differences in survival in *Dipteryx panamensis* seedlings in understorey environments at La Selva (Clark & Clark 1985). These results indicate large differences in the impact of herbivory between species and sites on seedling performance. Possible effects of herbivory on performance might be functional through its effect on leaf density, and this may explain the generally small direct impact of herbivory that we found in our study. Growth is also indirectly affected by herbivory and pathogens through the allocation of resources towards defence (Coley 1983). This was outside the scope of our study.

It should be noted, that the effect of herbivores and pathogens in our study could be underestimated if attack by these mortality agents leads to a swift death. Damage is then not likely to be important during the period over which growth rates are calculated. Moreover, herbivory and possible leaf fungi tend to be severely underestimated as damaged leaves are quickly shed and lost to observation (Coley & Kursar 1996).

Distance effects of parent trees on the dynamics of seedling populations have been widely studied in relation to the Janzen-Connell model (Janzen 1970, Connell 1971, review in Hammond & Brown 1997 (*in press*), mainly in field experiments involving even-aged seedlings. Effects of nearby parents on height growth of uneven-aged cohorts of saplings were demonstrated by Condit *et al.* (1994) for *Faramea occidentalis*, whereas an effect on recruitment was found for just 2-3 other species of many studied, all belonging to the most abundant species on BCI, Panama (Condit *et al.* 1992). A positive relation between survival and distance was found for 2 of 4 temperate *Carpinus* species (Shibata & Nakashizuka 1995). However, Itoh *et al.* (1995), in natural even-aged seedling populations of 4 Dipterocarp species, found no significant correlation between seedling survival and distance from the parent, nor did Connell *et al.* (1984) for even-aged mixed-species populations in Queensland. In our study, a quantitatively weak, positive relation between distance and growth but not mortality was demonstrated for *Dicymbe*, the commonest species in the plot. It is not clear which mechanism could be responsible for this combination of effects.

Seedling density was weakly and positively correlated with growth and survival in *Dicymbe* (Table 8, 9 and 10). At seedling densities which are not high enough for depressing growth rate through density-dependent effects, high seedling densities may be indicative of locally suitable conditions for growth and survival. As light availability is described in separate variables, these locally suitable conditions possibly concern water or nutrient availability. Itoh *et al.* (1995) and Connell *et al.* (1984) found no dependence of growth and/or mortality on local seedling density, whereas Puig & Fabre (1997) found a negative correlation between seedling density and survival in *Iryanthera hostmannii.* In most of these studies, seedling densities were low compared to *Dicymbe.*

The effect of elevation, negatively correlated with growth in *Chlorocardium*, is possibly interpreted as a moisture factor.

### Is seedling growth in the understorey predictable?

The results of this study provide a number of different answers for the question of predictability of seedling performance in the understorey of tropical rain forest. Seedling performance in this study was predictable, because we could establish correlations between performance and quantitative aspects of the seedling and its environment. All species responded in terms of growth to small variations in light availability. Differences in the size of seedlings, either as the result of a different age and growth history, or as the result of differences in response to minor variations in light availability, further contributed to differences in height growth and survival. The determinants of leaf growth remained more poorly understood. Furthermore it became apparent that size is mainly important when it is related to the size of neighbouring seedlings. The main patterns remained intact if the light gradient was reduced to less than 0.8% canopy openness (Table 10) for *Dicymbe*, but less so for *Chlorocardium.* Inter-specific differences further contributed to differences in performance which are already present among con-specific seedlings.

However, the value of this predictability is relative, because the study also showed that much variability of seedling growth and especially survival remained unexplained. The coefficients of determination for the growth regressions were low, and survival appeared to be independent of most measured variables, including light. Three factors contributed to this. First, the average and range of the growth response was very low (Table 5). This hampers the detection of significant contributions of the independent variables, especially if variation in these is also low, such as in light availability. Second, many continuous variables were entered in the analysis as classified variables. This was the case for light (4 Dawkins classes) and for herbivory, fungi and age. This lack of resolution in some explanatory variables could account for some unexplained variance. Third, a number of potentially important determinants of growth and survival was not measured. Addition of phosphorus, but not nitrogen or both, doubled growth of naturally established *Dicymbe* seedlings, whereas *Chlorocardium* stored phosphorus without increasing its growth rate (Raaimakers 1994). However, without knowledge of natural variability of P-availability within the plot it is difficult to determine whether this accounts for a part of the unexplained variance. Similarly, little is known about water. As far as field observations can tell, clear effects of variation in water availability within the plot becomes evident only after a very long period without rain. *Dicymbe*, but not the other two species, responded to drought with strongly increased mortality (R.J. Zagt, unpublished results). This did not happen during the study period. Other not measured factors affecting growth and mortality include root herbivory, presence of mycorrhiza (ectomycorrhiza are implicated in the dominance of Caesalpinoids; Newbery *et al.* 1988) and genetic variation between individuals.

The predictability of the response of a forest to manipulation of the canopy, as is often the objective of silvicultural systems, requires that (under the assumption that all species are 'available') seedling and sapling performance depends entirely on light (at gap level) and species-specific growth rates. This seemed not the case for the study species in the light range studied by us. First, although *Dicymbe* showed a higher growth and a stronger response to light than both other species, light and species explained only a small proportion of variance. Second, many other factors affected seedling performance (Tables 8-11). There was also no evidence that, over the light gradient studied, the order of growth response changed between the study species (Fig. 5), which would allow manipulation of relative species performance. The same conclusion was reached by Whitmore & Brown (1996), over a much larger light gradient.

These results show that manipulation of the light climate will not likely stimulate the performance of the commercially very important *Chlorocardium* in favor of the commercially uninteresting *Dicymbe*. Our study strongly suggests that adjusting the successional processes in gaps for the purpose of forest management requires a (generic) manipulation of light as well as a much more specific manipulation of the size hierarchy of competing seedlings. This was long ago realised by foresters, and liberation of (advanced) seedlings and saplings is prescribed in many silvicultural systems (Schultz 1960, de Graaf 1986). However, liberation thinning is rarely applied on a commercial scale owing to the high costs involved.

Lastly, predictable patterns of seedling performance resulting from seedling identity, size and abiotic setting may be disturbed by stochastic disruptions at the level of individuals (damage, herbivory, disease, gap formation) or community (drought, flooding etc.). The importance of size for determining differences in performance between seedlings indicates that the impact of stochastic size reductions may be considerable. We could not properly assess its consequences. The effect of herbivory was discussed above; and although we could establish that 13.2% of all seedlings suffered recorded physical damage over 4 year, the study was too short to compare pre- and post damage performance. Evidence from La Selva, Costa Rica, indicates that damaged seedlings have a lower survival probability (Clark & Clark 1991), but no information is available about growth rates.

The effect of stochastic events depends on the scale, intensity and frequency (Waide & Lugo 1992), and also specificity of occurrence. Events that occur at a low intensity and frequency may adjust individual seedling performances without severely affecting patterns of performance (*e.g.* the hierarchy of seedling sizes) that were previously present. This might be the case when animals trample a seedling bank or a branch comes down. Specific events, such as in the example of drought that specifically affects *Dicymbe* survival, or specific pests, more likely alter pre-existing trends in performance. Finally, in communities where severe stochastic disruptions take place, or where disruptions are frequent, seedling performance is expected to be unpredictable. In these communities, hierarchies in performance are re-established after each stochastic event.

## Conclusions

This study demonstrated that seedlings of late successional species significantly responded in terms of growth to variation in light availability over a relatively short light gradient in the rain forest. In addition, variation in size and species-specific differences in response to light enlarged the variation in response between individuals growing in the same small area of rain forest. Over the short gradients studied, there was no indication that species changed position in ranked relative performance. *Dicymbe* grew fastest and had highest survival, not only in the most shaded conditions but also in the more brightly illuminated microsites. The relation between plant size, both absolute (leaf density) and relative (rank) and growth was as important as light availability. Both are measures for light intercepting capacity of plants. Their importance strongly suggests that competition between individuals is a significant factor that structures community dynamics, also at the low light levels observed in the plot, and not only in the high light environments. These relations should be clarified in competition experiments, in which species, light and size are varied.

The study also revealed much variation in the response of seedlings. Without doubt a significant part of it is to be attributed to measuring error and the limited sensitivity of, especially, the Dawkins index. Still, much of the variation is probably real. It may imply that plants, albeit growing in average terms according to a certain species-specific strategy, are often merely coping with the reality of their environment. Strategies are often expressed in relative terms (relative growth rates, allocation patterns), which is a powerful way to assess inter-specific differences in growth and investment and interpret them in functional and adaptive terms. In the field however differences in absolute (realised) growth and survival rates will determine the outcome of succession, while it is less relevant whether this is accomplished by an individual with the best functional solutions to environmental constraints, or by an individual which is just coping well enough. Thus, variation in absolute growth and survival rates are not simple consequences of differences between individuals in life history attributes and access to resources, but also of size differences which are determined by a combination of species-specific characteristics (seed size, architecture, defence against pathogens and herbivores), growth history or chance factors (damage, disease) and of individual variation in these factors.

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chapter 7

# Seedling dynamics of *Chlorocardium rodiei* in logged-over rain forest in Guyana

*Roderick J. Zagt*

## Abstract

The germination, morphology growth and survival of *Chlorocardium rodiei* seedlings (<1.6 m tall) was studied between 4-7 years after logging in a 1.5 ha plot in exploited rain forest in Guyana. The physical impact of logging created a structurally heterogeneous residual forest consisting of skid-trails, dense secondary vegetation, forest remnants and tree crown zones. The effect of removal of adults on the seed shadow, differences in seedling morphology and performance between habitat types, and the response of transplanted seedlings to a range of light environments were studied. The exploited seedling population was compared with an undisturbed population.

*Chlorocardium* seed shadows were strongly concentrated around the remnant adult trees. The potential seed shadow was estimated to be 55% smaller in comparison with the pre-logging situation. Seedling distristributions showed a comparable pattern, with still a high number of seedlings found around stumps. Seed germination in the field and in the experiment was not related to canopy openness, and also not to habitat type.

Most seedlings were below the secondary canopy formed by colonizing species, seedling morphology and mortality were not different between habitat types. Differences in height growth between habitat types were accounted for by differences in crown illumination, while differences in leaf growth could not be accounted for by light. The differences were explained as the result of a different history of the light environment between habitat types.

Seedlings of the exploited population were on average 2.5 times as large as seedlings from the undisturbed population in leaf and branch number. However, in spite of a slightly higher growth rate, the exploited populations lost leaves at a much higher rate than the undisturbed populations. This was caused by the combination of a high leaf density (N of leaves per unit stem height) and low light conditions, which is the result of the rapid transition from high to low light environments in the exploited plot. The field exeriment confirmed that seedlings in high light conditions (representative of the early post logging period) stimulated height and leaf growth, but large seedlings transplanted in low light conditions suffered a similar negative growth and death as in the exploited plot. The relevance of these results for management of *Chlorocardium* is discussed. In spite of being overgrown by fast -growing colonisers, *Chlorocardium* seedlings proved to be very persistent in the vegetation 4-7 years after logging. However, in order to retain these seedlings and stimulate their growth, intensive and costly silvicultural management is required.

## Introduction

*Chlorocardium rodiei* (Greenheart) has been the mainstay of the Guyana forest industry since its beginning. The species provides a heavy and durable timber that is resistant to the action of marine borers (Fanshawe 1947, Gérard *et al.* 1996). It is easily available in large quantities in the tropical rain forest of the near interior of Guyana. Despite its long logging history, its appreciable significance for the local economy and strong symbolic meaning as an object of national pride, concerted efforts to develop a system that guarantees the continued availability of this commodity have been few and not very successful in their application (Clarke 1956, ter Steege 1990). Presently *Chlorocardium* is being logged in most of its natural range, and large areas of logged-over forest exist where derelict populations are left to regenerate, without a clear perspective of a future source of this timber.

Selective exploitation of timber in the tropical rain forest may cause extensive opening of the canopy (Macedo & Anderson 1993), thus creating a coarsely grained mosaic characterised by larger and smaller gaps of the same age that lie alternated with remnant patches of unchanged forest. Skid trails connect the stumps of the logged trees with the access road, and tree crowns and other logging debris lie piled up in some places. This forest replaces the more finely grained natural forest that is characterised by a mosaic of smaller gaps in many stages of regeneration (*e.g.* Martínez Ramos *et al.* 1988, van der Meer 1995). Although often reminiscent of the conditions in large natural gaps, establishment conditions in logging gaps differ from natural gaps in a number of important ways. Gaps caused by mechanical logging are often larger (Johns 1988, Uhl & Vieira 1989, ter Steege *et al.* 1996), and because they were created by cutting healthy trees (as opposed to natural gaps that are generally created by old and declining trees), crown zones occupied by twigs and leaves are larger.

The pulse of nutrients that is released from the decaying biomass and variation in mean and extreme light intensity, temperature and air humidity create spatially heterogeneous establishment conditions for seedlings (Schulz 1960, Brown 1993, Brouwer 1996). Heavy skidding machinery damages remnant above and below-ground vegetation and compacts or upturns the soil (de Foresta 1984, Hendrison 1990). This alters nutrient dynamics and hydrological characteristics of the soil (Malmer & Grip 1990, Jetten 1994, Brouwer 1996), and buries seeds or brings them from the soil seed bank to the surface (Pinard *et al.* 1996). It is well documented that establishment conditions for seedlings vary greatly along these gradients of light, temperature, water and nutrient availability and soil disturbance that characterise recently logged forest, and a large number of species, including a great many that were not present as an established individual prior to logging, may establish (De Zoysa *et al.* 1991, Hawthorne 1993, Pinard *et al.* 1996, Ek *in prep.*).

At a later stage of succession, a dense secondary stand develops (*cf.* de Foresta 1984, Saldarriaga *et al.* 1988, Saulei & Lamb 1991), and the micro-climatic conditions at soil level, change rapidly from typical of large gaps to typical of forest understories. There is some evidence (from natural gaps) that light levels below secondary canopies even drop below the levels found in mature forest (Clark *et al.* 1996). So, although logged forests are commonly regarded as sites where growth rates are increased and where individuals of canopy species are released from suppression by high light availability, for many seedlings and saplings of slowly growing late successional species this is a temporary situation and they inevitably enter a phase of prolonged low light availability. This may severely limit the species' potential of establishing in the canopy, especially for those species for which the remnant sapling population is the main source of new adults after removal of a large part of the reproductive population by logging.

Recent efforts have revealed that *Chlorocardium* sports many life history features which are not particularly helpful in re-establishing in recently logged forest. The growth rate of seedlings, juveniles and adults is slow (ter Steege *et al.* 1996, Chapter 8), so that many of them are soon below a dense canopy of fast growing individuals of other species. The population size distribution shows a marked deficiency in juveniles (ter Steege *et al.* 1996), causing new adults to be produced at a slow rate. The seeds are very large (38 g dry mass, Hammond & Brown 1995) and have a short range of (primary) dispersal (Zagt *in prep.*), implying that a large part of the logged forest is outside the dispersal range of surviving adults. Therefore, depending on the intensity of the logging operation, re-establishment of the *Chlorocardium* population in logged-over areas is to a large extent dependent on the seeds and seedlings that were present at the time of logging. The key phase for these seedlings is likely the very dark succession phase that follows after the establishment of a secondary canopy of fast growing species. Apart from species-specific growth and mortality rates, the success of these individuals may be dependent on the variable micro-site conditions encountered in logged forests, both before and after the establishment of an overtopping secondary canopy.

The general objective of this paper is to quantify germination, growth and survival of a remnant *Chlorocardium* seedling population in response to variation in habitat structure in logged forest 4-7 years after logging, and to compare this with an undisturbed population. Specifically, the following questions were addressed and associated hypotheses tested:

1. Is there variation in *Chlorocardium* morphology, germination, growth and mortality within logged forest, associated with habitat heterogeneity caused by logging?
2. What is the spatial effect on seed production of removal of adults?
3. Are growth, morphology and mortality of *Chlorocardium* seedlings in a logged area different from an undisturbed area?

These questions were addressed in series of related studies of a naturally established *Chlorocardium* population in a five year old logged area, that was monitored over a period of three years. This population was compared with a population growing in an undisturbed, but otherwise comparable area nearby. Furthermore, in order to assess growth and survival in conditions which are typical for the early post-logging period, but which were disappeared at the time of the study, a field experiment was done. The effect of light and morphology on growth and survival was studied for seedlings differing in age. Germination trials were done in this experiment, and in a separate experiment in logged forest. This study was set up to provide population biological information that is required for the scientific management of an over-exploited commercial species (*cf.* Putz 1993). It highlights the effect of a drastic change of resource availability over a short period of time on the growth and survival of seedling populations of a shade-tolerant species. The consequence of this change for the population dynamics and the management of *Chlorocardium* is discussed.

## Methods

### Study site

The study was conducted between 1991 and 1995 in the 1200 ha Ecological Reserve of the Tropenbos-Guyana Programme, located in the DTL timber concession *c.* 20 km south of Mabura Hill, central Guyana (5°13' N, 58°48' W). Average rainfall and temperature in the area are 2700 mm and 27°C, respectively (Jetten 1994). Rainfall follows a bimodal pattern with maxima in May-July and in December (Jetten 1994). The soil types in the area belong to one of two major groups: a group of clayey Plinthosols and a group of sandy and loamy soils of various types (Jetten 1994, Van Kekem *et al.* 1997). In the study area large undisturbed tracts of forest lie alternated with patches of logged-over though recovering forest. The vegetation of the area is classified as Evergreen Rain Forest (Mixed Forest) and Dry Evergreen Forest (ter Steege *et al.* 1993, 1996). The distribution of species and forest types respond strongly to the distribution of soil types (Davis & Richards 1934, Fanshawe 1952, ter Steege *et al.* 1993, Jetten 1994). The resultant communities are frequently dominated by one or a few species.

### Study species

*Chlorocardium rodiei* (Schomb.) Rohwer, Richter & v.d. Werff (Lauraceae, Greenheart) is a large canopy tree that is (co-) dominant in *Eschweilera-Licania* forest which occurs on brown sandy soils in Central Guyana (Fanshawe 1952, ter Steege *et al.* 1993). Furthermore it is common on laterite soils. The species is classified as a shade tolerant species requiring small gaps for its growth (ter Steege *et al.* 1994). Large individuals are often dispersed in clumps on gentle hill slopes, locally called 'reefs'. The species is nearly endemic to Guyana (ter Steege 1990). Flowering is annual, mainly in March-June (ter Steege & Persaud 1991); seed dispersal is barochorous with an unknown amount of secondary dispersal (Hammond *et al. in prep.*), mainly in February-May (Chapter 5). The seeds have an unusual, slow, germination behaviour. They germinate between 3 and 36 months after dispersal (Chapter 5). The growth of seedlings and adults is very slow (Chapter 6).

### Plot description

Growth and survival of *Chlorocardium* seedlings were studied between 1992 and 1995 in a 0.9 ha plot in a *c.* 4 ha tract of forest on brown loamy sand (classified as Ferralic Arenosol to Haplic Ferralsol) that was logged, in its primary state, in 1988. The average logging intensity for the entire tract and the plot was 19.5 and 21.1 trees ha$^{-1}$, respectively, representing a basal area of *c.* 6.6 and 8.1 m$^{2}$, respectively. Of all logged trees, 89% were *Chlorocardium*, and logging removed 56 and 49%, respectively, of the entire adult *Chlorocardium* population (defined as trees > 20 cm diameter at breast height, dbh). This logging intensity is high, but frequently observed in patches logged by traditional methods in the DTL concession area (R.J. Zagt, *unpublished data*) or elsewhere in Guyana (Bartica triangle, 19.3 stumps ha$^{-1}$ over 101 ha, Clarke 1956). There was no continuous canopy left in the plot, except in a number of small forest islands. The remaining stand of the 0.9 ha study plot after 7 years of regrowth contained 442 trees ≥10 cm dbh, with a basal area of *c.* 30.7 m$^2$. The canopy height of the secondary vegetation that established in the logging gaps varied between 6 and 8 m at that moment (1994).

### Habitat classification

The study plot was very densely vegetated, and therefore physically subdivided in ten 30 m by 30 m quadrates with cut lines which allowed access to all parts of the plot. A 2.5 m buffer zone around each line was excluded from the plot in order to avoid possible edge effects due to the increased access of light to the understorey. This reduced the effective plot size for seedling measurements to *c.* 0.6 ha. The structural environment of the study plot was mapped, and its area determined. Four different habitat types were distinguished, related to the impact of logging on vegetation and soil:

1 skid-trails, trails that were used by skidders to drag logs from the stump to the log loading bay from where they were transported onwards. These trails were devegetated as a result of skidding, and the soil was heavily disturbed (turned up, compacted). Colonisation of skid trails was primarily by pioneers and light demanding nonpioneers that establish after logging.

2 regrowth, areas where the canopy layer had disappeared but where the seedling and sapling bank nor the soil were disturbed. The amount of dead wood in the form of fallen trunks could be very high in regrowth areas. These areas were colonised by a very dense vegetation mainly consisting of pre-established seedlings and saplings.

3 tree-crowns, areas where crowns of cut or fallen trees came down and had buried the seedling bank. The difference with regrowth is that the development of secondary vegetation was arrested due to the high mass of leaves and branches.

4 remnant forest, patches where the original forest structure and the soil had remained intact, although light from adjoining logging gaps had locally stimulated the growth of pre-established seedlings and saplings.

All stumps were mapped.

### Distribution of seeds and seedlings around adults

In April-May 1992, all *Chlorocardium* individuals in a height range of 0.65-1.60 m in the plot were located, marked and mapped in a grid of 5 m by 5 m. Similarly, individuals in a height range of 0.01-0.65 m were mapped in a grid of 2.5 m by 2.5 m in an area of effectively 0.25 ha formed by four quadrates in the plot (May 1992, Fig. 1). All these individuals (0.01-1.6 m) are called seedling throughout this paper. The number of freshly fallen seeds per 5 m by 5 m subplot was determined once in the entire plot (May 1995). The distance between the centre of each grid cell and the nearest surviving adult and stump was calculated and classified in distance classes with a class width equal to the length of the grid-cell diagonal (3.5 m for the 2.5 × 2.5 m grid, 7.1

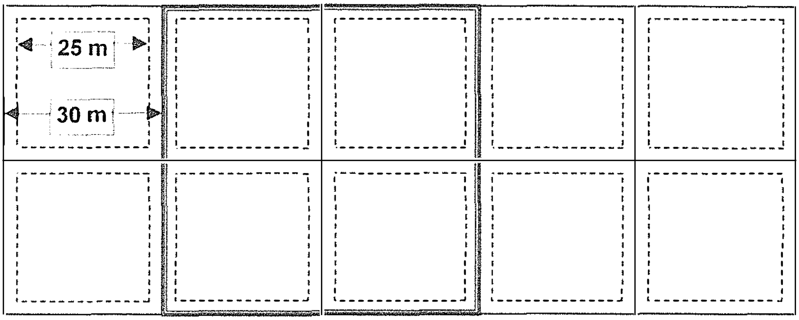

**Figure 1**
**Lay-out of the study plot in logged forest. The drawn lines represent the cut trails surrounded by a buffer zone of 2.5 m. The actual area inventoried is bordered by broken lines. The quadrates surrounded by triple borders were inventoried for *Chlorocardium* seedlings <0.65 m height.**

m for the 5 × 5 m grid). Seed and seedling distributions around stumps and surviving adults were determined, and comparisons between these two were made for a sample of grid cells that excluded grid cells that were at the same time within the seed shadow of a surviving adult and a stump. This limit was empirically determined at *c.* 14 m, based on the distribution pattern of freshly fallen seeds. Differences in seedling density around stumps and surviving adults were compared with Mann-Whitney unpaired rank tests.

### Three-year growth and survival

For each seedling between 0.65-1.60 m the following parameters were recorded: height till the highest meristem (main stem or branch, whichever was higher), number of leaves, number of branches, presence of cotyledons, and evidence of traumatic reduction in height, caused by, *e.g.*, breakage through branch fall. From stem height and leaf number, leaf density was calculated as the number of leaves per unit stem length (N of leaves per decimetre). The habitat of each seedling was recorded as one of the four habitat categories described above. In addition, the light climate in which the seedling was growing was characterised with the Dawkins crown index (Dawkins & Field 1978, Clark & Clark 1992, Chapter 6), a visual estimate of direct light availability. Due to the lack of seedlings with high Dawkins indices, we pooled Dawkins indices 1 and 2l (no direct light or some lateral light) and indices 2m-4 (medium amount of direct lateral light to full overhead light) for analysis. However crude, the index was demonstrated to correlate well with growth in *Chlorocardium* seedlings (Chapter 6).

The seedling population censuses were repeated yearly between 1992 and 1995 in the months April-May. At each census, the seedlings were re-measured, mortality was scored and new recruits were added to the measuring population. A small part (10%) of the plot was not measured in 1992, so 1993 is the first census with complete data on the distribution of seedlings, and these data were used for seedling distribution and morphological comparisons.

Growth and mortality rates of the seedling population in the logged plot were compared with a seedling population growing in an undisturbed plot that was studied previously (Chapter 6), about 2.5 km away from the logged plot. The soil and vegetation of this plot belong to the same type as the logged plot before exploitation, although the logged plot was somewhat more sandy and contained more species of a neighbouring forest type (Wallaba Forest on white sand *cf.* ter Steege *et al.* 1994), which was evident from a higher abundance of *Eperua falcata* in the logged plot than in the undisturbed plot. The density of adult *Chlorocardium* (prior to logging) was similar (logged: 41 trees ha$^{-1}$, undisturbed 38 trees ha$^{-1}$).

The size range and measuring procedures for the undisturbed *Chlorocardium* population were identical to the logged population, with the exception of habitat. Distinction was made between closed forest and regrowth, where regrowth consisted of a *c.* 0.25 ha (12%) large area in the undisturbed plot that had experienced major canopy disturbance and that resembled the regrowth habitat category in the logged plot in having a secondary canopy with comparable vegetation structure. Closed forest occupied *c.* 72% in 1994. Seedlings not belonging to these two habitat categories (*e.g.*, in gaps, 6%, or older building phase forest, 10%) were included for calculation of average growth and survival rates only, but not for tests for differences in growth and survival between the logged and undisturbed plots (see below).

Seedling height and leaf growth rates and survival probability in both plots were calculated following the procedures described in Chapter 6. Excluded from the analysis of growth and survival were seedlings that died after one enumeration, seedlings that recruited after the third enumeration, seedlings that suffered reductions in height as a result of traumatic damage or die-back, as well as seedlings with a very inconsistent growth pattern, *e.g.,* a large increase followed by a large decrease. Traumatic individuals (9.5% in logged, 18.5% in undisturbed plot over 3 years) were excluded because their growth did not reflect a functional response to resource availability, and because their immediate mortality was likely under-estimated (if the seedling was already decayed at recensus).

The growth rate was calculated as the regression coefficient of the linear regression of height or leaf number against time over the entire period (1-3 year) that the seedlings were present in the sample, rather than calculating yearly growth rates. This was done because growth was very slow in these seedlings, and therefore the influence of measuring errors relatively large. This lead to apparently large fluctuations in yearly growth rate in the same individuals. This effect is enhanced by the occurrence of discontinuous growth, with a large height increase and many new leaves in one year and no growth in the next year.

Survival was calculated as 3 year survivorship, including only seedlings that were present at the first enumeration. Although overall survivorship is also reported, analysis of survival was only done on the sample of seedlings for which growth was known (*i.e.* excluding seedlings that were present during a single enumeration).

The objective of the field study was to determine whether there were (1) differences in morphology, growth and survival of *Chlorocardium* seedlings between the logged and undisturbed plots and (2) differences between habitat types and sites within the seed shadow of surviving versus logged *Chlorocardium* adults. The size and morphology of *Chlorocardium* seedlings were compared between the logged and undisturbed plot, and within the logged plot, between habitat categories and between seedlings growing closer to stumps *vs.* seedlings growing closer to surviving adults. Comparisons were made with Mann-Whitney unpaired rank tests (simple contrasts) or Kruskal-Wallis anova (habitat type), using the 1993 census as the basis for comparison.

Height and leaf growth were studied with linear multiple regression models containing continuous and dummy variables. Lines were fitted with least squares regression. The difference between the logged and undisturbed plot was tested by fitting a model containing variables for initial plant size (height and leaf density at the first measurement, natural log transformed), presence of cotyledons, light (the two pooled Dawkins index classes), plot, habitat and the interactions plot × plant-size, plot × light and plot × habitat. The Dawkins index at the last census that a seedling was present was used for analysis. Although some gaps were created in the undisturbed plot (2.7% of the area over three year), this adequately described the Dawkins index of most seedlings throughout the study period. The light environment at seedling level in the logged plot was dark and not variable (in terms of Dawkins index). Only seedlings growing in habitats characterised as forest remnant (mature forest) and regrowth were incorporated in the comparison between the logged and undisturbed plots, so differences in seedling growth could be interpreted as an effect of logging (or plot) rather than different habitat composition within the plots.

Within the logged plot, the significance of the factors habitat (three dummy variables representing the four habitat types) and stump (a dummy variable that was '1' if the nearest adult was a stump and '0' if it was a surviving adult) was evaluated against models containing a constant, or a constant and the parameters for plant size (stem height, leaf density and presence of cotyledons), and/or light. In this way it could be assessed whether the effect of habitat or stump was an independent effect, or merely an effect of habitat associated differences in light availability, or initial plant size. The effect of adding a variable was tested with a variance ratio test. The ratio of the increase in explained variance of the model divided by the number of variables added, and the residual mean square error of the complete model was evaluated against an F-distribution with $p$ and N-$q$-1 degrees of freedom, where $p$ is the number of variables added to the model, N the total number of observations, and $q$ the total number of variables. It was necessary to natural log transform (absolute) height and leaf growth before analysis to ensure that the residuals were distributed normally.

The same procedures were repeated for survivorship. Survivorship was studied with multiple logistic regression, and the effect of adding a factor was quantified as the increase in likelihood of the model. The response variable was the logit of the probability of survival. The parameter coefficients were estimated by a quasi-newton procedure that minimised the negative log likelihood function of the model. The difference in log likelihood of models with and without the variable of interest was tested as -0.5 × $\chi^2$, with df. equal to the number of estimated parameters.

### Field experiment 1: the effect of light on growth, morphology and germination

The light conditions at ground level in exploited forest change rapidly in the first years after logging. The effects of light environment, age and morphology (leaf density) on growth were tested in a field experiment which was carried out near the undisturbed plot. In the forest nine experimental sites representing three stages in the forest cycle were identified: three recent gaps (of which two were very small), three gaps with a dense layer of *c.* 1-3 m high saplings, and three forest understorey sites, all within *c.* 3 ha of forest. Each site was circular with a radius of 5 m. At 15 positions per site (N=135), randomly determined in a 1 × 1 m grid, one wel-established seedling aged more than one year, one recently germinated seedling, and four seeds were implanted in a triangle with sides of *c.* 0.6 m. Old *Chlorocardium* seedlings were grown from seed in March 1990 in 2.5 L plastic bags which were left for 15 months in a nursery in a large clearing where light was reduced to 50% of the ambient light. In June 1991, when the transplantation took place, the seedlings were *c.* 0.40 m tall. They were divided into three groups according to their stem height and branch number. An equal number of seedlings from each size group was assigned to each site. The potting bag of each seedling was carefully cut, and the seedlings were planted with most of the potting soil attached (in order not to damage the roots). Because the seedlings had likely exhausted the potting medium they were given a single dose of NPK fertiliser after planting and left to acclimate for six months. The newly germinated seedlings were collected from the surrounding forest. They were less than 2 months old, had 2-4 leaves and no leaf losses, and were not lignified yet. Because they were germinating in the understorey, their height was not much less than the old seedlings (0.25-0.30 m). The seeds were introduced in April 1992, because in June 1991 there was insufficient fresh seed available.

The first measurement was in January 1992, followed by measurements in July 1992 and September 1993. All measurements were non-destructive. The following variables were measured: stem length, length of all branches, and number of leaves. From these, branch and leaf density, and stem, leaf and total (stem + branch) length growth were determined as before. The light environment of each seedling was quantified with hemispherical photography (Whitmore *et al.* 1993, ter Steege 1996) at each site at the end of the measuring period. On three uniformly overcast days, black and white photographs (125 ASA, a red filter was used for improved contrast) were taken at 65 cm height in the middle between the two seedlings at each position with a levelled camera mounted with a fisheye lens. The images were scanned at 350x350 pixels and canopy openness was determined with the program Winphot 5.0 (ter Steege 1996).

Although the experiment was set up as a nested design, it became clear that true replication of gap size (light environment) and developmental stage of the regenerating vegetation was impossible, even within the experimental sites as a result of internal gap

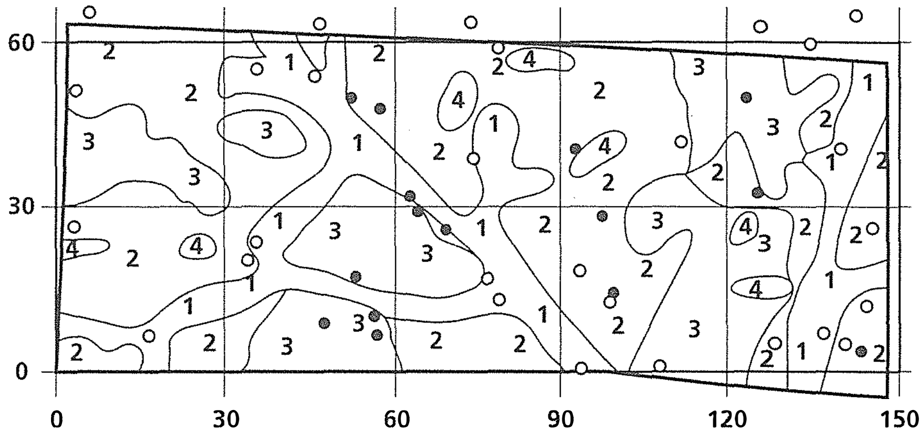

**Figure 2**
**Distribution of stumps and habitat types in the logged plot near Mabura Hill.**

heterogeneity. Instead, the plant sites were considered as sampling units, not the experimental sites. The data are analysed with multiple regression analysis as described above. A high correlation between seedling age and leaf density made the results of multiple regression analysis involving both seedling types simultaneously very unstable. Instead, the data were analysed separately for the young seedlings and the old seedlings, and any differences observed between the two age groups can not be formally supported in statistical terms. Height growth rate, leaf growth rate and survival were related to height and leaf density at the first measurement and canopy openness. The signed natural log of absolute height growth and the signed square root of absolute leaf growth were used for analysis.

The germination of seedlings (defined as the extension of a shoot) was scored five times till January 1993, 41 weeks after seeding. At that time 74% of all seeds had shown a relevant response (dead or germinated). For each sampling unit (4 seeds) it was determined how many seedlings had developed a shoot (including seedlings that had died subsequently), and how many had died, and the probability for each sampling unit to have 4, ≥3, ≥2 or ≥1 shoots and surviving individuals, respectively, after 41 weeks was regressed against ln (canopy openness) with logistic regression.

### Field experiment 2: the effect of habitat type on germination

Possible differences in germination of *Chlorocardium* between habitat type was studied in a germination experiment. In the same tract of logged forest where the logged plot was located, the vegetation was classified in habitat types as described above. Two by two meter germination plots were randomly positioned in areas previously classified as regrowth (4 plots), forest remnant (4) and skid trail (5), and additionally in three large gaps in the logged area that were recently opened by clearing secondary vegetation on skid trails (3 plots). This last type was added to obtain information of germination in a situation that is typical for the period just after logging, when there is

**Table 1**

**Distribution and density of *Chlorocardium* seeds around adults in the logged plot near Mabura Hill, Guyana, in May 1995, and hypothetical distribution and number of seeds before exploitation, if the same pattern of seed distribution is assumed. Seed density is expressed per grid cell of 25 $m^2$.**

| | Around surviving adults | | | | | | Around adults and stumps | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Distance to adult (m) | Plots | | Plots with seeds | | Seeds | | Plots | | Expected N of | |
| | N | % | N | % | N | Density | N | % | Plots with seeds | Seeds |
| 0 - 7.1 | 83 | 23.1 | 69 | 83.1 | 576 | 6.9 | 170 | 47.2 | 141.3 | 1179.8 |
| 7.1 - 14.1 | 122 | 33.9 | 34 | 27.9 | 134 | 1.1 | 165 | 45.8 | 46.0 | 181.2 |
| 14.1 - 21.2 | 75 | 20.8 | 1 | 1.3 | 3 | 0.0 | 25 | 6.9 | 0.3 | 1.0 |
| >21.2 | 80 | 22.2 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 0.0 | 0.0 |
| | 360 | | 104 | 28.9 | 713 | 2.0 | 360 | | 187.6 | 1362.0 |

little vegetation. There were no germination plots in tree crown habitat. In April 1993, in each germination plot 16 freshly fallen *Chlorocardium* seeds were introduced and left to germinate. Mortality and germination (defined as before) were scored at approximately monthly intervals between June 1993 and April 1994 (53 weeks after introduction; 11 measurements). Differences in survival and germination per habitat type at the last measurement were tested with one-way anova on square root transformed numbers of survivors and germinated seedlings, respectively, per germination plot. Seed removal, presumably by *Myoprocta acouchi* (Red Acouchy) and other rodents (Hammond *et al. in prep.*), was also scored and tested in the same way. The open gaps had a canopy openness of *c.* 30% (Houter 1997); the openness of the remaining plots was not measured, but they were all very dark (canopy openness probably all <3%).

All statistical analysis was done with the Statistica package (Statsoft Inc. 1993).

## Results

The distribution of stumps and habitat types is given in Fig. 2. There were 18 *Chlorocardium* and 4 other trees felled in this area, of which 16 were removed. There were 19 surviving *Chlorocardium* adults left, most of which were rejected by the fellers because they were hollow, crooked, forked *etc.* Forty-nine percent of the plot area was classified as regrowth, 27% as remnant forest, 20% as skid-trail and 4% as tree crown habitat.

### Distribution of seeds around adults

During the survey of May 1995, a total of 713 freshly fallen seeds was registered in the plot (Table 1). The distribution pattern was strongly contracted around the surviving adult trees in the plot, with very few seeds found beyond 14 m from the parent bole. Taking this pattern as a base for estimation, the theoretical reduction in seed

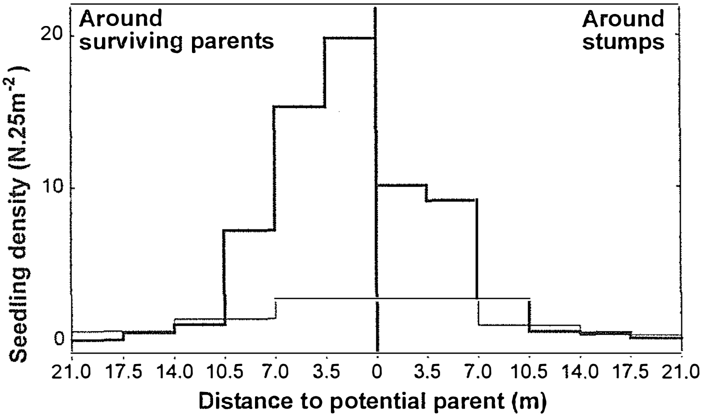

**Figure 3**
Distribution of *Chlorocardium* seedlings around surviving parent trees (left side) and stumps (right side) in a logged area near Mabura Hill, Guyana. Bold lines: seedlings <0.65 m height; thin lines: seedlings 0.65-1.60 m height. Seedling density was sampled at different grid cell sizes, but is expressed per 25 m$^2$. Only plots within 14 m from one parent category and more than 14 m from the other parent category are used. Gridcells used around stumps: n=37 (large seedlings) and 145 (small seedlings). Around surviving adults: n=64 and 113 grid cells. Note the difference in width of distance classes between small and large seedlings.

number and distribution in the study plot due to logging was 52% and 55%, respectively, compared to the pre-logging situation (Table 1). This is about the same as the reduction in number of parents (49%). The estimate does not take into account the effects of parent size or possible changes in reproduction caused by the opening of the canopy by logging. A relation between parent size and reproductive output could not be demonstrated in a limited field study due to high inter-individual variability in seed production and overlapping seed shadows (M. Berkhout, K. Stelma & R.J. Zagt, *unpublished results*).

### Seedling distribution around adults

Seedling distribution around parents was studied for large seedlings (≥0.65 m) in the entire plot (0.9 ha) at a large grid cell size (5 × 5 m), and for small seedlings (<0.65 m) in the smaller subplot (0.25 ha) at a reduced grid cell size (2.5 × 2.5 m). Seedling density dropped off rapidly with increasing distance to the nearest potential parent (Fig. 3). The seedling density was highest below the (former) crown (7 m or less from the bole). The seedling distribution in the plot was still strongly affected by the seed shadows left around logged trees: the density of large seedlings per grid cell within 14 m around stumps was even not different from density around surviving adults (Fig. 3; cells within 14 m of both a stump and a survivor were excluded; Mann-Whitney unpaired ranks test Z=1.06, p=0.29, N = 113 (cells around stumps) and 64 (surviving adults)). The density of small seedlings was much lower around stumps than around

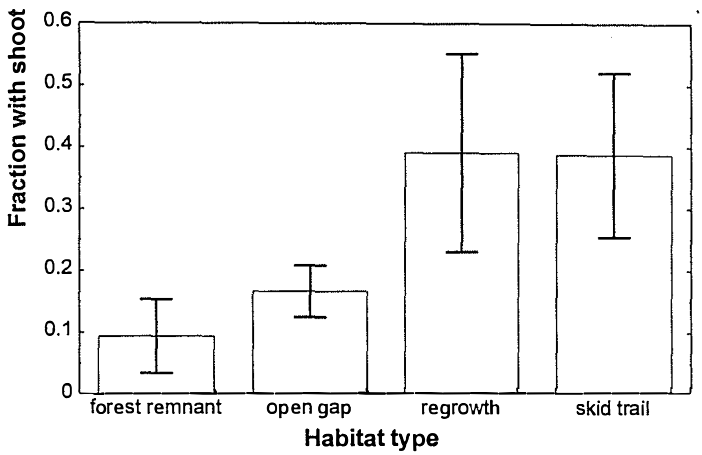

**Figure 4**
**Germination (± se) after 53 weeks of *Chlorocardium* seeds per habitat type in a logged forest near Mabura Hill, Guyana. n=3-5 replicates of 16 seeds per habitat type. The fraction germinating seeds was not different between habitat types (one-way anova p>0.05).**

surviving adults (Mann-Whitney unpaired ranks test Z=3.34, $p<0.001$, N = 110 (cells around stumps) and 136 (surviving adults)).

### Germination

There was no relation between 41 week seed germination or survival and canopy openness in field experiment 1, as determined by logistic regression of germination or survival and openness (effect of addition of ln (openness) to a model with a constant only; both $\chi^2 <1.6$, $p>0.21$, n=134). At each sampling site of 4 seeds, there were 1.8 ± 0.1 surviving seeds left at that time (46%; including the germinated seeds), and 0.9 ± 0.1 (s.e.) seeds had produced a shoot (22%).

Germination after 53 weeks in experiment 2, in which seeds were germinated in plots that were distributed over the various habitat types in logged forest, was 27±6% over the 16 sites. The large variation in germination and survival was not related to habitat type (one-way anova germination $F_{3,12}=1.5$; survival $F_{3,12}=1.9$, $p>0.05$ in both cases, Fig. 4). A major source of seed loss was removal by rodents, which accounted for 25-94% of treatment totals in experiment 2. Although there was no difference in removal rate between habitat types ($F_{3,12}=1.1$, $p>0.05$), seed removal by rodents certainly contributed locally to differences in germination percentage. The fate of seeds that were removed outside the germination plot could not be monitored.

### Patterns of seedling abundance, size and morphology between plots, habitat types and nearest adult types in the logged forest

Seedling abundance seemed to be higher in the logged than in the undisturbed plot, despite the reduced adult density in the former (Table 2). There were strong differenc-

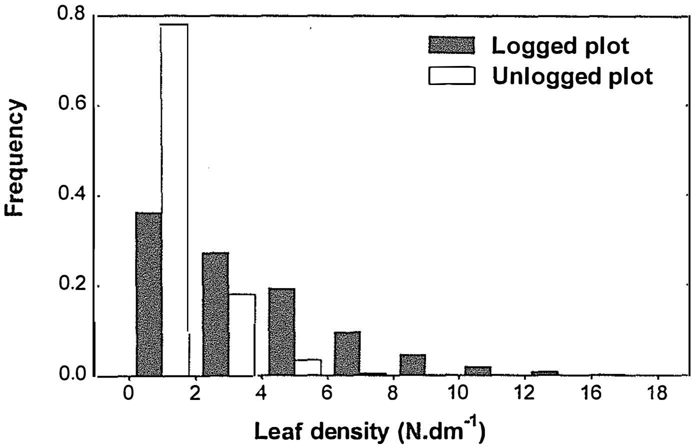

**Figure 5**
**Comparison of the distribution of leaf density in *Chlorocardium* seedlings in a logged and undisturbed area near Mabura Hill, Guyana in 1993. n=842 (undisturbed plot) and 458 (logged plot).**

es in height, number of branches and number of leaves between seedlings growing in both plots (Table 2). The seedlings in the logged plot were on average about 2.5 times as large as seedlings in the undisturbed plot in all these aspects, except height. The difference in branch and leaf density were not only present in the mean, but also in the range: seedlings with leaf density >4 $\mathrm{dm}^{-1}$ were virtually absent in the undisturbed plot, but frequent in the logged plot (4 *vs.* 36% of all seedlings, Fig. 5).

The seedlings were not randomly distributed over the four habitat types ($\chi^2 = 53.8$, d.f.= 3, $p<0.001$), but were over-represented in areas classified as regrowth, and under-represented in remnant forest patches (Table 3). A substantial number of seedlings apparently survived the physical impact of logging because they grew closely to stumps on skid trails.

There were no differences between habitat types in seedling height, leaf number and leaf density (Kruskal-Wallis anova $H<1.8$ in all cases, $p>0.61$, n=458), but there was difference in branch number and branch density ($H>9.1$ in both cases, $p<0.03$, n=458). Seedlings growing in skid-trails and regrowth had a higher number of branches and branch density than remnant forest and tree crowns (Mann-Whitney unpaired ranks test $Z>2.8$ in both cases, $p<0.01$, n=458). In contrast, there were highly significant differences in these characters between individuals growing nearest to stumps and individuals growing nearest to surviving adults (Table 2). This was paralleled by a significant difference in Dawkins index between these seedlings (Mann-Whitney unpaired ranks test, Z=3.2, psurvivor).

## Changes in morphology, and growth and survival between plots

For surviving seedlings, leaf density remained constant in the undisturbed plot throughout the study period, but in the logged plot it steadily decreased (Fig. 6), even

**Table 2**

**Comparison of seedling density and some morphological characters between the logged (n=458) and the undisturbed plots (n=842, top) and between individuals growing closer to stumps (n=235) and closer to surviving adults (n=223; bottom, only in the logged plot). All data are from 1993. Means (s.e.) of morphological characters are reported. All differences were highly significant (p<0.001, Mann-Whitney unpaired ranks test), except height difference between stump and adult (p<0.01).**

| | Undisturbed plot | | Logged plot | | |
|---|---|---|---|---|---|
| | Mean | s.e. | Mean | s.e. | Ratio logged/non-logged |
| Seedling density (N $ha^{-1}$) | 437 | | 747 | | 1.7 |
| Height (cm) | 80.9 | (0.6) | 89.3 | (0.9) | 1.1 |
| N of branches | 2.4 | (0.1) | 6.2 | (0.2) | 2.6 |
| Branch density (N $dm^{-1}$) | 0.3 | (0.0) | 0.7 | (0.0) | 2.4 |
| N of leaves | 12.2 | (0.5) | 32.9 | (1.3) | 2.7 |
| Leaf density (N $dm^{-1}$) | 1.4 | (0.0) | 3.6 | (0.1) | 2.6 |

| | Near to stump | | Near survivor | | |
|---|---|---|---|---|---|
| | Mean | s.e. | Mean | s.e. | Ratio stump/survivor |
| Height (cm) | 91.7 | (1.2) | 86.9 | (1.2) | 1.1 |
| N of branches | 7.1 | (0.2) | 5.4 | (0.2) | 1.3 |
| Branch density (N $dm^{-1}$) | 0.8 | (0.0) | 0.6 | (0.0) | 1.3 |
| N of leaves | 39.8 | (2.0) | 26.2 | (1.5) | 1.5 |
| Leaf density (N $dm^{-1}$) | 4.2 | (0.2) | 3.0 | (0.2) | 1.4 |

**Table 3**

**Seedling density per habitat type of *Chlorocardium* (≥0.65 m) in a logged area near Mabura Hill, in 1993.**

| Habitat type | N of seedlings | Density (N $m^{-2}$) |
|---|---|---|
| Skid-trail | 108 | 0.09 |
| Regrowth | 308 | 0.10 |
| Remnant forest | 71 | 0.04 |
| Tree-crown | 33 | 0.14 |
| Total | 520 | 0.08 |

though seedling height in both areas increased. The same pattern as for leaf density was observed for branch density (data not shown).

Seedlings in the logged plot lost as much as eleven leaves per year but had a high, however gradually decreasing yearly survivorship, whereas seedlings in undisturbed

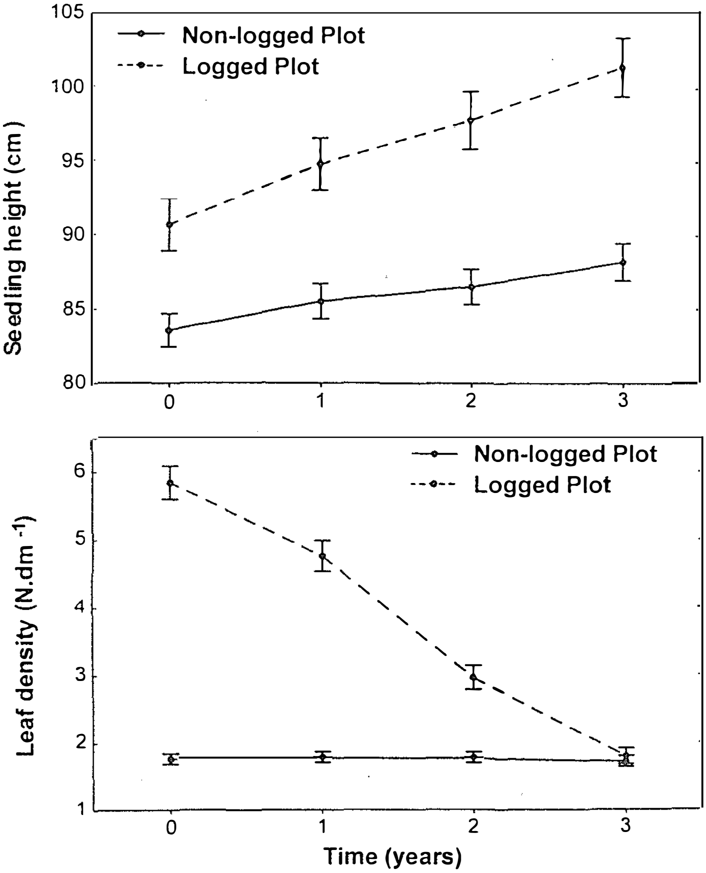

**Figure 6**

**Mean (± se) height (above) and leaf density (below) of *Chlorocardium* seedlings in a logged and undisturbed area near Mabura Hill, Guyana over three years. n=289 (undisturbed plot) and 145 (logged plot) seedlings that survived throughout the measuring period.**

plot had an approximately constant leaf number and a gradually increasing survivorship (Table 4, Figs. 6, 7). Seedling height growth was low in both plots, however slightly higher in the logged plot. In the logged plot, very few individuals showed an increase in both height and leaf number, and leaf and height growth were not correlated (Table 4).

Seedlings in those areas in the logged and the undisturbed plot which had a comparable habitat structure (closed forest sites and sites in gaps with regrowth) had a barely different height and leaf growth, when the effects of light and morphology were accounted for (Table 5a). Although there were no main plot effects, the response of height growth to light was different between the logged and the undisturbed plot, and the same was true for the effect of cotyledons. The light was very low and little variable in the forest and gap understorey sites in the undisturbed plot, so there was no significant relationship between light and growth there. It is stressed that the explanatory

**Table 4**
**Average annual growth rates for *Chlorocardium* in logged and unlogged tropical rain forest near Mabura Hill, Guyana. Growth rates are regression coefficients of seedling height or leaf number against time, with 2-4 observations per seedling. Seedlings with recorded stem breakage were excluded. Height and leaf growth were significantly different between plots (at $p<0.001$) as determined by t-tests. Correlation is Pearson correlation coefficient between height and leaf growth (performed on log-transformed data). Significant correlation coefficients are indicated with asterisks: ***$p \leq 0.001$; ns $p>0.05$. In the last column is the percentage seedlings that had a positive height growth and a stable or increasing number of leaves.**

| Site | N | height growth average ± SE (cm $y^{-1}$) | leaf growth average ± SE (N $y^{-1}$) | correlation | % growing individuals |
|---|---|---|---|---|---|
| Logged plot | 407 | 3.2 ± 0.2 | -11.4 ± 0.6 | $0.04^{ns}$ | 7 |
| Undisturbed plot | 723 | 2.0 ± 0.1 | -0.2 ± 0.1 | 0.16*** | 40 |

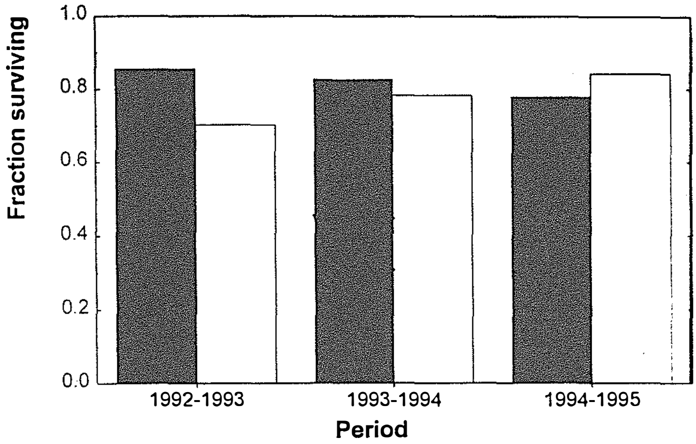

**Figure 7**
**Survivorship per census interval of *Chlorocardium* seedlings in logged (filled bars) and undisturbed (open bars) tropical rain forest near Mabura Hill, Guyana. Initial population sizes were n=310, 408 and 388 for the logged plot, and n=665, 654 and 715 for the undisturbed plot.**

power of the variables describing height growth was very low. In contrast to height growth, the $R^2$ for leaf growth was higher, and the effect of light was strongly significant. The effect of light was different between the two plots, as well as the effect of leaf density.

In the same seedling sample, there were no differences between patterns of seedling survival in both plots, except for the effect of leaf density. The positive effect of leaf density on survival was less in the logged plot than in the undisturbed plot, and the effect of cotyledons was opposite in both plots (Table 5b)

**Table 5**

**Partial correlation between plant and habitat characteristics and height and leaf growth (a), and regression coefficients for the relation between these variables and survival (b) for *Chlorocardium* seedlings growing in closed forest and regrowing gap sites in the logged and undisturbed plots, determined with multiple regression (growth) and logistic regression (survival). The dummy variables used are Dawkins index (two dummies), plot (0-unlogged plot, 1-logged plot) and habitat (0-regrowth, 1-closed forest). For logistic regression, the coefficients for the dummies are given for each level of the underlying variable separately. The joint effect of the dummies representing the same underlying variable were not significant in any case. Asterisks give the level of significance of the partial correlation coefficients: ***p≤0.001; **p≤0.01; *p≤0.05; no symbol: not significant. n=863 seedlings.**

| a | Height growth | Leaf growth |
|---|---|---|
| Ln-initial height | 0.01 | 0.01 |
| Ln-initial leaf density | 0.12 *** | -0.03 |
| Cotyledons | 0.12 *** | 0.05 |
| Dawkins index | 0.06 | 0.19 *** |
| Plot | 0.00 | -0.05 |
| Habitat | -0.02 | 0.01 |
| Plot × Leaf density | -0.01 | -0.22 *** |
| Plot × Cotyledons | -0.08 * | -0.03 |
| Plot × Dawkins | 0.08 * | 0.10 * |
| Plot × Habitat | -0.02 | 0.06 |
| $R^2$ | 0.08 *** | 0.58 *** |

| b | 3 yr Survival |
|---|---|
| Constant | -14.43 *** |
| Ln-initial height | 2.89 *** |
| Ln-initial leaf density | 3.39 *** |
| Cotyledons | 0.67 |
| Dawkins 2l | 0.09 |
| Dawkins 2m-4 | 0.10 |
| Plot | -0.02 |
| Habitat | 0.00 |
| Plot × Leaf density | -2.10 * |
| Plot × Cotyledons | -0.82 |
| Plot × Dawkins 2l | -0.29 |
| Plot × Dawkins 2m-4 | 1.20 |
| Plot × Habitat | 0.36 |
| $\chi^2_{11}$ | 116.4 *** |
| N | 543 |

### The effect of habitat heterogeneity on growth and survival in the logged plot

Seedlings growing in different habitat types showed a different height growth rate, but sequential fitting of different regression models indicated that this difference was largely attributable to differences in light between these habitat types (Table 6a). However, the effect of habitat type on leaf growth remained highly significant even after inclusion of the variables plant size (initial stem height, leaf density and presence of cotyledons) and light. The effect of habitat type was due to the difference between regrowth and the other three types, with leaf growth of seedlings growing in regrowth areas being reduced by 0.5 ln units compared to the remaining seedlings. The strongest correlates of height growth in the full model were leaf density (partial correlation coefficient P*r*=0.26, p<0.001) and light (P*r*=0.19, p<0.001), and for leaf growth it was leaf density (P*r*=-0.48, p<0.001), followed by habitat type (P*r*=0.22, p<0.01) and light (P*r*=0.15, p<0.001).

**Table 6**

**Effect of fitting habitat heterogeneity to sequential (a) multiple regression models of height and leaf growth and (b) logistic models of the probability of survival of *Chlorocardium* seedlings in the logged plot. The effect is tested of adding the variable for habitat structure (HABITAT) to models already containing plant characteristics (PLANT: initial height and leaf density, presence of cotyledons), LIGHT (Dawkins index), and identity of the nearest parent (STUMP: stump or surviving adult). n=408 (growth), 249 (survival), df for the F-test varies between (3,404) and (3,398), for the $\chi^2$-test it is always 3.**

| a | Height growth | | | | Leaf growth | | | |
|---|---|---|---|---|---|---|---|---|
| Model | $R^2$ | F | $F_{change}$ | p | $R^2$ | F | $F_{change}$ | p |
| HABITAT | 0.03 | 4.6 | 4.6 | <0.01 | 0.07 | 10.0 | 10.0 | <0.001 |
| PLANT | 0.09 | 13.0 | | | 0.21 | 34.8 | | |
| PLANT, HABITAT | 0.12 | 9.1 | 4.9 | <0.01 | 0.26 | 23.6 | 10.1 | <0.001 |
| PLANT, LIGHT | 0.14 | 13.2 | | | 0.24 | 25.7 | | |
| PLANT, LIGHT, HABITAT | 0.16 | 9.3 | 2.6 | 0.053 | 0.28 | 19.7 | 7.5 | <0.001 |
| PLANT, LIGHT, STUMP | 0.16 | 12.6 | | | 0.26 | 23.3 | | |
| PLANT, LIGHT, STUMP, HABITAT | 0.17 | 8.9 | 1.5 | >0.05 | 0.30 | 18.6 | 7.0 | <0.001 |

| b | Survival | | |
|---|---|---|---|
| Model | $\chi^2$ | $\chi^2_{change}$ | p |
| HABITAT | 5.3 | 5.3 | 0.15 |
| PLANT | 38.2 | | |
| PLANT, HABITAT | 43.7 | 5.5 | 0.14 |
| PLANT, LIGHT | 39.9 | | |
| PLANT, LIGHT, HABITAT | 44.0 | 4.2 | 0.25 |
| PLANT, LIGHT, STUMP | 43.7 | | |
| PLANT, LIGHT, STUMP, HABITAT | 46.8 | 3.1 | 0.37 |

Similarly, there was a significant difference in height and leaf growth between individuals growing in the vicinity of stumps and of surviving adults, independent of the effects of plant size, habitat type and light (Table 7a). Individuals growing closer to a stump grew faster than individuals growing closer to a surviving adult. There was no distance effect; but just an effect of the state (logged or surviving) of the nearest adult *Chlorocardium* (recall that 93% of the total plot area was within 14 m from the nearest stump or surviving adult, Table 1).

**Table 7**
**Effect of fitting the effect of nearest adult identity (stump or survivor) stump to sequential (a) multiple regression models of height and leaf growth and (b) logistic models of the probability of survival of *Chlorocardium* seedlings in the logged plot. See Table 6 for further explanation.**

| a | Height growth | | | | Leaf growth | | | |
|---|---|---|---|---|---|---|---|---|
| Model | $R^2$ | F | $F_{change}$ | p | $R^2$ | F | $F_{change}$ | p |
| STUMP | 0.04 | 18.1 | 18.1 | <0.001 | 0.01 | 3.3 | 3.3 | >0.05 |
| PLANT | 0.09 | 13.0 | | | 0.21 | 34.8 | | |
| PLANT, STUMP | 0.12 | 13.1 | 12.5 | <0.001 | 0.23 | 30.0 | 12.7 | <0.001 |
| PLANT, LIGHT | 0.14 | 13.2 | | | 0.24 | 25.7 | | |
| PLANT, LIGHT, STUMP | 0.16 | 12.6 | 8.3 | <0.01 | 0.26 | 23.3 | 8.9 | <0.01 |
| PLANT, LIGHT, HABITAT | 0.16 | 9.3 | | | 0.28 | 19.7 | | |
| PLANT, LIGHT, HABITAT, STUMP | 0.17 | 8.9 | 5.0 | <0.05 | 0.30 | 18.6 | 7.4 | <0.01 |

| b | Survival | | |
|---|---|---|---|
| Model | $\chi^2$ | $\chi^2_{change}$ | p |
| STUMP | 6.7 | 6.7 | <0.01 |
| PLANT | 38.2 | | |
| PLANT, STUMP | 42.8 | 4.6 | <0.05 |
| PLANT, LIGHT | 39.9 | | |
| PLANT, LIGHT, STUMP | 43.7 | 3.8 | 0.050 |
| PLANT, LIGHT, HABITAT | 44.0 | | |
| PLANT, LIGHT, HABITAT, STUMP | 46.8 | 2.8 | >0.05 |

Seedling survival was not different between habitat types, and the state of the nearest adult was correlated with the survival probability only if only plant size or light were included in the model (Table 6b, 7b). The strongest correlate of survival was initial leaf density (data not shown, *cf.* Table 5).

### Field experiment 1: morphology, growth and survival in relation to light

In the field experiment, there were no qualitative differences between seedling height and leaf growth in relation to leaf density (at the start of the experiment) and canopy openness (Table 8), although the effect was stronger after 20 than after 6 months, for leaf growth than for height growth, and for one year old seedlings than for new seedlings. In contrast to the seedlings from the natural populations, there was a

**Table 8**

**Partial correlations between leaf density, canopy openness and the interaction between leaf density and canopy openness, and growth of stem length and leaf number in the field experiment, after 6 and 20 months. Asterisks give the level of significance: ***p≤0.001; **p≤0.01; *p≤0.05; no symbol: not significant.**

| | height growth (cm $y^{-1}$) | | leaf growth (N $y^{-1}$) | |
|---|---|---|---|---|
| Measurement | 6 months | 20 months | 6 months | 20 months |
| **Young seedlings** | | | | |
| Leaf density | -0.09 | -0.18 | -0.25 * | -0.24 |
| Openness | -0.14 | -0.16 | -0.08 | -0.26 |
| Leaf density × Openness | 0.09 | 0.20 | 0.17 | 0.38 * |
| $R^2$ | 0.04 | 0.05 | 0.09 | 0.29 ** |
| N | 77 | 41 | 77 | 41 |
| **Old seedlings** | | | | |
| Leaf density | -0.10 | -0.22 | -0.25 ** | -0.23 * |
| Openness | -0.11 | -0.23 * | -0.33 *** | -0.35 ** |
| Leaf density × Openness | 0.16 | 0.29 * | 0.39 *** | 0.43 *** |
| $R^2$ | 0.11 ** | 0.23 *** | 0.30 *** | 0.49 *** |
| N | 115 | 81 | 115 | 81 |

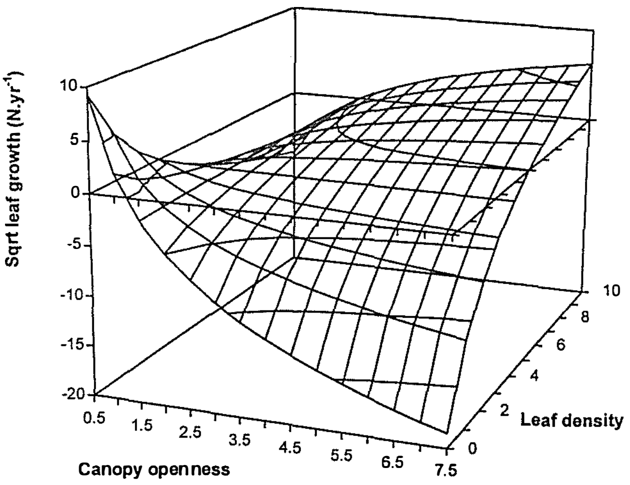

**Figure 8**

The modelled effects of leaf density and canopy openness on fitted leaf growth for one year old *Chlorocardium* seedlings in the field experiment (table 8). Leaf density was determined at the first measurement, and leaf growth was determined over 20 months thereafter. Leaf growth is given as the signed square root of absolute leaf growth. Note that the strongly negative predicted leaf growth values for seedlings with high light, low leaf density represent extrapolation given by the regression equation; they are not supported by data points.

strong interaction between the effects of light and leaf density on height and leaf growth. This effect compensated and dominated the negative effects of initial leaf density and canopy openness (these results suffered somewhat from moderately correlated initial leaf density (after 6 months of growth) and canopy openness for the old seedlings (r= 0.34; p<0.01; n=81); this was not the case for the young seedlings). A positive leaf growth rate was predicted only for those seedlings which had a low leaf density in low light environments, and a high leaf density in high light environments (illustrated for 1 year old seedlings in Fig. 8). Height growth was less responsive (because a negative growth response is not possible) but the pattern was comparable. There was no effect of initial height.

The number of branches per plant depended on the height of the plant, not on the light environment. This relation was found for younger plants at the end of the study, and for older plants at the first measurement (correlation between N of branches and ln plant height $r=0.25$, $n=42$ and $r=0.66$, $n=133$, respectively; $p<0.001$ in either case). However, 20 m later the number of branches for older plants was also dependent on the light environment: partial regression coefficients with N of branches were $Pr=0.75$ ($p<0.001$) for ln height, and $Pr=0.24$ ($p<0.05$) for ln openness; $F_{2,78}=94.1$, $R^2=0.71$, $p<0.001$. Only a relatively small portion of new stem and branch biomass was invested in growth of the main stem (*i.e.*, height growth): in fast growing individuals (>40 cm over 20 m; these had no branch losses) under high light, less than *c.* 20% of total net length growth took place in the main stem. Clearly, this percentage is higher in individuals with few branches or higher branch losses.

Survivorship of the older seedlings was strongly and positively affected by initial stem height and leaf density, but not by canopy openness (effect of ln(openness) on survival in a model containing ln(height) and ln(leaf density): $\chi^2=0.2$, $p>0.05$, $n=133$ for older seedlings, $\chi^2=0.5$, $p>0.05$, $n=110$ for younger seedlings).

## Discussion

The results of this study clearly indicate that there were substantial differences between the logged and undisturbed plots in terms of *Chlorocardium* morphology, growth and survival. Individuals in the logged plot were larger, had more branches and leaves, grew slightly faster in height than seedlings in the undisturbed plot and had, at least in the first year of the study, a higher survival rate. The most salient feature of the seedlings in the logged plot was their very high leaf loss rate (Fig. 6, Table 4) with the average leaf number per seedling dropping from 42.1 in 1992 to 15.7 in 1995. These results confirm that 4-7 years after exploitation, the logged plot had become a very dark environment for those seedlings that grow below the secondary canopy.

### Responses to the removal of adults

Apart from a reduced seed production in the plot, the removal of parents had a strong effect on the spatial distribution of seeds. The potential seed shadow (< 14 m from the parent) dropped from 93 to 57% of the total plot area. This implies that establishment of new adult trees outside that area depends on pre-established seedlings, and on seeds that are dispersed out of the direct seed shadow of the parent by rodents (Forget 1994). Although there are indications that secondary dispersal occurs occasionally (Hammond *et al.* in review), there is no insight yet in the significance of secondary dispersal for the population dynamics of the species. The removal of adults had not yet led to a depletion of seedlings (≥0.65 m) around stumps compared to surviving adults, although smaller seedlings were more common around survivors (Fig. 3). This suggests that most seedlings (≥0.65 m) in the plot were established before or just after logging, and that more recent cohorts have not been very successful yet in reaching this size class. At 10-20 years after logging, a clear positive relation was found between the size of the remnant adult population per ha and the percentage 'area with abundant seedlings' by Clarke (1956) and ter Steege (1990), indicative of the increasing impact of the remaining adults on seedling abundance in logged-over forests. The seedling density (0-1.5 m height) in the logged plot was slightly higher than seedling density in untreated logged-over forest at Moraballi, which was 550-650 $ha^{-1}$ (ter Steege 1990).

### Germination

There was no clear relation between germination and habitat, nor light (Fig. 4). This is in contrast to Fanshawe (1947) and ter Steege *et al.* (1994), who found no germination in large gap environments compared to 15-20% germination (after 12 weeks, this may have affected this result) in small gaps and understorey. The latter ascribed this to drought and sunburn. Although these effects were visually evident in the seeds germinating in the high light environments in both germination experiments, some seeds survived and germinated. Germination success in darker environments was limited by the attack of insects, rodents and fungi (*cf.* Hammond *et al. in prep.*). These different constraints to germination in different habitats did not lead to differences in germination after *c.* 1 year. This is consistent with Hammond *et al.* (*in prep.*), who found no effect of canopy openness on germination in undisturbed forest.

### Responses to habitat heterogeneity

Habitat heterogeneity as created by the felling and skidding of trees did not lead to important differences in germination, morphology (except branch number and density), height growth or survivorship 4-7 years after logging. The apparent effect of habitat on height growth was removed when the effect of light was taken into account (Table 6). However, there was a strong statistical effect of habitat type on leaf growth (or rather: rate of leaf loss), even when the effect of light and plant size were accounted for. Seedlings in regrowth lost leaves faster than elsewhere. Because the branch density in this habitat (and in skid-trails) was higher than elsewhere, but leaf number equal, and therefore leaf number per unit stem and branch length lower, their past rate of leaf loss has likely also been higher (assuming constant internode-lengths, ter Steege *et al.* 1994). These two habitats had experienced the greatest rate of change in microenvironment compared to forest remnants and tree-crowns: the light intensity in the forest remnants was low before and after logging, whereas in tree-crown habitat a dense secondary vegetation had not yet formed, so that it has always remained light since logging. The data suggest that the seedlings had probably reached a larger size (more branches, more leaves) in regrowth (and possibly skid-trails) than elsewhere as a result of higher post-logging light availability in these disturbed areas, but that the establishment of the secondary canopy and associated drastic change in light availability led to a high rate of leaf loss (see also below).

There was a somewhat unexpected, strong effect of nearest parent state (cut or surviving) on morphology and growth, and a tendency towards an effect on survival of *Chlorocardium* seedlings. The difference in morphology might be explained from differences in light availability, as the light availability around stumps just after logging is almost by definition higher than around surviving adults. From Table 7 it can be concluded that the effect on growth is only partly explained by differences in light, and partly by plant size and habitat type, but in all cases there remains a difference between stump and surviving adult neighbourhoods. There are several possible explanations for this effect. A methodological explanation is that the Dawkins index is not sensitive enough to remove all variation due to light from the regression model. The Dawkins index is a measure for direct light, while there may be differences in indirect light between sites with the same Dawkins index. Ecological interpretations include the possibility of different carry-over effects caused by past light environments between stumps and adults, and the Janzen-Connell model, which predicts that seedlings growing in the close vicinity of the parent experience a higher pressure from insect predators and diseases associated to that parent (or nearby conspecific seedlings) than seedlings growing farther away (Janzen 1970, Connell 1971, Hammond & Brown *in press*). Logging provides an unintended test of distance-dependent effects of adults by removing the parent and leaving the original seedling distribution around the parent more or less intact. The effect of adult removal on growth (and the tendency towards and effect on survival) seems to support the hypothesis that (living) adults exert a negative influence on nearby offspring. This is remarkable, because an earlier study of growth and survival of *Chlorocardium* seedlings in the undisturbed plot had not revealed a distance effect (Chapter 6).

### Skid-trails

The percentage area under skid-trail in this small plot was relatively high compared to areas where skidding was executed in a planned fashion (Hendrison 1990), but comparable to areas with uncontrolled skidding (*e.g.* Gullison 1995). Although the sandy nature of the soil at the site may prevent that compaction leads to the deterioration of the soil structure that is commonly associated with skidding (Bruynzeel & Critchley 1994, Jetten 1994), much larger nutrient losses due to leaching than in disturbed zones outside skid-trails were demonstrated by Brouwer (1996) in a study at a nearby site. These losses concerned all solutes except $Na^+$ and $Cl^-$, and were particularly significant for $NO_3^-$. Furthermore, higher $Al^{3+}$ concentrations and lower pH were demonstrated for skid-trails, and the recovery of the vegetation was slower there (Brouwer 1996). Even though these changes potentially affected the composition and establishment and growth rates for colonising plants, and skid-trails are easily recognisable 4-7 year after logging, their effect on *Chlorocardium* growth and survival during this period was none. The tendency to higher leaf loss was probably more attributable to the history of the light environment on skid-trails than to differences in soil compaction or fertility. Possible differences in growth and survival of *Chlorocardium* between different habitats caused by logging, if any, seem therefore to be limited to the early post-logging phase of high light availability. Differences in early post-logging establishment and performance by pioneer species between different habitats created by logging were demonstrated by Uhl *et al.* (1981), de Foresta (1984) and Pinard *et al.* (1996).

By the end of the study period the skid trails tended to become brighter than adjacent regrowth areas as a result of the different accumulation of Leaf Area Index due to the nature of colonisers in both areas: late-successional species with a long leaf life-span and deep crowns in regrowth, and early successional species with a short leaf life-span and shallow crowns on skid-trails (R.J. Zagt, *personal observation*)

### Differences between the logged and undisturbed plots

Unlike the logged plot, there were no rapid changes in seedling morphology in the undisturbed plot (Fig. 6). The observed differences in mean height and leaf growth rate between the two plots (interaction terms) could largely be explained by differences in light and plant size rather than logging-related differences between the plots, although the response of height growth to the presence of cotyledons, and the response in leaf growth to leaf density was different between the plots (Table 5). In the logged plot cotyledons had no effect, which is understandable if it is assumed that most of the seedlings in this plot were 4-7 years old, and the cotyledons not functional any more. The difference in response to light and to leaf density might be a methodological artefact, or point at differences in the efficiency of the leaves. An artefact effect of light might be caused by differences in diffuse light as observed above, or because the use of this subjective index was unconsciously scaled to the range of light environments in both plots (the plots were enumerated in different periods of the year). The difference may also be real and point to a higher light use efficiency by seedlings in the logged plot compared to the undisturbed plot, *e.g.*, because the maximum rate of photosynthesis per unit leaf area is higher (see below). There were no independent effects of plot on leaf and height growth.

Yearly survival in the logged plot had a lightly decreasing trend (Fig. 7). Although this trend is light, it is expected to become stronger, considering the rapid leaf loss in the surviving seedlings. The increasing trend in yearly survivorship in the undisturbed plot is somewhat puzzling, as there seemed to be no major differences in meteorological conditions between years.

### The effect of light and leaf density on growth

Light and leaf-density were both important components of (short-term) growth. A strong interaction between the two was evident in the field experiment (Fig. 8), but not in the demographic plots. In both plots there was a tendency for this interaction, but the range in light environments was probably too small (much less than the 0-7% in the experiment) to detect a significant effect. A positive leaf growth rate was only achieved by seedlings with a high leaf density growing in high light or seedlings with a low leaf density growing in low light. The latter concerned the recently germinated seedlings that were growing on cotyledonary reserves rather assimilates produced by photosynthesis. Fig. 8 shows that problems experienced by the older seedlings transplanted to the low light sites in the experiment and the seedlings in the logged plot were very comparable. Not only did both groups of seedlings temporarily pair low light availability with high leaf density, they also had achieved most of their growth in high light conditions. Most of the leaves and branches were constructed in a past when light availability was (much) higher. These leaves were probably characterised by a low SLA (specific leaf area, leaf area per unit leaf mass) (*cf.* ter Steege *et al.* 1994), a high maximum photosynthetic rate per unit of leaf area (but see Raaimakers *et al.* 1995) and a relatively high light compensation point. Once shaded, these leaves probably experience carbon deprivation, which causes the plant to decline and eventually die, unless they adjust themselves or are timely replaced by shade-adapted leaves (Popma & Bongers 1991, Kitajima 1996). Although new leaves continue to be constructed, the negative leaf growth rate suggests that this is not sufficient to maintain leaf area and to improve the carbon balance of the seedlings. Moreover, once a new leaf is constructed, the light climate has likely further decreased, *etc.*

The remarkable difference in leaf number between the logged and undisturbed plot (Table 2), was not caused by a different pattern of growth in the light or in the dark, but by a difference in branch number, which was related to a larger seedling size and higher branch retention in the logged plot. In the experiment, *Chlorocardium* produced 2 branches on every node over the entire light range, and therefore the number of branches of the seedlings in the field experiment was dependent on height and independent of the light climate. Light was important for the growth and survival of existing branches. Under low light conditions the branches do not grow, shed leaves and die, explaining a light effect on branch number for older seedlings at the end of the study (data not shown). In the high light treatments of this experiment, where seedlings grew fast in height, branch length and leaf number, only 20% of new stem length was invested in height growth, and the rest in lateral growth and the development of a high leaf density. This was also observed by Cornelissen (1993) for subtropical *Castanopsis.* This shows that *Chlorocardium* is not competitive in the sense that it tries to overtop neighbouring seedlings, but that it has probably a more conservative strategy in which a high survival rate prevails over a high growth rate (a 'pessimist' *sensu* Kohyama 1987). Indeed, survival of *Chlorocardium* seedlings was strongly dependent on leaf density, but not dependent on light (Table 5). This may explain why *Chlorocardium* is still present in the logged plot, under a dense secondary canopy where very few other seedlings of similar size are left (R.J. Zagt, *personal observation*), and why mortality rate increased towards the end of the study period, when leaf density became low (*cf.* Fig. 7)

### Silvicultural aspects of the management of Chlorocardium

The results of this study show that *Chlorocardium* seedling demography in logged areas 4-7 years after logging is characterised by slow growth, high leaf loss rates and probably increasing mortality rates. There are substantial differences in morphology, and hence visual vitality, between seedlings growing in the logged plot and seedlings in undisturbed areas, but the evidence indicates that these differences are decreasing rather than increasing. Together with the results of the field experiment (where only individuals transplanted to high light environments (>4% canopy openness) had substantial height and leaf growth), this shows that soon after logging *Chlorocardium* has a period of rapid growth, mainly in branches and leaves, but that this period ends when competing vegetation starts to overtop the seedlings. The growth and survival trends observed after five years can still largely be interpreted as a consequence of the growth during the early post-logging period. Historical observations of favourable response of *Chlorocardium* seedlings to logging or silvicultural treatment which are based on single measurements (*e.g.*, Clarke (1956), also Hawthorne (1993) for timber tree regeneration in Ghana) should therefore be interpreted with some caution, and be followed up by monitoring of growth and survival.

The return of *Chlorocardium* as a major component of the vegetation in the logged plot is limited by the reduced dispersal distance of new seeds, poor growth of the seedlings and the near absence of juvenile trees (the number of juveniles between 5 and 20 cm dbh in the study plot was 1, and 7 for the entire 4 ha tract). The mortality rate of these seedlings is not expected to decline as long as the seedlings continue to loose leaves at the rate they did during the study period. A change in this trend is only expected if the light environment below the secondary canopy improves (a trend that seems to be present on some of the skid trails), but this will not lead to the high growth rates that are needed to produce the large juveniles and adults that maintain a logging cycle of 20-40 years (*cf.* Chapter 8). A silvicultural remedy against competition of smaller commercial trees by secondary vegetation in exploited forest is the killing of non-commercial competitive trees (refinement), such as prescribed in the CELOS silvicultural system and others (de Graaf 1986, Jonkers 1987, Maître 1991). However, this is only expected to be successful, where logging is light (leaving scope for refinement) and in forest that is rich in juvenile *Chlorocardium* trees that are the main beneficiaries of this treatment. In a situation such as the logged plot (broken canopy, no advanced regeneration but high seedling density), silvicultural treatment should target the larger seedlings, and be very specific, *i.e.* should consist of liberation thinning of the more vital (tall and leafy) *Chlorocardium* seedlings. Treatments showing a high degree of specificity (concentrated around and above groups of seedlings, saplings and juveniles) gave the best results in terms of increased growth and higher seedling densities in earlier silvicultural experiments (*e.g.*, Prince 1971 in ter Steege 1990; in heavily logged-over forest). However, if *Chlorocardium* indeed has a strategy favouring survival over growth, competing seedlings and saplings will probably benefit more of this treatment than *Chlorocardium* itself, just like they did after logging. This implies that the treatment needs to be repeated often (*cf.* Clarke 1956). High costs, the rather high skills required for liberation thinning and the absence of short-term returns make such an operation a very unlikely one. Independent of these considerations, reduction damage (to advanced regeneration and to seeds and seedlings dispersed below the tree crowns) and maintenance of an adult population with a seed shadow that approximates the extension of the pre-logging seeds shadow are a prerequisite maintain ecologically and economically significant *Chlorocardium* populations.

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chapter 8

# The response of tropical trees to logging: a cautious application of matrix models

*Roderick J. Zagt & René G.A. Boot*

## Abstract

The population dynamics of the shade-tolerant species *Dicymbe altsonii*, *Chlorocardium rodiei* and the understorey species *Duguetia neglecta* in undisturbed and exploited rain forest in Guyana was studied. All three species were very abundant components of the vegetation, but they differed in regeneration strategy, and only *Chlorocardium* is exploited. Four population censuses were carried out from 1992-1995 in 2.5 ha (undisturbed) and 3.6 ha (exploited) plots near Mabura Hill, Guyana. Size-dependent growth-, mortality and fecundity rates were determined and integrated in population matrix models. Tree life-span and age at first reproduction were estimated using three methods: matrix models, growth projection and by determining the $^{14}C$ content (for *Chlorocardium*). Matrix models were also used to simulate the effects of exploitation and silvicultural intervention.

The results showed considerable inter-specific differences. *Dicymbe* had high mean growth rates in all size classes, while *Chlorocardium* and *Duguetia* were slow growers. *Dicymbe* and *Duguetia* had very low seedling mortality. *Dicymbe* and *Chlorocardium* but not *Duguetia* had higher growth rates in the exploited plot than in the natural plot in most size classes. The matrix models indicated population growth rates close to 1 for *Chlorocardium* and *Duguetia* in both plots, while *Dicymbe* had population growth rates of 1.03-1.14. Age estimates depended strongly on the method and assumptions used. Age at first reproduction ranged from 160-220 (-310) years for *Dicymbe*, 206-280 (-350) for *Chlorocardium* and 64-100 (-115) for *Duguetia*, and mean total life-span of all species ranked among the highest when compared to 7 other species.

Modelled timber resources were projected to decrease for at least 100 years after exploitation of *Chlorocardium*. This decrease could be stopped by liberating seedlings (strongest effects) or advanced juveniles, or similar methods that improved growth or reduced mortality of these stages (reduction of damage, increasing pre-logging juvenile abundance). Repeated logging was, paradoxically, projected to be beneficial for the recovery of timber resources. However, the results of the simulations were strongly dependent on the assumptions used to calculate post-logging growth rates. In all simulations, *Dicymbe* was projected to increase its abundance much stronger than *Chlorocardium*.

It is concluded that there is some scope for sustainable exploitation of *Chlorocardium*, but only with substantial silvicultural intervention.

## Introduction

Even though the causes for the depletion of timber resources in many countries lie beyond the biology of the timber species, an imperfect knowledge of the ecology and demography certainly forms a major obstacle to the use of tropical rain forest tree species in those places where silviculture is preferred over tree-mining (Swaine *et al.* 1987, Hubbell & Foster 1992, Putz 1993, Boot & Gullison 1995, Condit 1995, Condit *et al.* 1995b, Bruenig 1996). In some areas where relatively fast growing merchantable species occur in high densities the ecological aspects of sustainable forest management are well understood (Bruenig 1996) or even 'solved' (Whitmore 1995). However, this is not the case for Greenheart (*Chlorocardium rodiei*), the main commercial timber species in Guyana. Despite considerable recent efforts (reviewed in ter Steege *et al.* 1995, 1996), the ecology of this species remains elusive. In summary, the species produces very large seeds but rather small seedlings which are barely dispersed beyond the crown area; its seeds germinate very slowly (3-36 months); the seedling may remain dependent on its cotyledons for several years, and have the capacity to survive for two years in absolute darkness but for just months in the understorey, the plants grow slowly in height and in diameter throughout their lives, and hardly respond in growth to increases in light or nutrient availability, further, the species is common as a seedling and as an adult but relatively rare as a sapling and juvenile (ter Steege 1990, Boot 1994, 1996, Raaimakers *et al.* 1995, Hammond *et al. in prep.*, Chapters 5, 6). To crown this puzzling picture, in many forests in central Guyana, *Chlorocardium* shares a dominant position in the canopy with *Dicymbe altsonii*, a species which outperforms it in all these aspects (Boot 1994, Chapter 6). Presently, *Chlorocardium* is being selectively over-exploited over much of its natural range (ter Steege *et al.* 1996). After exploitation, the residual population is recovering slowly, if at all (*e.g.*, Chapter 7).

The general issue of this paper is to integrate the demographic aspects of *Chlorocardium* ecology in a population model, and to compare its population dynamics with two other species which are also very common in the same forests: *Dicymbe altsonii*, a canopy species, and *Duguetia neglecta*, an understorey species. Differences in dynamics between an exploited and an undisturbed population of these three species are then used to assess the sensitivity to and scope for management of *Chlorocardium.*

There are several approaches to modelling tree population dynamics. The basic distinction is the modelling unit, which ranges from individuals to groups of individuals grouped in classes. Individual based models simulate tree growth as a function of location, size and resource availability (Liu & Ashton 1995), and therefore have the greatest capacity of incorporating the mechanistic base of tree population dynamics. Within this group of models, growth-yield models and gap models can be distinguished on the base of purpose (timber management *vs.* study of ecological mechanisms) and modelling philosophy (Liu & Ashton 1995). For temperate tree communities these models have been successfully developed and applied to a variety of purposes (*e.g.*, the gap models FORET (Shugart & West 1977) and SORTIE (Pacala *et al.* 1993)), but their large data requirement has limited their application to the species-rich forests of the tropics (*e.g.* Shugart *et al.* 1981, Vanclay 1989, Gourlet-Fleury & Montpied 1995).

When data are scarce, population matrix models (Lefkovitch 1965) may be more appropriate to describe tree population dynamics. The basic assumption of these models is that population dynamics can be satisfactorily described by means of growth, reproduction and survival of individuals which are organised in size classes or stages. The great advantage of these models is that they have clear and well understood mathematical attributes which can be interpreted in biological terms (Caswell 1989, Cochran & Ellner 1992). Their simple structure provides a powerful tool for quantifying the demographic consequences of differing demographic properties between species (Silvertown *et al.* 1993), populations (*e.g.*, Olmsted & Alvarez-Buylla 1995) or even between different life history pathways within a population (*e.g.*, van Groenendael *et al.* 1994). Matrix models have found quite extensive application in tropical trees and palms (*e.g.*, Hartshorn 1972, Alvarez-Buylla 1994), not only for species, but also for groups of species (Favrichon 1994) or complete forest stands (Osho 1991). However, matrix models are not mechanistic but descriptive, and the inherent assumptions that the behaviour of all individuals in a class can be described by mean vital rates, that population dynamics is independent of initial state, and that they are constant in time (implying that they are unaffected by changes in the environment) are not realistic. This limits the usefulness of these models for, for example, the evaluation of exploitation regimes for large trees (Boot & Gullison 1995), although this approach has sometimes been applied (Mendoza & Setyarso 1986). Several researchers have developed methods to cope with these problems (density-dependence of vital rates: Alvarez-Buylla (1994), explicit inclusion of gap dynamics: Horvitz & Schemske (1986), Alvarez-Buylla (1994)). These developments provide important insights in the impact of these aspects, but they also add new assumptions to the model, and give up some of the advantages of matrix models, without gaining the versatility of individual models.

For the three species in the Guyanese rain forest, having no earlier data on population dynamics (except growth rates of larger *Chlorocardium* size classes), we chose a matrix modelling approach. In spite of the relatively limited dataset, this allowed a comparison between the species, and between populations growing in an undisturbed and an exploited area. Because not all assumptions of matrix models are likely held, particularly in the logged site, we limit our comparison to the simplest, most transparent form, and try to cope with transgressions of the assumptions by a cautious application rather than by adding complexity to the model.

In order to practically apply knowledge about the population dynamics of a species for management, it is necessary to put a time scale to population dynamical processes. Polycyclic silvicultural systems based on natural regeneration (de Graaf 1986) are concerned with the continuous production of timber from a single stand in cycles of planned silvicultural intervention. Therefore, it is important to be able to estimate how long a cohort of trees will take to grow from seedling to adult, when it starts to reproduce and how long its reproductive life is. The estimation of tree age is a major problem in tropical trees. In the aseasonal tropics tree rings are generally not formed

(Worbes 1989). Several approaches were developed to estimate species-specific size-age relations from tree increment data (Lieberman & Lieberman 1985b). Another approach is recent and specifically utilises population transition matrices (Cochran & Ellner 1992).

In this paper, we assemble matrix population models for *Chlorocardium*, *Dicymbe* and *Duguetia* in tropical rain forest dominated by these species in Guyana. The data cover over three years of growth in contrasting habitats: a pristine site and a site that was logged 5 years prior to the study. We asked whether the populations of these species were increasing or decreasing, and in which facets of their life history they differ. We compare this with 7 other species with published matrix models. A further objective was to assess the response of these species to logging by comparing population dynamics before and after exploitation, and to identify the size-classes which most affect the population growth rate. Next, we estimated age-size relations for all three species in order to determine how long it takes to mature and how long a tree lives. We compared the results of three different methods (matrix estimates, growth projection and carbon-dating) and assessed the effect of different assumptions for two of these methods. Finally, we compared the effect of different possible management options on post-logging population dynamics of *Chlorocardium*. In every step of this analysis, we tried to assess the biological relevance and limits of the matrix projection method.

This study adds six new matrix models to the still limited matrix literature for tropical woody species, plus two that we assembled from literature data (for *Prioria copaifera*). For the first time matrices for different but sympatric woody species are presented, and for woody species populations that have been exploited. Also new is the application of the methods of Cochran & Ellner (1992) for age-based life-history parameters to tropical woody tree species.

## Methods

### Field procedures

#### *Species and site description*

The study was conducted between 1991 and 1995 in the 1200 ha Ecological Reserve of the Tropenbos-Guyana Programme, located in the DTL forest concession *c.* 20 km south of Mabura Hill, central Guyana (5°13' N, 58°48' W). Average rainfall and temperature in the area are 2700 mm and 27°C, respectively (Jetten 1994). Rainfall follows a bimodal pattern with maxima in May-July and in December (Jetten 1994). Several landforms are distinguished in the concession area; the study area itself was in the sedimentary plains (Van Kekem *et al.* 1997), which are relatively flat (slopes up to 9°). The soil types in the Reserve area belong to one of two major groups: a group of clayey Plinthosols and a group of sandy and loamy soils of various types (Jetten 1994, Van Kekem *et al.* 1997). The distribution of species and forest types respond strongly to the distribution of these soil types (Davis & Richards 1934, Fanshawe 1952, ter Steege *et al.* 1993, Jetten 1994). The resultant communities, which are classified as Evergreen Rain Forest (Mixed Forest) and Dry Evergreen Forest (ter

**Table 1**
**Comparison of plant and life history characters of the three study species. Based on Chapters 3 and 5, Hammond & Brown (1995), H. ter Steege, *personal communication*, and unpublished data R.J. Zagt, which refer to the situation in the study plot.**

| | *Dicymbe altsonii* | *Chlorocardium rodiei* | *Duguetia neglecta* |
|---|---|---|---|
| Distribution | central Guyana | central Guyana | Guyana, Surinam |
| Regeneration strategy | gap-dependent | gap-dependent | shade-tolerant |
| Seed dry weight (mean, g) | 5.7 - 8.5 | 38.9 - 41.6 | 0.3 |
| Fruiting | biannual | annual | annual? |
| Seed crop in plot ($ha^{-1}$) | 40 000[1] | 5 000 | ? |
| Dispersal mechanism | dehiscion | gravity/ (mammals) | birds? |
| Germination | direct | delayed | direct? |
| Seedling height [2] (m) | 0.35 | 0.40 | 0.05 |
| Branching type | orthotropic | plagiotropic | plagiotropic |
| Leaf form | compound, alternate[3] | simple, opposite | simple, alternate |
| DBH at maturity (cm) | 25 | 21 | 2? |
| Maximum height (m) | 35 - 40 | 35 - 40 | 20 |
| Maximum DBH (cm) | 150 | 120 | 15 |

[1] in a fruiting year.
[2] with fully expanded first leaves.
[3] except first pair, which is opposite.

Steege *et al.* 1993, 1996), are frequently dominated by one or a few species. In the study area large undisturbed tracts of forest lie alternated with patches of logged-over though recovering forest.

### *Study species*

Three species were selected for this study. All three are widespread and very common species in central Guyana, and they represent a range of non-pioneer regeneration strategies (Table 1).

*Dicymbe altsonii* Sandw. (Caesalpiniaceae, Clump Wallaba) is a large canopy tree that can be classified as a gap-dependent species (Chapter 6). The species is distributed in a small area in central Guyana and north-western Brazil (Cowan & Lindeman 1989). In the study area, *Dicymbe* occurs exclusively on sandy and loamy soils, over a broad hydrological gradient (ter Steege *et al.* 1993). It is dominant or co-dominant in a number of forest types (Fanshawe 1952, ter Steege *et al.* 1993, Jetten 1994).

*Chlorocardium rodiei* (Schomb.) Rohwer, Richter & v.d. Werff (Lauraceae, Greenheart) is also a large canopy tree which is logged selectively but on a large scale throughout Guyana. It is classified as a gap-dependent species (ter Steege *et al.* 1994). The species is nearly endemic to Guyana (ter Steege 1990), and occurs on brown loamy sands and laterite, usually on gentle hill slopes. It is considered a dominant in *Eschweilera-Licania* forest (Fanshawe 1952, ter Steege *et al.* 1993).

**Table 2**
**Sampling scheme for demographic study of three rain forest tree species near Mabura Hill, Guyana. The total sampled area (in ha, except for the first column, which is in m²) per size range (heights, h and diameters, dbh in cm) is given.**

| *Chlorocardium* | h 0-0.65 | h 0.65-1.3 | h 1.30- dbh 1 | dbh > 1 | |
|---|---|---|---|---|---|
| Undisturbed Plot | 950[1] | 2.0 | 2.0 | 2.5 | |
| Exploited Plot | 250[1] | 0.6 | 0.9 | 3.6 | |
| *Dicymbe* | dbh 0-1 | dbh 1-2.5 | dbh 2.5-4 | dbh 5-10 | dbh > 10 |
| Undisturbed Plot | 950[1] | 2.0 | 2.0 | 2.5 | 2.5 |
| Exploited Plot | 250[1] | 0.3 | 0.9 | 1.4 | 3.6 |
| *Duguetia* | h 0-1.3 | h 1.3 -dbh 4 | dbh > 4 | | |
| Undisturbed Plot | 950[1] | 2.0 | 2.5 | | |
| Exploited Plot | 250[1] | 0.9 | 1.4 | | |

[1] These plots (25 m² × 38 (undisturbed plot) and 10 (exploited plot)) are referred to as seedling sample plots in the text.

*Duguetia neglecta* Sandw. (Annonaceae, Yarri yarri) is an understorey tree that rarely exceeds 10 cm in diameter (at breast height, dbh). It can be classified as a shade-tolerant species. The species occurs on brown loamy sands and laterite, and is distributed in Guyana and Surinam.

### Plot description

The demography of these species was studied between 1991 and 1995 in two permanent plots located in *Chlorocardium*-rich forest that has variously been described as 'well-drained mixed forest' (ter Steege *et al.* 1993) or as *Eschweilera-Licania* and *Eschweilera-Dicymbe* associations (Fanshawe 1952), on brown loamy sand (Ferralic Arenosol to Haplic Ferralsol) belonging to the Berbice Formation (van Kekem *et al.* 1997). One plot, the undisturbed plot (2.5 ha), was established in primary forest (described in Chapter 6). The total tree density in this plot was 397 trees $ha^{-1}$ (dbh ≥10 cm) with an estimated basal area of 39.3 $m^2$ and a canopy height of 30-40 m. A second plot, the exploited plot (3.6 ha), was located *c.* 2 km from the undisturbed plot and was unaffected by human activity until 1988, when it was logged. The study covers the period between 4 and 7 years after logging. The average logging intensity was 19.5 trees $ha^{-1}$, representing a basal area of *c.* 6.6 $m^2$. Of all logged trees, 89% were *Chlorocardium*, and logging removed 56% of the adult *Chlorocardium* population (defined as trees >20 cm dbh). Forty-nine percent of a 1.35 ha area within this plot was classified as regrowth (canopy destroyed by logging, but soil and seedling populations undisturbed), 20% as skid-trail (soil and vegetation destroyed by the action of skidder machines), 27% as remnant forest and 4% as tree crown habitat (Chapter 7). The remaining stand after 7 years of regrowth contained 328 trees ≥10 cm dbh per ha, with a

**Table 3**
**Size classes distinguished in this study. The size classes for *Chlorocardium* and *Dicymbe* are identical when expressed as height classes. In terms of dbh they are slightly different. Lfd is leaf density, the number of leaves per decimetre of stem.**

|  |  | *Dicymbe* |  | *Chlorocardium* |  | *Duguetia* |  |  |
|---|---|---|---|---|---|---|---|---|
| Class | Height (m) | Dbh (cm) | Lfd (N dm$^{-1}$) | Dbh (cm) | Lfd (N dm$^{-1}$) | Class | Height (m) | Dbh (cm) |
| *1* |  | yearlings |  | seeds |  | *1* | <0.15 |  |
| *2* | <0.45 |  | <0.5 |  | <1.0 | *2* | <0.30 |  |
| *3* | <0.45 |  | >0.5 |  | >1.0 | *3* | <0.65 |  |
| *4* | <0.80 |  | <0.5 |  | <1.0 | *4* | <1.30 |  |
| *5* | <0.80 |  | >0.5 |  | >1.0 | *5* |  | <1.0 |
| *6* | <1.56 |  | <0.5 |  | <1.0 | *6* |  | <2.0 |
| *7* | <1.56 |  | >0.5 |  | >1.0 | *7* |  | <3.0 |
| *8* | <3.13 | <1.5 |  | <1.4 |  | *8* |  | <4.0 |
| *9* | <6.25 | <3.4 |  | <3.1 |  | *9* |  | <5.0 |
| *10* | <12.50 | <7.6 |  | <6.6 |  | *10* |  | <6.0 |
| *11* | <25.00 | <17.4 |  | <20.9 |  | *11* |  | <7.0 |
| *12* | <30.00 | <24.9 |  | <31.0 |  | *12* |  | ≥7.0 |
| *13* | - | <52.5 |  | <55.4 |  |  |  |  |
| *14* | - | <80.0 |  | <80.0 |  |  |  |  |
| *15* | - | ≥80.0 |  | ≥80.0 |  |  |  |  |

basal area of *c.* 30.7 m$^2$ and a strongly broken canopy. The canopy height of the secondary vegetation that established in the logging gaps varied between 6 and 8 m in 1994.

It is difficult to assess to what extent both demographic plots were comparable in their primary state. The population structures of the larger size classes that were not so much affected by logging and regrowth suggest that adult densities were similar in both plots before logging (see results).

In this paper, we provide a detailed demographic study of tree populations at two locations, and strictly speaking we can not extrapolate our results to other areas. The general soil type of the study plots ('brown sands and loams') occupies *c.* 43% of the 218.000 ha concession of DTL (van Kekem *et al.* 1997). Inventories of other areas (3 areas of 2.5 ha) in the Ecological Reserve indicated that tree densities of the study species within the Ecological Reserve were variable, but broadly comparable with the undisturbed plot (*Chlorocardium* ≥10 cm dbh: 9, 16, 30 and 38 trees per ha; *Dicymbe* ≥10 cm dbh: 78, 78, 49 and 74 trees per ha; *Duguetia* ≥4 cm dbh: 113, 53, 41 and 67 trees per ha; the fourth figure referring to the undisturbed plot, R.J. Zagt, *unpublished results*). The logging intensity within the DTL concession varies strongly between locations and with management policy. Three *c.* 1 ha tracts elsewhere in the concession had much higher logging intensities of 29, 30 and 36 trees per ha (Zagt 1995). However, the logging intensity in the exploited plot was similar to reported intensities elsewhere in Guyana (Bartica triangle, 19.3 stumps ha$^{-1}$ over 101 ha, Clarke 1956). On the basis of these three arguments, we assume that these plots were not dissimilar to many other forests in central Guyana where *Chlorocardium* and *Dicymbe* co-dominate.

### *Sampling scheme and data collection*

Population censuses of the study species were carried out annually (four times) between 1991 and 1995, in October-January (undisturbed plot) and March-May (exploited plot; from 1992 onwards). The size of the sampled area depended on the species and the abundance of a particular size class (Table 2). Difficult terrain conditions limited the sampled area for seedlings of the smallest category in the exploited plot. The maximum sampled population size per species in any year was: *Chlorocardium* undisturbed 2092, exploited 592, *Dicymbe* 4870, 1749, *Duguetia* 1351, 200.

All individuals belonging to the study species were located, labelled and mapped in the appropriate subplots. For individuals in the seedling sample plots, height (up to 4 m), leaf density (number of leaves per decimetre stem length, Chapter 6), Dawkins index and evidence of damage were recorded. The Dawkins index is a rapid, subjective and semi-quantitative way to assess the direct but not diffuse light environment for individual trees and seedlings (Dawkins & Field 1978, Clark & Clark 1992). Six classes were distinguished:

1: no direct or lateral light in the crown;

2l, m and h: low, medium and high amounts of lateral light (*e.g.*, seedlings growing next to a canopy gap);

3 and 4: less and more, respectively, than half of the crown directly illuminated from above (seedlings growing in a gap, canopy trees).

Individuals taller than 1.3 m were marked with a painted ring at breast height or higher if irregularities or buttresses were encountered, and their diameter was recorded with a vernier caliper (trees <4 cm dbh) or pi-graduated tape (trees >3 cm dbh). Diameter was measured till the nearest 0.05 cm (pi-tape) or 0.01 cm (caliper; average of two perpendicular measurements). Seedling and sapling heights (<4 m) were measured yearly. The height of trees >4 m was determined once during the study period by simultaneously measuring the tree and a 2 m reference stick, with a Suunto clinometer. Mortality was scored at re-census; in addition, any individual recorded as not found for at least two censuses was considered to have died at the first census that it was not found.

## **Matrix models of population dynamics**

### *Establishment of size classes*

Stage-based matrix models require populations to be organised in biologically meaningful classes characterised by individuals with comparable growth and mortality rates and fecundity. Therefore we based our classification on a height and maturity criterion. Height is the main measure of success for juvenile individuals of species that mature in the canopy. We established a diameter-height relation for the two canopy species by regressing height against diameter with a logistic growth equation. For each

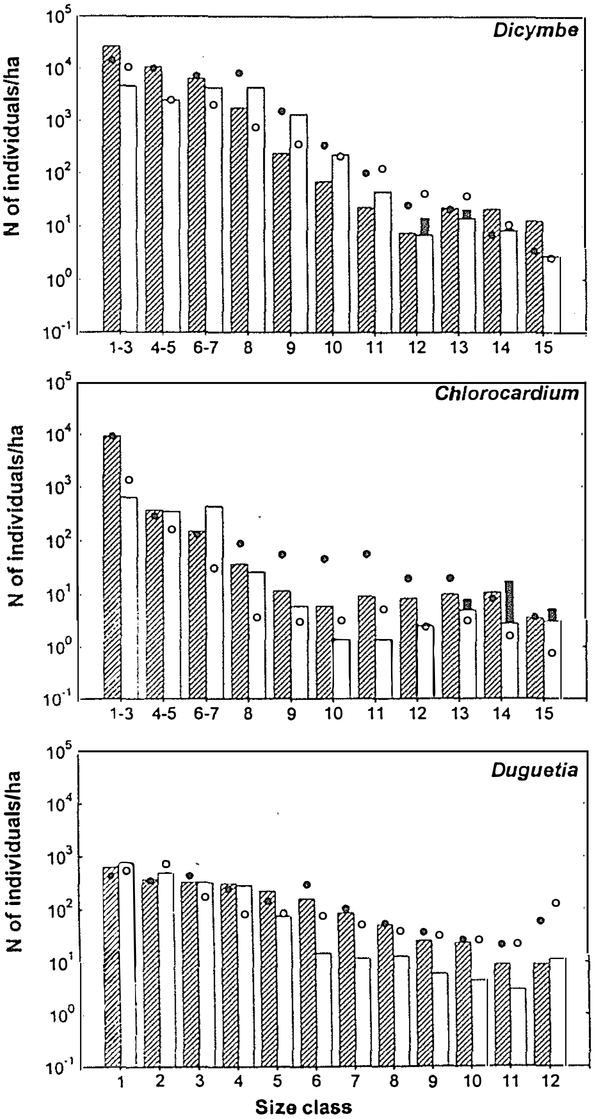

**Figure 1**

Population size distributions of the three study species at the third census (1993-4, bars), and projected stable size distributions obtained from matrix modelling (dots). Dark bars and dots are undisturbed populations, light bars and dots the exploited populations. The black bars in classes 12-15 for *Dicymbe* and *Chlorocardium* concern destroyed (by logging) and cut individuals, respectively. Some destroyed individuals were probably missed, so these are minimum estimates. Destroyed individuals belonging to smaller size classes could not be identified. *Dicymbe* ($p<0.001$) and *Duguetia* ($p<0.05$) but not *Chlorocardium* had different population size distributions between both plots when tested with 2-sample Kolmogorov-Smirnov tests performed on size classes >1.3 m tall (*Chlorocardium* and *Dicymbe*: classes 8-15, *Duguetia*: 5-12). Present and stable population size distributions were different in all cases ($p<0.001$). The population size distributions of *Chlorocardium* and *Dicymbe* differed from each other in both plots ($p<0.001$).

individual we recorded whether it belonged to the canopy (criterion in case of doubt: Dawkins index 3 or higher) and whether it was fertile or not (inspection with binoculars). We then defined a transitional class of individuals. Smaller individuals were not in the canopy and not fertile, larger individuals were all in the canopy and fertile. Then we calculated the upper and lower height limits of this class and defined the juvenile classes by repeatedly halving the height of the lower transitional class boundary (Table 3), and calculating the corresponding diameter. Individuals were assigned to classes on the basis of their diameter. We adjusted the lowest seedling height class by setting the limit slightly above the observed height of seedlings with stems that are not yet lignified. These seedlings have different vital rates than older seedlings and we wanted to avoid that they would be distributed over several classes. The lowest size class was seeds for *Chlorocardium* (which maintains a *de facto* seed bank, Chapter 5) and first year seedlings for *Dicymbe.* The three seedling classes up to 1.56 m tall were each subdivided into two classes based on leaf density. Seedlings with a low leaf density (defined as <1 and <0.5 leaf per decimetre stem for *Chlorocardium* and *Dicymbe,* respectively) show high mortality and slow growth (Chapter 6), and were classified separately from seedlings with a higher leaf density. Mature trees were classified by diameter, in three classes. Trees above 80 cm were considered senescent (most are hollow (ter Steege 1991) and many are shedding large branches), and the remaining diameter range was divided in two equal parts. In this way, *Chlorocardium* and *Dicymbe* had an equal number of classes (15), which allows the comparison of life histories using matrix models (Enright *et al.* 1995).

The classification of *Duguetia* was carried out in a different way for several reasons: the tree does not reach the canopy, some classes were poorly represented, a relatively low percentage of individuals was observed with flowers or fruits and there was no clear distinction possible between fertile and non-fertile classes. Therefore we simply distinguished eight 1 cm diameter classes, and four seedling classes of doubling height.

### *Growth and mortality rates*

Matrix population models are parameterised with four types of stage specific vital rates: $P_i$, the stage-specific probability per time unit (one year in this paper) of surviving and remaining in the same size class *i* (stasis); $G_i$, the probability of surviving and progressing to a larger size class (growth); $R_i$, the probability of surviving and regressing to a smaller size class, and $F_i$, the number of offspring per individual. Mortality is $1-\sigma_i$, with survival $\sigma_i=P_i+G_i+R_i$.

The most straightforward method of determining survival $\sigma_i$ and growth $G_i$ is the recording of relative frequencies of actual deaths and transitions, and this is the method that has frequently been used for transition matrices of tropical trees (*e.g.*, Hartshorn 1972, Enright & Ogden 1979, Alvarez-Buylla 1994). However, stage-dependent mortality determined by observing actual deaths in small and short-term studies tells little about the mortality pattern of the species, and actual transitions between size-classes in long-lived, slow-growing species with wide class intervals are rarely observed. The observed vital rates are then strongly dependent on the within class size distribution of the individuals, and easily assume unrealistic values (*e.g.,* no deaths, no growth). A number of studies involving palms (*e.g.*, Olmsted & Alvarez-Buylla 1995, Svenning & Balslev 1997) calculate transition probabilities from estimated stage durations $T_i$ (Caswell 1989 p. 84). Mean stage durations are calculated from class width and mean growth rate $\gamma_i$, and growth transition probabilities $G_i$ are then derived as $\sigma_i / T_i$. This approach tacitly assumes that no transitions are possible between non-neighbouring stages, and that regression (negative growth) does not occur. This is a reasonable assumption for classes which are defined by diameter, but not for the (narrow) seedling classes which are defined by height. Very fast growers will be able to jump a stage during one year, whereas others that suffer traumatic height reduction will be pushed back into a smaller size class. Therefore, we derived growth transitions $G_i$ and survival probabilities $\sigma_i$ for seedling classes (1-7 in *Chlorocardium* and *Dicymbe*, 1-4 in *Duguetia*) on the basis of observed transition frequencies, which were averaged over the three years of study. Large sample sizes warrant this approach in most instances; however some classes in the exploited plot had very small sample sizes.

We did not estimate mean growth $\gamma_i$ and survival $\sigma_i$ by taking their class means. Matrix modelling assumes that growth rates can be described by their mean, which is ideally derived from the mean growth trajectory that individuals follow over their lives. The general shape of size-dependent growth is expected to show an optimum at intermediate size, with the increasing leg representing the innate tendency of plants towards exponential growth, and the decreasing leg the effects of senescence and the worsening balance between assimilating and respiring tissues in the tree (Zeide 1993). Therefore, we approach mean diametrical growth of large individuals by fitting a growth equation through all the data and calculating a stage specific mean growth rate for the class midpoint. We used the Hossfeld IV equation to estimate size-dependent growth rate $\gamma$, which is

$$\gamma = \frac{b \times c \times D^{(c-1)}}{\left( b + \frac{D^c}{a} \right)^2} \tag{1}$$

where D is diameter at breast height, and a, b and c are fitted parameters (Zeide 1993). The dependent variable in (1) was average yearly growth rate per individual, calculated by linear regression of tree diameter (2-4 measurements) against time (in days since the first census). This minimised the effect of measuring errors on the very small growth rates that we observed. Trees with large (>0.1 cm) decreases in diameter or damaged paint rings were omitted from this analysis. This removed 0-3% of the individuals per species from the sample. We approached the standard deviation by fitting a second model through the residuals about the mean (*cf.* Condit *et al.* 1995b).

Similarly, mortality is not expected to be constant throughout the life of a tree, but to be higher at smaller tree sizes, when trees are sensitive to suppression due to shading and to physical damage, and at larger sizes, when trees become senescent. As we have no a-priori knowledge about the shape of the relation between size and survival rate, we used the flexible logistic model proposed by Huisman *et al.* (1993) for species response analysis to estimate probabilities of survival $\sigma$. This model describes an optimum function with potentially unequal rates of increase and decrease:

$$\sigma = \frac{1}{1 + e^{(a+b \times D)}} \times \frac{1}{1 + e^{(c+d \times D)}} \qquad (2)$$

where D is diameter, a, b, c and d are fitted coefficients and b and d have opposite signs. The (binary) dependent variable was survival over three years, because yearly survival was very high and death sometimes takes a long time for a large tree. We fitted models (1) and (2) with non-linear regression that minimised the residual sum of squares in an iterative way. We then determined $G_i$ as $\sigma_i \times \gamma_i$ / (class width of *i*) = $T_i^{-1} \times \sigma_i$, and $P_i \times (1-T_i^{-1}) \times \sigma_i$, where $\gamma_i$ and $\sigma_i$ were calculated for the midpoint of class *i*.

Simple comparisons of growth between species, size classes or Dawkins classes were evaluated with non-parametric tests. The Mann-Whitney unpaired rank tests was used for comparisons between plots or between *Chlorocardium* and *Dicymbe* (per size class). The relation between growth and Dawkins index (per species and per plot) was evaluated with Spearman rank correlations. Because not all classes contained sufficient data, individuals of different classes were pooled in seedlings (which are below the secondary canopy in the exploited plot), subcanopy individuals (which are in or above the secondary canopy, but below the original primary canopy in the exploited plot) and canopy individuals (in the primary canopy). Differences between species, per plot and pooled size category, were calculated with Kruskal-Wallis anova.

### *Reproduction*

Due to the high density of adults, it was impossible to determine size-dependent reproductive output per tree. Instead, we estimated the total reproductive output in the plot from the density of current year's seed and seedling cohorts that survived till December, and divided this by the number of adults in the population (classes 12-15 for *Chlorocardium*, classes 13-15 for *Dicymbe*). The sample in the exploited plot was not adequate to obtain a reliable estimate for reproductive output in this plot. Because we lacked data on differences in fecundity rate between size classes and between the plots, we assigned all reproductive classes in both plots the same fecundity value. Although this is a simplification of reality, the error is probably minor because projected matrix behaviour of trees has been shown to be relatively little affected by differences in fecundity (Caswell 1989, Peters 1991).

Unlike both other species, *Dicymbe* reproduces biannually, with flowering years followed by off-years. A two-year projection interval seems appropriate for the population matrix model of this species. However, for reasons of comparability we assumed that in the population matrices *Dicymbe* was an annual reproducer, with a crop size equal to half the biannual crop size.

We ignored in the matrices for *Dicymbe* the species' potential for vegetative reproduction through stem suckers (Chapter 4). This underestimates the total reproductive

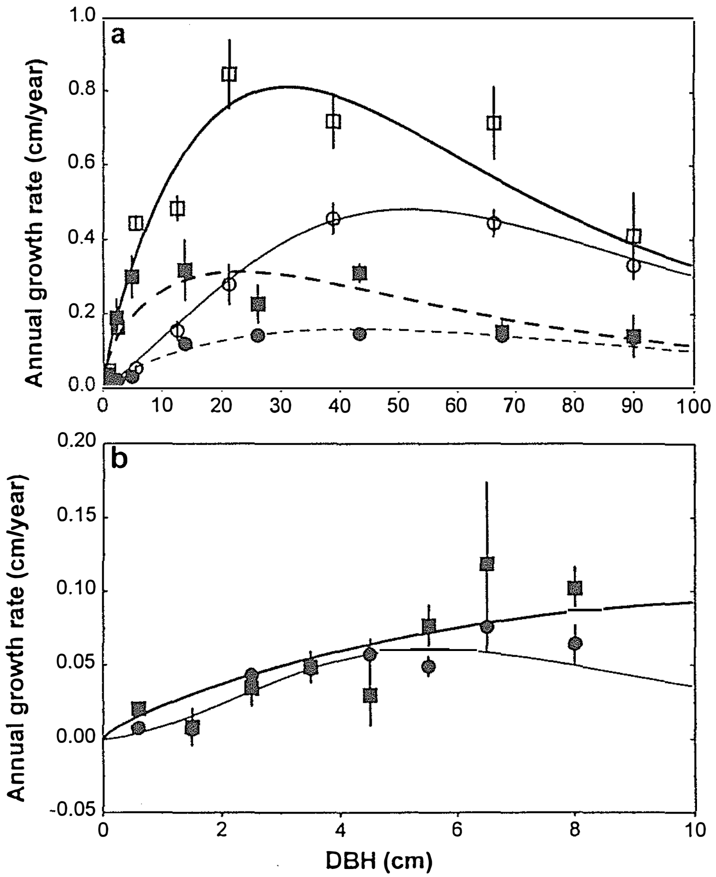

**Figure 2**

**Diameter-growth relations for the study species, fitted with Hossfeld IV growth equations. Averages per size class (±s.e.) are plotted for reference. a. *Dicymbe* (open symbols, drawn lines) and *Chlorocardium* (closed symbols, broken lines). b. *Duguetia*. Squares are trees in the exploited plot, dots in the undisturbed plot. Sample sizes: see Table 5.**

output, but because 'reproduction' occurs only when a stem sucker replaces the parent tree when it dies, its contribution to regeneration is hard to quantify (it is equal to a fraction of the annual mortality of adults).

For *Duguetia*, which is probably bird-dispersed, we never found viable seed away from trees. We therefore determined per capita fecundity by determining the number of recently germinated seedlings in the seedling sample plots, and distributing this output over the size classes on the basis of the number of fecund individuals per class. We averaged the per capita fecundities over classes 9-12 because it is likely that we overlooked a considerable number of reproductive individuals; the lower percentage of reproductive individuals in classes 7 and 8 is probably real. Individuals in the exploited plot were assigned the same $F_i$.

**Table 4**

**Size-class dependent growth, mortality and fertility rates for *Dicymbe* (a), *Chlorocardium* (b) and *Duguetia* (c) in undisturbed and exploited forest near Mabura Hill, Guyana. Growth is a mean over three years, and individuals were assigned to the size class in which they spent most of the time. Fertile is the percentage of trees that was observed with flowers or fruits at least once during the study period. Flowering for *Chlorocardium* is cumulative over 1992-1995; for *Dicymbe* is for 1993 only. Reproduction in *Duguetia* represents an underestimate. No fecundity data are available for the exploited plot. Standard errors for growth result from inter-individual variation; standard errors for mortality from inter-annual variation.**

| (a) | Undisturbed plot | | | | Exploited plot | | | |
|---|---|---|---|---|---|---|---|---|
| | | Growth[2] (cm $y^{-1}$) | Mortality (% $y^{-1}$) | Fertile | | Growth[2] (cm $y^{-1}$) | Mortality (% $y^{-1}$) | test[5] |
| Class | N[1] | mean ± se | mean ± se | (%) | N[1] | mean ± se | mean ± se | |
| *1* | | -[4] | 27 ± 11 | | | -[4] | 40 ± 38 | |
| *2* | 58 | 1.6 ± 0.3 | 40 ± 4 | | 5 | 5.1 ± 1.6 | 49 ± 8 | * |
| *3* | 382 | 3.1 ± 0.1 | 13 ± 1 | | 82 | 2.7 ± 0.4 | 32 ± 5 | ns |
| *4* | 101 | 2.1 ± 0.3 | 12 ± 2 | | 4 | 4.1 ± 0.8 | 21 ± 21 | * |
| *5* | 598 | 4.9 ± 0.2 | 4 ± 1 | | 58 | 6.0 ± 0.7 | 7 ± 3 | ns |
| *6* | 197 | 3.8 ± 0.4 | 6 ± 2 | | 7 | 7.3 ± 2.2 | 12 ± 2 | ns |
| *7* | 248 | 7.3 ± 0.5 | 2 ± 1 | | 94 | 8.7 ± 0.9 | 2 ± 1 | ns |
| *8* | 659 | 0.02 ± 0.00 | 1 | 0 | 344 | 0.05 ± 0.00 | 4 | *** |
| *9* | 445 | 0.02 ± 0.00 | 1 | 0 | 472 | 0.16 ± 0.01 | 2 | *** |
| *10* | 142 | 0.05 ± 0.01 | 2 | 0 | 210 | 0.44 ± 0.02 | 0 | *** |
| *11* | 52 | 0.15 ± 0.03 | 1 | 0 | 100 | 0.48 ± 0.03 | 1 | *** |
| *12* | 20 | 0.28 ± 0.05 | 2 | 14 | 22 | 0.85 ± 0.09 | 1 | *** |
| *13* | 49 | 0.46 ± 0.04 | 0 | 52 | 42 | 0.72 ± 0.07 | 0 | ** |
| *14* | 51 | 0.44 ± 0.04 | 0 | 80 | 22 | 0.71 ± 0.10 | 2 | * |
| *15* | 25 | 0.33 ± 0.03 | 1 | 79 | 4 | 0.41 ± 0.12 | 0 | ns |

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[1] Class 1-7: sample size for calculation of growth rates; sample sizes for calculation of mortality were larger.

[2] Class 2-7 (*Duguetia* 1-4): height growth, excluding damaged individuals; class 8-15 (*Duguetia* 5-12): dbh growth.

[3] Height growth rates inflated by germinating individuals.

[4] Yearlings remain only 1 year in this class and spend the majority of their time in other classes.

[5] Results of three Mann-Whitney tests: on growth between plots (left), on growth between *Chlorocardium* and *Dicymbe* in undisturbed plot (middle) and idem in exploited plot (right; only in table for *Chlorocardium*). * p≤0.05; ** p≤0.01; *** p≤0.001; ns not significant; - not tested.

| (b) | Undisturbed plot | | | | Exploited plot | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Growth[2] (cm y$^{-1}$) | Mortality (% y$^{-1}$) | Fertile | | Growth[2] (cm y$^{-1}$) | Mortality (% y$^{-1}$) | test[5] | | |
| Class | N[1] | mean ± se | mean ± se | (%) | N[1] | mean ± se | mean ± se | | | |
| *1* | 222 | | 63 ± 5 | | 208 | | 59 | | | |
| *2* | 112 | 16.9 ± 1.7[3] | 72 ± 9 | | 1 | 15.8[3] | 92 ± 8 | - | *** | - |
| *3* | 50 | 6.6 ± 1.1[3] | 54 ± 9 | | 12 | 1.5 ± 1.3 | 14 ± 7 | ** | *** | ns |
| *4* | 294 | 2.0 ± 0.2 | 51 ± 5 | | 19 | 3.1 ± 1.5 | 69 ± 33 | ns | ns | ns |
| *5* | 261 | 1.7 ± 0.2 | 13 ± 3 | | 148 | 2.2 ± 0.3 | 9 ± 4 | * | *** | *** |
| *6* | 72 | 1.1 ± 0.4 | 32 ± 5 | | 22 | 3.2 ± 1.7 | 66 ± 8 | ns | *** | ns |
| *7* | 156 | 2.4 ± 0.3 | 4 ± 1 | | 205 | 3.6 ± 0.3 | 5 ± 0 | ** | *** | *** |
| *8* | 89 | 0.01 ± 0.00 | 2 | 0 | 39 | 0.04 ± 0.01 | 1 | ns | ns | ns |
| *9* | 29 | 0.02 ± 0.01 | 0 | 0 | 12 | 0.19 ± 0.05 | 2 | ** | ns | ns |
| *10* | 15 | 0.03 ± 0.01 | 0 | 0 | 3 | 0.30 ± 0.06 | 0 | ** | ns | ns |
| *11* | 22 | 0.12 ± 0.02 | 1 | 4 | 5 | 0.32 ± 0.08 | 0 | ** | ns | ns |
| *12* | 21 | 0.14 ± 0.02 | 0 | 73 | 9 | 0.23 ± 0.05 | 0 | ns | ns | ** |
| *13* | 24 | 0.15 ± 0.02 | 0 | 96 | 18 | 0.31 ± 0.03 | 2 | *** | *** | *** |
| *14* | 28 | 0.14 ± 0.02 | 3 | 96 | 9 | 0.15 ± 0.03 | 0 | ns | *** | *** |
| *15* | 7 | 0.13 ± 0.01 | 0 | 100 | 6 | 0.14 ± 0.06 | 0 | ns | * | ns |

| (c) | Undisturbed plot | | | | Exploited plot | | | |
|---|---|---|---|---|---|---|---|---|
| | | Growth[2] (cm y$^{-1}$) | Mortality (% y$^{-1}$) | Fertile | | Growth[2] (cm y$^{-1}$) | Mortality (% y$^{-1}$) | test[5] |
| Class | N[1] | mean ± se | mean ± se | (%) | N[1] | mean ± se | mean ± se | |
| *1* | 44 | 0.9 ± 0.2 | 25 ± 4 | | 18 | 1.0 ± 0.4 | 31 ± 8 | ns |
| *2* | 28 | 1.0 ± 0.3 | 6 ± 3 | | 9 | 1.3 ± 0.4 | 3 ± 3 | ns |
| *3* | 25 | 2.2 ± 0.8 | 0 ± 0 | | 6 | 0.8 ± 0.4 | 4 ± 4 | ns |
| *4* | 19 | 2.6 ± 0.9 | 2 ± 1 | | 3 | 1.5 ± 1.7 | 4 ± 4 | ns |
| *5* | 417 | 0.01 ± 0.00 | 1 | 0 | 69 | 0.02 ± 0.00 | 2 | * |
| *6* | 281 | 0.01 ± 0.00 | 0 | <1 | 11 | 0.01 ± 0.01 | 0 | ns |
| 7 | 163 | 0.04 ± 0.00 | 1 | 11 | 11 | 0.04 ± 0.01 | 0 | ns |
| *8* | 100 | 0.05 ± 0.01 | 0 | 29 | 13 | 0.05 ± 0.01 | 2 | ns |
| *9* | 60 | 0.06 ± 0.01 | 3 | 53 | 7 | 0.03 ± 0.02 | 0 | ns |
| *10* | 54 | 0.05 ± 0.01 | 0 | 51 | 6 | 0.08 ± 0.01 | 6 | ns |
| *11* | 19 | 0.08 ± 0.02 | 2 | 45 | 3 | 0.12 ± 0.06 | 0 | ns |
| *12* | 22 | 0.06 ± 0.01 | 1 | 65 | 16 | 0.10 ± 0.02 | 4 | ns |

*Basic manipulations*

We used six Lefkovitch (1965) matrices to describe the population dynamics of the study species (3 matrices per plot). The population dynamics is described by

$n_{t+1} = M \times n_t$

where $n_t$ is a $m \times 1$ vector whose entries $n_i$ give the population size distribution at time $t$, and M is a $m \times m$ population matrix whose elements $m_{ij}$ represent the vital rates, the contribution of class $j$ individuals to class $i$ after one projection interval. M is the sum of survival matrix P and birth matrix B, with $p_{ij} = P_i$ (probability of remaining in the same size class) for $j=i$, $p_{ij} = G_{ij}$ (probability of growth) for $j<i$, and $p_{ij} = R_{ij}$ (probability of regression) for $j>i$. $F_j$, the number of offspring per individual, are the elements $b_{ij}$ of B, with $i=1$ for all our study species.

Following methods described by Caswell (1989), we describe the asymptotic behaviour of M by calculating the dominant eigenvalue $\lambda_1$ for each matrix, and its associated right and left eigenvectors $w_1$ and $v_1$. These are interpreted as a measure for the finite rate of increase ($\lambda_1$), the stable population size distribution ($w_1$) and stage-specific reproductive values ($v_1$) for populations growing at a rate $\lambda_1$. The present status of the populations was assessed by calculating the rate of convergence $\rho=\lambda_1 / |\lambda_2|$, where $|\lambda_2|$ is the real part of the second largest eigenvalue. A low rate of convergence ($\approx 1$) indicates that a population is approaching asymptotic behaviour very slowly and that transient behaviour is more relevant for describing the population dynamics of the species.

To assess the sensitivity of $\lambda_1$ to changes in the $m_{ij}$, we derived sensitivity and elasticity matrices S and E using standard procedures (Caswell 1989, de Kroon *et al.* 1984). The $s_{ij}$ give the rate of change in $\lambda_1$ to absolute changes in $m_{ij}$, the $e_{ij}$ do the same for proportional changes in $m_{ij}$. The $e_{ij}$ sum to 1 (de Kroon *et al.* 1984, Mesterton-Gibbons 1993), and therefore depend on each other. Moreover, the likelihood of a proportional change in $m_{ij}$ depends on the biological variability of the $m_{ij}$, which is not the same for each size class. Hence, we consider the summed $e_{ij}$ per stage as a better measure for the contribution of its demographic rates to population growth than the individual $e_{ij}$. These sums are equal when taken over columns or over rows (van Groenendael *et al.* 1994).

Although the methodology for their application has been developed (de Kroon *et al.* 1987, Alvarez-Buylla 1994, Takada & Nakashizuka 1996), we did not incorporate density-dependent dynamics and patch dynamics in the model, for the following reasons. Intra-specific density-dependence has been shown for tropical trees but only in very common species using a very large data-set (Condit *et al.* 1994), or in seeds and seedlings of some species (Janzen-Connell effect, Hammond & Brown (*in press*)). Our species are common, but the data-set is from an area which is too small to detect the effect of varying density on sapling and seedling growth and survival. Furthermore, growth- and survival-reducing effects of a high density are not expected to be limited to intra-specific interactions, but would rather be species-independent, through, *e.g.*, asymmetric competition for light (Weiner 1990, Kohyama 1992a). This requires a model for the entire stand rather than one species. Moreover, new assumptions will apply to the matrix model, while it will loose its attractive asymptotic characteristics (population growth rate, elasticity analysis *etc.*). The inclusion of patch-dynamics assumes that species have different dynamics in gaps, building phase patches and mature forest. Although for pioneers this might be a satisfactory simplification, for climax species it is not. In each patch type a large range of light environments is found between very dark and very light (for these plots: see Chapter 6), and an appropriate model would require the dynamics of light environments rather than the dynamics of patches. This information is not available.

To compare the three study species with other species, we took the following published matrices for (sub-)tropical trees (not palms): *Pentaclethra macroloba* (shade-tolerant canopy species; Hartshorn 1972), *Cecropia obtusifolia* (pioneer; Alvarez-Buylla 1994, 1983-1990 global matrix), *Araucaria cunninghamii* (shade-tolerant? canopy species; Enright & Ogden 1979), *Brosimum alicastrum* (shade-tolerant? canopy species; Peters 1991, recalculated from Table 14.1, females and hermaphrodites only), *Grias peruviana* (shade-tolerant understorey species; Peters 1996), and *Pinus palustris* (light-demanding? canopy species; Platt *et al.* 1988; B estimated by proportionally distributing 245 recruits over adult size classes using Fig. 4). In addition, we introduce 2 new matrices for the shade-tolerant canopy species *Prioria copaifera* from data provided by Condit *et al.* 1993a, Table 1, estimating B from data provided in the text. (We assumed that the species started reproducing at dbh=32 cm rather than 64 cm, as stated in the text). Matrix *Prioria* 1 is based on census data from 1982-1985; *Prioria* 2 refers to the period 1985-1990. All matrices include seeds and seedlings, except *Pinus* (lower dbh limit 2 cm) and *Prioria* (1 cm dbh). All projection intervals are 1 year, except *Pinus*, for which it is 4 years. The *Pinus* and *Prioria* matrices are given in Appendix A.

### Size-age relations

#### *A matrix modelling approach*

Recently, Cochran & Ellner (1992) derived formulas to estimate age-based life history characters from stage-classified matrices. We used these formulas to calculate the survivorship function $l_x$, the stage-specific conditional total life span (the sum of $183_i$, the mean age of reaching stage *i*, and $\Omega_i$, the life expectancy for individuals in stage *i*, for a cohort born at $t$=1), and the mean age at which a newborn enters the first reproductive class (which equals the $\tau_i$ for the first reproductive class in our species). Furthermore, we calculated generation times and $p_{i,a}$, the stable stage-specific age distribution. All calculations are based on survival matrix **P**. For formulas and derivations we refer to Cochran & Ellner (1992).

#### *Growth trajectories*

We contrast the age estimates derived from matrix modelling with estimates of tree age derived from growth projection, based on the method of Lieberman & Lieberman (1985b), to which we added a mortality model. We let virtual trees grow from a dbh of 1.4 cm (class 9, *Chlorocardium*, *Dicymbe*) and 1 cm (class 6, *Duguetia*) with annual increments that were based on the growth equation (1) with the species-specific fitted coefficients. The projection was continued until a random number between 0 and 1 (drawn at each time-step) was equal to or more than the size-specific survival rate pre-

**Table 5**

**Spearman rank correlations between Dawkins index and growth for three species in undisturbed and exploited forest near Mabura Hill, Guyana. The individuals are grouped in three classes: seedlings (height growth; *Dicymbe* classes 2-7, *Chlorocardium* 4-7, *Duguetia* 1-4), subcanopy (dbh growth; *Dicymbe* and *Chlorocardium* 8-11, *Duguetia* 5-12) and canopy (dbh growth, rest). There were no *Duguetia* in the canopy. Significance levels are denoted by asterisks: *** p≤0.001; ns not significant.**

| | | Undisturbed | | Exploited | | N |
|---|---|---|---|---|---|---|
| Seedlings | *Dicymbe* | 0.19 | *** | 0.29 | *** | (1576, 250) |
| | *Chlorocardium* | 0.41 | *** | 0.49 | *** | (783, 398) |
| | *Duguetia* | 0.32 | *** | 0.29 | ns | (116, 36) |
| Subcanopy | *Dicymbe* | 0.40 | *** | 0.69 | *** | (1298, 1126). |
| | *Chlorocardium* | 0.49 | *** | 0.70 | *** | (155, 57) |
| | *Duguetia* | 0.25 | *** | 0.53 | *** | (1115, 137) |
| Canopy | *Dicymbe* | 0.03 | ns | 0.11 | ns | (144, 90) |
| | *Chlorocardium* | 0.30 | *** | 0.17 | ns | (80, 42) |

dicted by equation (2). The annual increment was determined according to three different scenarios: (1) random growth, resulting from a normal distribution with size-specific mean and a standard deviation given by equation (1) fitted through the residuals around the mean; (2) (size-specific) mean growth plus one standard deviation; this reflects the often-made assumption that only fast growing trees reach maturity (*e.g.*, Liu & Ashton 1995); (3) 'Auto-correlated' growth: either the mean of the 10 previous growth rates, or the size-specific growth given by equation (1), whichever was higher. To this rate (3) a random standard error was added as in scenario 1. Scenario 3 was not designed to present a realistic growth trajectory, but rather to assess the effects on mean and variance in size-age relationships of individual growth histories which are characterised by periodic accelerations. In the forest this is possible if trees are released from competition by gap formation or exploitation. Both very slow and very fast growth histories occur in scenario 3, as is also possible in real trees differing in site conditions or genetic background. We ran the simulations *c.* 2500 times over a maximum of 500-600 years.

From these data we report projected maximum life-span and the mean age at reaching reproductive age.

### *$^{14}$C determinations*

A third method to estimate tree age, only done for *Chlorocardium*, was by analysing three wood samples taken from the core of three large freshly cut trees (dbh 110, 92 and 90 cm) for their $^{14}$C content. The samples were analysed by Accelerator Mass Spectrometry at the R.J. van de Graaff Laboratory of the Department of Subatomic Physics, Utrecht University (sample numbers UtC 4973-4975).

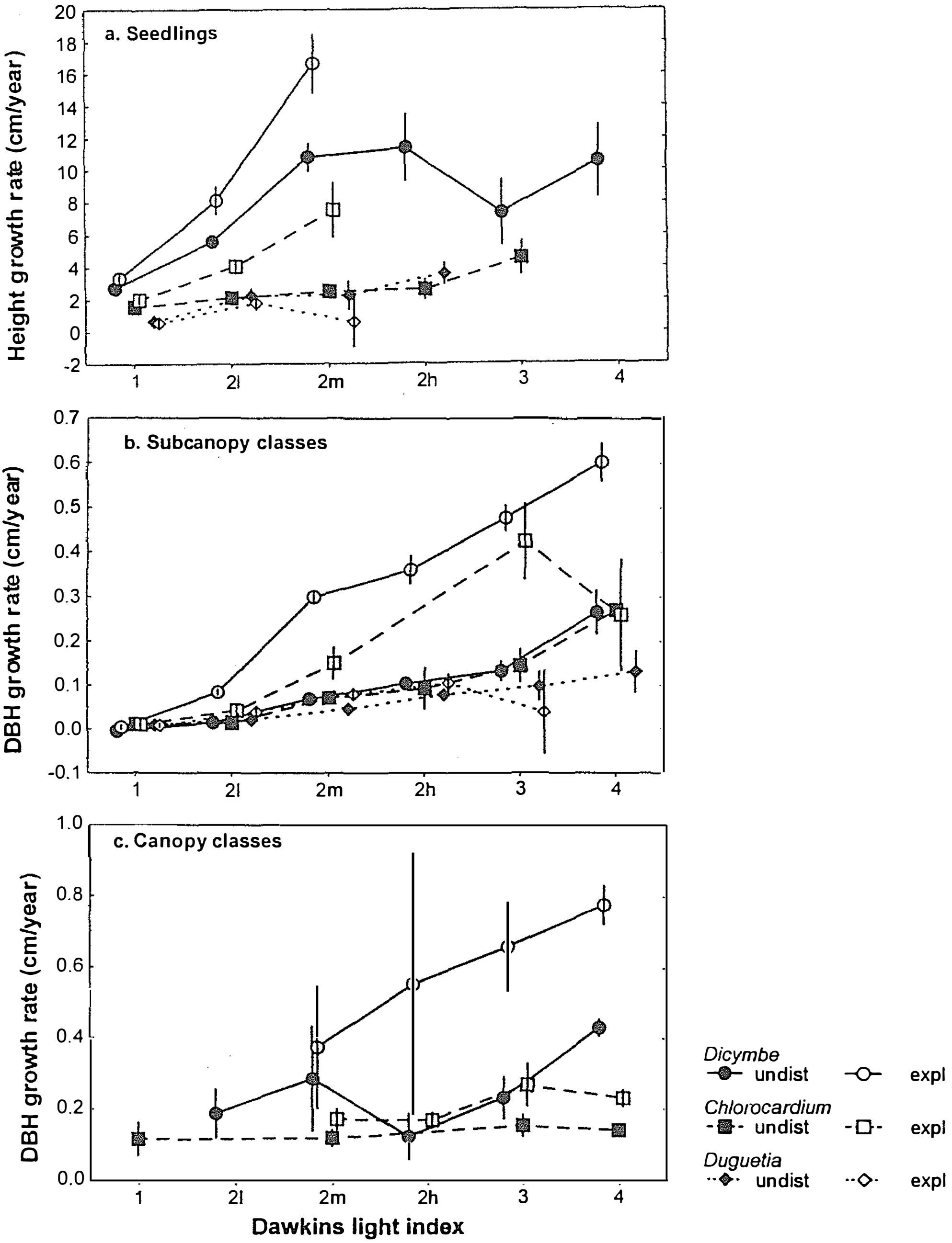


**Figure 3**

Relation between Dawkins index and growth for three groups of pooled size classes per species: a. seedlings (*Dicymbe* class 2-7, *Chlorocardium* 4-7 (growth in 2-3 was not light driven *cf.* Table 1), *Duguetia* 1-4); b. subcanopy classes (*Dicymbe* and *Chlorocardium* 8-11, *Duguetia* >4); c. Canopy classes (classes (*Dicymbe* and *Chlorocardium* >11). ○ ●, *Dicymbe*; □ ■, *Chlorocardium*; ◇ ◆, *Duguetia*. Closed symbols, undisturbed plot; open symbols, exploited plot. Lines are solely drawn to guide the eye.

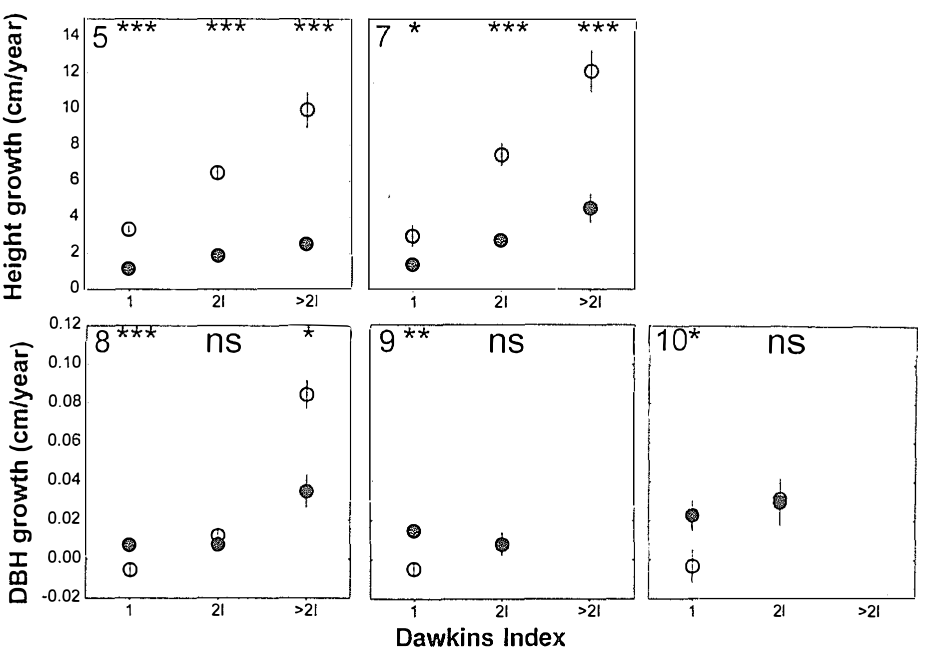


**Figure 4**

Comparison of mean (±s.e.) growth of *Dicymbe* (open dots) and *Chlorocardium* (closed dots) per light class (Dawkins index) with increasing size. Numbers refer to size classes. Height growth is given for classes 5 and 7, which are the high leaf density classes. Dbh growth is given for remaining classes. Plants with Dawkins index 2m and more are pooled; where absent there were too few observations. Results Mann-Whitney tests per light class are given by asterisks: * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$; ns not significant.

## Exploitation

Our data describe the current vital rates of populations 4-7 years after logging. The asymptotic behaviour of population matrices provides little information about the population parameters that are subjected to strongly varying vital rates (Boot & Gullison 1995), as is expected in the case of logging. Therefore we simulated population responses of *Chlorocardium* to logging by creating matrices that varied with time since logging. We followed the development of the population in terms of population size and amount of timber (defined as trees belonging to classes 13 and 14, 31-80 cm dbh; larger trees are usually hollow, ter Steege 1990) by sequentially multiplying the population vector $n_t$ with these matrices. We assessed the consequences of a number of logging scenarios based on the following considerations and assumptions:

### *Growth stimulation*

Growth stimulation is maximal just after logging after which it gradually dissipates over a period of 20 years. Hereafter the vital rates are the same as in the undisturbed forest. We modelled this by fitting an equation derived from (1) through the data of

*Chlorocardium* growth rates of both plots combined. Fitted parameter *b* (which gives the slope of the response function at small dbh, Zeide 1993) was made linearly dependent on time since logging, where time was 6 years for the exploited plot and 20 years for the undisturbed plot. This might give a somewhat optimistic estimate of the length of the period with increased growth rates and of the first year growth (which is often not so high due to damage and physiological acclimation). We compared this with the same scenario, in which growth in the first year after logging was lower (equal to second year), and to a scenario in which growth in the first 10 years was given by the exploited population, and thereafter by the undisturbed population.

It was evident that possible positive effects of logging on growth and survival of *Chlorocardium* seedlings had largely disappeared by the time the study began (Chapter 7). Because we had no strong quantitative data, we studied the effect of various estimates for growth transitions between the leafy seedling classes (classes 3, 5 and 7), reduced mortality transitions and reduced regression transitions between leafy and leaf-poor seedling classes. Transitions from seeds to other classes, multi-step transitions and regressions between height classes (*e.g.*, from 4 to 2) were considered unaffected by logging. We also assumed that seed germination in the exploited plot did not respond to canopy openness (Chapter 7), although other data exist that suggest that germination is reduced (*cf.* Chapter 5, ter Steege *et al.* 1994, Hammond *et.al. in prep.)*, and that regressions between size classes were the consequence of damage, not of resource (light) scarcity. We only report the hypothetical effects of increasing growth transitions for seedlings (observed growth transitions increased by factors 2, 4 and 6 over 5 years, while simultaneously adjusting stasis).

### *Damage reduction*

Although there is some information on the relation between extraction rate and light availability in gaps in a similar forest (ter Steege *et al.* 1994), we have insufficient data to assess how different logging intensities affect the transition probabilities. We therefore assumed that the modelled growth stimulation was independent of extraction rate and damage to the residual stand. We calculated the effect of extraction rates of 50, 40 and 30% of the original timber stand under this assumption. Lower extraction rates would certainly affect growth rates negatively.

Damage to the residual stand depends on logging intensity (*e.g.*, Johns *et al.* 1996, Hendrison 1990), but we had no quantitative data. We assumed that logging and skidding damage to large saplings and pre-adults (class 8-11) was 5% as in careful logging, and we report the effect of varying damage to seedlings (classes 1-7: 25, 15 and 5% of the initial population destroyed). Growth and survival on skid trails may be different than elsewhere in the plot in the period just after logging, but at 4-7 years after logging this was not the case for *Chlorocardium* (Chapter 7). We made no distinction between skid-trails and other habitats in the simulations.

### *Silvicultural intervention and repeated logging*

Three forms of silvicultural intervention were considered: (a) thinning of the secondary vegetation, leading to extension of the phase of fast seedling growth from 5 to 10

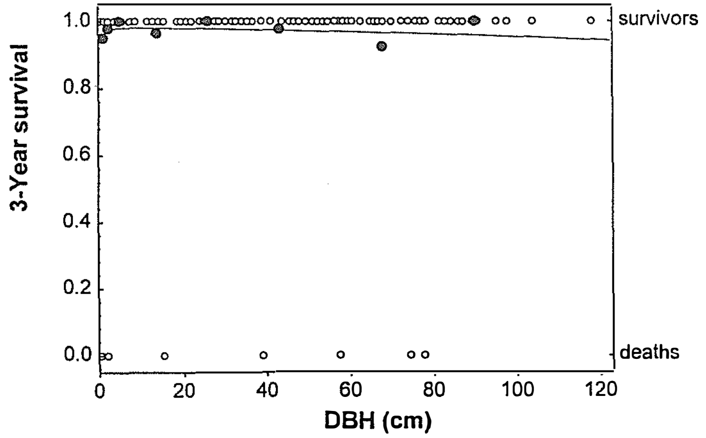


**Figure 5**
**Results of logistic fitting of survival in relation to stem diameter for *Chlorocardium*. The data for both plots were combined. Drawn line: survival curve predicted by equation (2). O: tree fates after three years: died (y=0) or survived (y=1). ●: observed three-year survival per size class, plotted at the size class midpoint. These points are added for reference; the function was fitted with the open dots. Other species gave comparable results.**

years. (b) pre-logging liberation of large saplings and pre-adults (classes 10-11). We modelled this simply by adjusting abundance in the pre-logging population vector. (c) Liberation of large saplings and pre-adults. This was done by assigning them transitions belonging to the first 7 years of post-logging growth rates for 3 times during a 20 year period following logging (slightly adapted from De Graaf 1986).

Our data concern the response of a population to first-time logging, and nothing is known about responses during subsequent logging cycles. We calculated the effect of various logging cycles assuming that the population response to logging would be the same after each exploitation.

For comparison, we simulated the response of *Dicymbe* to logging of *Chlorocardium* under identical conditions. All simulations were run over 400 years.

## Results

### Population structure and abundance

*Dicymbe* was the most abundant species of the three in both plots (Fig. 1). The high abundance of *Dicymbe* saplings between 0 and 7 cm dbh (classes 8-10) in the exploited plot compared to the undisturbed plot reflect a strong response to logging. In many logging gaps, but also in forest remnants that received a lot of lateral light, *Dicymbe*, and not saplings of true pioneers such as *Cecropia* spp. or *Goupia glabra*, dominated the secondary vegetation. The adult population of *Chlorocardium* in the logged plot was strongly reduced by logging and consisted in majority of rejected trees (hollow, rot, crooked, or forked). In both plots *Chlorocardium* was poorly represented in juve-

**Table 6**

**Fitted parameters for the size-growth (Hossfeld IV) and size-survival (Huisman-Olff-Fresco) functions obtained for undisturbed and exploited populations of three tree species in the rain forest near Mabura Hill, Guyana. Explained variance for the survival model is not reported, because this gives little information about the fit of logistic models.**

| | *Dicymbe*[1] | | *Chlorocardium*[2] | | *Duguetia* | |
|---|---|---|---|---|---|---|
| | undist. | expl. | undist. | expl. | undist. | expl. |
| Size-growth (eq. 1) | | | | | | |
| a | 59.06 | 86.36 | 22.59 | 32.93 | 0.62 | 4.47 |
| b | 217.43 | 16.80 | 119.25 | 18.05 | 290.33 | 76.31 |
| c | 2.14 | 1.74 | 1.76 | 1.54 | 2.55 | 1.74 |
| Variance expl. (%) | 53.7 | 41.0 | 55.0 | 42.8 | 11.4 | 23.3 |
| Size-survival (eq. 2) | | | | | | |
| a | -2.12 | -1488 | -4.01 | | -4.36 | -4.91 |
| b | -0.15 | -244 | 0.01 | | 0.16 | 1.35 |
| c | -5.53 | -4.31 | -3.03 | | -2.97 | -3.38 |
| d | 0.02 | 0.01 | -0.66 | | -2.43 | -1.29 |

[1] **Survival only fitted for individuals ≥3.4 cm dbh due to incomplete survival data for classes 8-9.**

[2] **Survival data for both plots lumped due to low mortality in exploited plot.**

nile size classes (9-11). This lack of juveniles was particularly pronounced in the exploited plot. This parallels results obtained in other logged areas near Mabura, and is arguably caused by logging damage (Zagt 1995). The logged plot had a higher abundance of large *Chlorocardium* seedlings (6-7). *Duguetia* was characterised by a relatively flat population size distribution. Individuals <7 cm dbh were underrepresented in the exploited population compared to the undisturbed population.

### Growth, mortality and reproduction

In both plots, *Dicymbe* had a higher mean growth rate than *Chlorocardium* for all size classes except the smallest seedling classes. However, the variation in growth rate was large and differences between species were only significant in adult and seedling size classes when tested with Mann-Whitney U-tests (Fig. 2a, Table 4). The high growth rate of *Chlorocardium* in the small size classes (2-3) was mainly due to germinating seedlings that grew on cotyledonary reserves. *Duguetia* had slow average growth rates (Fig. 2b, Table 4). When tested over the same diameter range (*Chlorocardium* and *Dicymbe* classes 8-10, *Duguetia* classes 5-12), *Duguetia* had the same growth rate as *Chlorocardium* ($p>0.17$), but less than *Dicymbe* ($p<0.001$) in both plots (Mann-Whitney tests).

In the exploited plot, *Dicymbe* and *Chlorocardium* grew faster than in the undisturbed plot for most size classes. For *Duguetia* there was hardly any difference in growth rate between undisturbed and exploited populations. However, most *Duguetia* in the exploited plot grew below the secondary canopy, so the difference in growth between both plots is not necessarily caused by a lack of response to light.

Most correlations between Dawkins index and growth rates in pooled size classes were highly significant and positive (Fig. 3, Table 5), showing that growth rates increased with increasing crown illumination in all species. The exception is formed by individuals in the canopy, which showed little response, whereas the response in the subcanopy classes was strong. There seemed to be a stronger response to light in exploited than in undisturbed populations for *Chlorocardium* and *Dicymbe*, particularly for the subcanopy size classes (Fig. 3b; Mann-Whitney tests; *Dicymbe*: 10 of 13 comparisons significant at $p \leq 0.05$; *Chlorocardium* 6 of 11; *Duguetia*: 2 of 8). Interspecific differences in growth per light class in the subcanopy were rarely significant when tested with Kruskal-Wallis anova: in the undisturbed plot there were interspecific differences in growth in the three lowest Dawkins classes; in the exploited plot this was only in class 2m (data not shown). The interpretation of this pattern is complex, because the effects of light (Fig. 3) and size (Fig. 2) are confounded. We further analysed the relation between light, size class and species (*Dicymbe* and *Chlorocardium*) in the undisturbed plot (where sufficient individuals were available). The results showed that seedlings (the leafy classes 5 and 7) of *Dicymbe* had a higher height growth than *Chlorocardium*, independent of Dawkins index (Fig. 4; also Chapter 6). For (diameter) growth of larger size classes (8-11) this was different. At low light (Dawkins index 1), *Dicymbe* had a lower growth than *Chlorocardium*, while at Dawkins 21 there was no significant difference, and at higher light classes *Dicymbe* had a higher growth rate (although the data were few for high light classes).

Mortality of larger saplings and trees (height >1.3 m) was a rare occurrence and was generally limited to one or two individuals per size class over the entire study period (Table 4, Fig. 5 for *Chlorocardium*). Seedling mortality was much higher.
*Chlorocardium* had the highest seedling mortality, *Duguetia* had the lowest mortality and it was strongly concentrated in the smallest size class. For *Chlorocardium* and *Dicymbe*, the mortality in size classes with a low leaf density (classes 2, 4 and 6) was consistently higher than in classes with a high leaf density (classes 3, 5 and 7). Exploited seedling populations tended to have higher average seedling mortality than their undisturbed counterparts, but in *Chlorocardium* this varied per size class. The fitted parameters for the growth and mortality functions are given in Table 6. The dataset was too small to analyse light-dependent mortality. Previous results for seedlings in the undisturbed plot indicated that mortality is only higher in the lowest light class (Dawkins index 1; Chapter 6).

*Dicymbe* and *Chlorocardium* flowered from the moment they reached the canopy. In *Chlorocardium* flowering was annual and most individuals flowered each year. *Dicymbe* flowered in 1991 (before the populations were marked), 1993 and started but failed in 1995 (because of drought). We could only collect data for 1993. About 60% of the potentially reproductive population was actually flowering (Chapter 3) individuals in the transitional class were generally not flowering. It is unknown whether the remaining 40% were flowering in other years. Flowers and fruits in *Duguetia* were difficult to find and the data from Table 4 represent a cumulative result over three years. Exploited populations seemed to differ in a number of respects from their undisturbed counterparts. All *Chlorocardium* from class 12 and up flowered each year and appeared to produce more flowers, but less seed in the exploited plot. *Dicymbe* trees were flowering rather poorly in this plot, and the number of flowering *Duguetia* that was found was very low. Still, several trees with over 10 fruits were found (compared to a maximum of 4 fruits for the undisturbed population). However, we have no strong quantitative data to support these observations and we assume for the purpose of this paper that fecundity in either population was the same for all three species.

The density in December of seeds and just germinated seedlings in the seedling sample plots in the undisturbed plot was estimated at 0.4 ± 0.2 $m^{-2}$ (sd over three years) for *Chlorocardium*, 1.9 ± 0.0 $m^{-2}$ (1991 and 1993) for *Dicymbe* and 0.02 ± 0.01 $m^{-2}$ (three years) for *Duguetia*. This led to average fecundity estimates of 125, 195 and 0.47, respectively, per potentially mature individual per year. The fecundities for the small individuals belonging to classes 7 and 8 were reduced in proportion to the small number of fertile individuals in these classes. All fecundity estimates should be considered as very rough.

### Matrix models

Table 7 summarises the growth, survival and fecundity data of the six populations in transition matrices. The transitions for the seedling classes (*Chlorocardium* and *Dicymbe* 1-7, *Duguetia* 1-4) were calculated from actually observed transitions and show a considerable amount of regression to smaller size classes, particularly from classes with high to classes with low leaf density (*e.g.*, from class 5 to 4 in *Chlorocardium*, undisturbed). In these classes multi-step transitions were also observed. The fecundities for the exploited and undisturbed populations are taken to be the same. *Chlorocardium* and *Dicymbe* differ in the fecundity of transition class 12. *Chlorocardium* was characterised by a high juvenile mortality and slow growth rates (Table 4). *Dicymbe* was a fast grower in all size classes, and produced many seeds, but not at an annual basis. *Duguetia* was a slow growing species and had a very low fecundity, but suffered very low seedling mortality. The demographic parameters that can be derived from these matrices are presented in Table 8. *Chlorocardium* and *Duguetia* have $\lambda_1$ which are very close to unity, indicating that these populations are increasing or decreasing at slow rates. In contrast, both *Dicymbe* populations are expected to strongly increase their numbers if the present conditions were maintained. The $\lambda_1$ of 1.14 in the exploited population has no long-term meaning because of the strongly changing demographic conditions in that plot, but it does confirm that *Dicymbe* is in a period of strong proliferation after logging.

The stable population structures (given by the dominant right eigenvectors; Fig. 1) are different from present population structures in all populations when tested with Kolmogorov-Smirnov two sample tests (assuming equal population sizes; all $p<0.001$). Stable population size distributions of *Dicymbe* show a higher relative abundance of subadult trees (classes 9-12). This tendency is very strong for *Chlorocardium*, although the relative scarcity of class 9 and 10 individuals, characteristic for undisturbed populations, is also present in stable populations. The data suggest that if total population siz-

**Table 7**

**Population transition matrices for undisturbed and exploited populations of three tree species from the rain forest near Mabura Hill, Guyana.**

**(a) Population matrix for *Dicymbe*, undisturbed population**

| *1* | *2* | *3* | *4* | *5* | *6* | *7* | *8* | *9* | *10* | *11* | *12* | *13* | *14* | *15* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 195 | 195 | 195 |
| 0.129 | 0.270 | 0.143 | 0.013 | 0.004 | 0.003 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0.496 | 0.135 | 0.494 | 0.010 | 0.013 | 0 | 0.001 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0.014 | 0.093 | 0.026 | 0.476 | 0.100 | 0.019 | 0.012 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0.087 | 0.097 | 0.206 | 0.220 | 0.748 | 0.015 | 0.021 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0.056 | 0.015 | 0.700 | 0.197 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0.002 | 0 | 0.006 | 0.079 | 0.177 | 0.673 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0.029 | 0.076 | 0.980 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.009 | 0.980 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.014 | 0.965 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.016 | 0.975 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.017 | 0.958 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.038 | 0.981 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.016 | 0.981 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.016 | 0.996 |

**(b) Population matrix for *Dicymbe*, exploited population**

| *1* | *2* | *3* | *4* | *5* | *6* | *7* | *8* | *9* | *10* | *11* | *12* | *13* | *14* | *15* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 195 | 195 | 195 |
| 0.039 | 0.023 | 0.040 | 0 | 0.021 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0.173 | 0.083 | 0.171 | 0 | 0.021 | 0 | 0.003 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0.039 | 0.062 | 0.044 | 0.146 | 0.140 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0.116 | 0.193 | 0.153 | 0.453 | 0.435 | 0 | 0.012 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0.038 | 0.511 | 0.303 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0.029 | 0 | 0.069 | 0 | 0.158 | 0.180 | 0.433 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0.092 | 0.167 | 0.761 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0.004 | 0.009 | 0.157 | 0.767 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.179 | 0.828 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.157 | 0.872 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.111 | 0.799 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.186 | 0.930 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.055 | 0.938 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.040 | 0.970 |

**(c) Population matrix for *Chlorocardium*, undisturbed population**

| *1* | *2* | *3* | *4* | *5* | *6* | *7* | *8* | *9* | *10* | *11* | *12* | *13* | *14* | *15* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0.112 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 125 | 125 | 125 | 125 |
| 0.172 | 0.158 | 0.164 | 0.022 | 0.025 | 0.004 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0.051 | 0.039 | 0.203 | 0 | 0.027 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0.036 | 0.062 | 0.050 | 0.421 | 0.241 | 0.088 | 0.008 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0.006 | 0.022 | 0.041 | 0.034 | 0.544 | 0.040 | 0.030 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0.001 | 0 | 0 | 0.015 | 0.005 | 0.470 | 0.070 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0.002 | 0.028 | 0.078 | 0.829 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0.004 | 0.026 | 0.972 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.014 | 0.975 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.016 | 0.979 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.014 | 0.986 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.007 | 0.978 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.014 | 0.984 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.006 | 0.983 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.006 | 0.986 |

**(d) Population matrix for *Chlorocardium*, exploited population**

| *1* | *2* | *3* | *4* | *5* | *6* | *7* | *8* | *9* | *10* | *11* | *12* | *13* | *14* | *15* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0.120 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 125 | 125 | 125 | 125 |
| 0.135 | 0 | 0.049 | 0.077 | 0.013 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0.029 | 0 | 0.612 | 0.000 | 0.074 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0.101 | 0.083 | 0.097 | 0.204 | 0.070 | 0.113 | 0.016 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0.029 | 0 | 0.097 | 0.021 | 0.704 | 0.007 | 0.026 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0.010 | 0.009 | 0.206 | 0.176 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0.037 | 0.016 | 0.721 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0.013 | 0.927 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.058 | 0.932 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.058 | 0.948 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.045 | 0.975 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.019 | 0.962 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.030 | 0.980 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.011 | 0.981 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.008 | 0.986 |

**(e) Population matrix for *Duguetia*, undisturbed population**

| *1* | *2* | *3* | *4* | *5* | *6* | *7* | *8* | *9* | *10* | *11* | *12* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 0.628 | 0.028 | 0 | 0 | 0 | 0 | 0.17 | 0.44 | 0.80 | 0.80 | 0.80 | 0.80 |
| 0.121 | 0.798 | 0.044 | 0.011 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0.108 | 0.890 | 0.046 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0.009 | 0.066 | 0.873 | 0.007 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0.046 | 0.929 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0.056 | 0.978 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0.016 | 0.961 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0.032 | 0.945 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.047 | 0.935 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.057 | 0.930 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.060 | 0.930 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.058 | 0.985 |

**(f) Population matrix for *Duguetia*, exploited population**

| *1* | *2* | *3* | *4* | *5* | *6* | *7* | *8* | *9* | *10* | *11* | *12* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 0.550 | 0.061 | 0.042 | 0 | 0 | 0 | 0.17 | 0.44 | 0.80 | 0.80 | 0.80 | 0.80 |
| 0.141 | 0.879 | 0 | 0.042 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0.030 | 0.821 | 0.089 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0.095 | 0.786 | 0.005 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0.042 | 0.949 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0.028 | 0.960 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0.030 | 0.946 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0.043 | 0.934 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.054 | 0.923 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.063 | 0.913 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.071 | 0.905 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.077 | 0.977 |

es would remain the same, timber (classes 13 and 14) will be less abundant in stable populations than in the present populations.

The real part of the second largest eigenvalue, $\lambda_2$ was not much lower than $\lambda_1$ in all populations, leading to damping ratios $\rho$ which were not far from 1 (Table 8). This means that the period required to reach asymptotic behaviour and stable population size distribution may belong.

**Table 8**

**Demographic parameters derived from population transition matrices constructed for the study species near Mabura Hill and for a number of other tree species (see methods). $\lambda_1$ - dominant eigenvalue of the matrix; $\lambda_P$ - eigenvalue of the matrix assuming zero fecundity; $\rho$ - damping ratio; $\mu$ - generation time.**

| Species | | $\lambda_1$ | $\lambda_P$ | $\rho$ | $\mu$ | (sd) |
|---|---|---|---|---|---|---|
| *Chlorocardium* | undist. | 0.998 | - | 1.011 | 302 | (135) |
| *Dicymbe* | undist. | 1.028 | 0.996 | 1.019 | 467 | (267) |
| *Duguetia* | undist. | 1.006 | 0.985 | 1.023 | 200 | (93) |
| *Chlorocardium* | exploit. | 1.003 | 0.986 | 1.025 | 188 | (97) |
| *Dicymbe* | exploit. | 1.135 | 0.970 | 1.076 | 71 | (37) |
| *Duguetia* | exploit. | 0.990 | 0.977 | 1.020 | 141 | (61) |
| *Pentaclethra* | | 1.002 | - | 1.028 | 115 | (46) |
| *Pinus* | | 1.012 | 0.899 | 1.112 | 140 | (76) |
| *Cecropia* | | 1.012 | 0.932 | 1.308 | 27 | (17) |
| *Prioria 2* | | 1.018 | 0.988 | 1.028 | 193 | (94) |
| *Prioria 1* | | 1.019 | 0.988 | 1.031 | 174 | (89) |
| *Grias* | | 1.020 | 0.980 | 1.073 | 90 | (57) |
| *Araucaria* | | 1.020 | 0.984 | 1.039 | 208 | (109) |
| *Brosimum* | | 1.067 | 0.986 | 1.089 | 127 | (87) |

Sensitivity, the response of $\lambda_1$ to changes in transition probabilities, varied by several orders of magnitude between the matrix elements, with *Chlorocardium* showing the largest range and *Duguetia* the smallest (Fig. 6). Changes in growth probabilities generally had a larger effect on $\lambda_1$ than changes in stasis. The exploited and undisturbed populations had rather similar sensitivities, except for seedling stages. The summed elasticity values per class show that proportional changes in the vital rates of the pre-reproductive size class have the largest effect on $\lambda_1$ for *Chlorocardium* and *Duguetia*, but not for *Dicymbe*. In this species elasticities are about equal in all stages that are defined on diameter (8-15), and peak in the class of 'small adults' (just as exploited *Chlorocardium*). The largest size class has low elasticity except for *Duguetia*. None of the species was very sensitive to changes in fecundity: their sensitivity is about a factor 10 lower than the lowest non-fecundity element in all species, and elasticity is well below 1%, except for exploited *Dicymbe* populations (max. 2.5%).

## Age estimates

Survivorship matrices P were used to construct the survivorship function $l_x$, the expected fraction of newborns that is still alive after $x$ years (Fig. 7). This reveals large differences between the population matrices. Both *Chlorocardium* populations suffer a high initial mortality, and have a similar survivorship curve, whereas *Dicymbe* and *Duguetia* have rather different survivorship between plots. After *c.* 40 years the survival

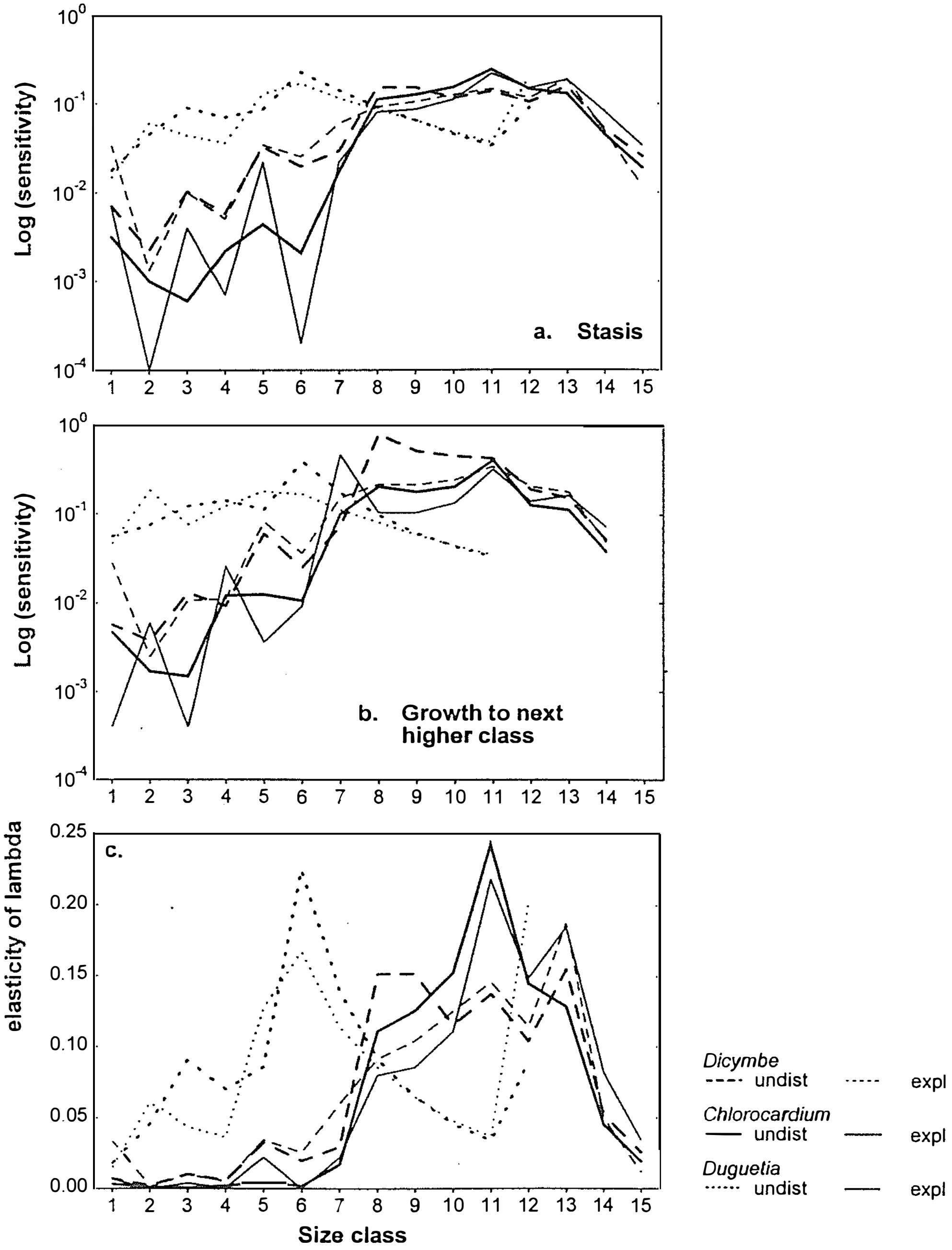


**Figure 6**

Sensitivity (a, stasis, b, growth to the next larger size class) and elasticity analysis (c) for the population matrices of the six study populations. Note the log scale in the sensitivity figures. Elasticity values of each class are summed.

**Table 9**
**Projected mean age at reaching stage *i*, $\tau_i$, for the six study populations, assuming unchanging vital rates. Between brackets is the standard error.**

| | *Dicymbe* | | *Chlorocardium* | | *Duguetia* | |
|---|---|---|---|---|---|---|
| | undisturbed | exploited | undisturbed | exploited | undisturbed | exploited |
| *1* | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| *2* | 4 (4) | 3 (1) | 2 (1) | 2 (1) | 4 (2) | 3 (2) |
| *3* | 2 (2) | 2 (1) | 2 (1) | 3 (2) | 9 (5) | 11 (8) |
| *4* | 8 (6) | 3 (1) | 3 (2) | 3 (2) | 20 (14) | 17 (9) |
| *5* | 4 (2) | 3 (1) | 3 (1) | 3 (1) | 39 (26) | 25 (13) |
| *6* | 12 (6) | 5 (2) | 5 (4) | 8 (5) | 54 (31) | 46 (24) |
| *7* | 10 (6) | 4 (2) | 6 (2) | 7 (4) | 100 (55) | 71 (34) |
| *8* | 19 (11) | 7 (4) | 12 (6) | 10 (5) | 126 (60) | 89 (39) |
| *9* | 69 (51) | 11 (5) | 47 (36) | 24 (14) | 144 (63) | 104 (41) |
| *10* | 119 (71) | 15 (6) | 87 (53) | 39 (20) | 159 (64) | 117 (43) |
| *11* | 147 (76) | 21 (8) | 135 (71) | 58 (27) | 173 (66) | 129 (45) |
| *12* | 187 (86) | 29 (11) | 206 (100) | 98 (48) | 188 (67) | 139 (46) |
| *13* | 211 (89) | 34 (12) | 252 (110) | 124 (55) | | |
| *14* | 264 (103) | 48 (18) | 314 (126) | 174 (74) | | |
| *15* | 317 (116) | 64 (24) | 373 (139) | 227 (90) | | |

rates were projected to be similar for all species, but at that moment there were still 75-410 surviving individuals of *Dicymbe* and *Duguetia* for each surviving *Chlorocardium.* The other species for which this could be calculated show a variety of survivorship curves, which were all more closely to *Chlorocardium* than to the other two species. *Cecropia* showed the lowest survivorship; *Dicymbe* and *Duguetia* by far the highest.

Individuals from undisturbed populations that reach the largest size class did so at a mean estimated age $\tau_i$ of over 300 years for the two canopy species and just below 200 years for *Duguetia* (Table 9). The expected remaining life-span in this class (Fig. 8) depended strongly on the accuracy of the estimate for the survival rate $\sigma$. *Dicymbe* individuals entering class 15, with $\sigma_{15} = 0.996$, had a life expectancy of 250 years $(=1/(1-\sigma_{15}))$ in that class, almost certainly an over-estimate. *Chlorocardium,* with 1% lower survival, had a much reduced life expectancy of 71.4 years. Summation of $\tau_i$ and life expectancy of this class yields the expected total life-span of 445, 567 and 254 years, for *Chlorocardium*, *Dicymbe* and *Duguetia*, respectively. The projected mean ages for the smallest size classes in *Chlorocardium* and *Dicymbe* show, remarkably, that *Chlorocardium* is projected to reach the same size class at a younger mean age than *Dicymbe* (Table 9). The possible reason is that *Chlorocardium* suffers high seedling mortality, which prevents seedlings from remaining very long in one size class before growing into the next. This depresses mean ages, even though growth rates are smaller than for *Dicymbe.*

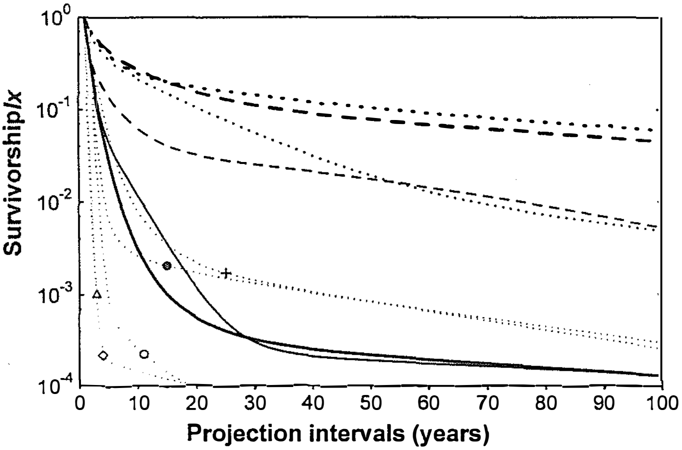


**Figure 7**

**The projected survivorship function $l_x$ for the six study populations and five species with published population transition matrices. Drawn lines, *Chlorocardium*; broken lines, *Dicymbe*; stippled lines, *Duguetia*. Bold lines, undisturbed populations; fine lines, exploited populations. The other species are identified by the following symbols plotted on their respective lines: ◇ *Araucaria*; ○ *Brosimum*; △ *Cecropia* (only for newborn type seeds); ● *Grias*; + *Pentaclethra*. *Pinus* and *Prioria* are not given because of different start diameters. The functions for exploited populations have indicative value only.**

The standard deviations for all estimates of mean age obtained with these projection methods were very large. The within class distribution of ages, *p*, in the largest *Chlorocardium* class showed a very wide and flat age distribution, with 1.3% of the individuals estimated to have an age over 1000 years, and a similar percentage below 200 years (data not shown). The projections for the exploited populations indicated that, on average, large size classes are reached more rapidly there. Clearly, these figures were strongly affected by the increased growth rates in the exploited plot, a situation that will not last long enough to produce these individuals in subsequently unmanaged situations.

The estimated time periods needed to reach reproductive size and the largest size class was high for the study species when compared to the other tree species (Fig. 8). *Araucaria* approached *Chlorocardium* and *Dicymbe* in mean expected age at death for the largest size class. The shortest life-span was projected for the pioneer *Cecropia* (<30 years for the largest individuals).

We also calculated generation time $\mu$, the mean age at which newborns produce offspring (Table 8). This measure does not assume stable stage distribution (unlike other possible measures for generation time, Cochran & Ellner 1992). The study species show the longest generation times (although inflated for *Dicymbe*, for the reasons mentioned above); *Araucaria* and *Prioria* had the next longest generation times.

**Table 10**
**Comparison between survivorship until a certain diameter (in % surviving of the original number of individuals present at 1.4 cm dbh) predicted by the scenarios for auto-correlated growth and mean growth, for *Chlorocardium* and *Dicymbe*. Trees growing with mean growth rate have a much smaller chance to reach a certain diameter than trees growing with auto-correlated growth rate. Survivorship was calculated over *c.* 2500 simulations per species and over 500 years. A similar pattern is present for *Duguetia*, in another diameter range.**

| | *Dicymbe* | | *Chlorocardium* | |
|---|---|---|---|---|
| dbh | mean scenario | auto-correlated scenario | mean scenario | auto-correlated scenario |
| 20 | 1.6 | 4.6 | 10.8 | 17.4 |
| 30 | 1.3 | 4.3 | 5.7 | 11.1 |
| 50 | 1.1 | 3.9 | 1.7 | 4.8 |
| 80 | 1.0 | 3.0 | 0.0 | 1.3 |

## Growth trajectories

The three scenarios used to project virtual tree growth trajectories yielded widely different size-age relationships. In Fig. 9, a typical growth history for a *Chlorocardium* tree is depicted, illustrating the consequences of the three different projection scenarios for life-time growth rates. For all species, the age-size relation projected with the auto-correlated scenario was between those predicted by mean growth and by fast growth (1 standard deviation above the mean; Fig. 10). The mean scenario was hardly capable of producing mature trees within 250 years after reaching 1.4 cm dbh (*Chlorocardium* and *Dicymbe*). This effect was stronger than is apparent from Fig. 10, because much fewer individuals survive to reach a certain size in the mean scenario than in the auto-correlated scenario (or in the fast scenario)(Table 10). For example, in *Chlorocardium* not a single tree was predicted to survive to 80 cm dbh in 2700 runs of 500 years, assuming a mean growth scenario. The age-size trajectories produced by the auto-correlated scenario were quite comparable to the (population matrix based) estimates for the mean age of reaching size class *i*, $\tau_i$, except for *Chlorocardium*. The mortality function had large impact on the various trajectories. For example, of an initial population of 1000 individuals, 778 are expected to survive 50 years at a survival rate of 0.995 (as in *Dicymbe* class 14), while this figure is only 547 at a survival rate of 0.988 (*Chlorocardium* class 14). A low mortality rate and small mortality differences between classes (as in *Dicymbe*) 'slows' the age-size relationship to a considerable extent, while a higher, gradually increasing mortality (as in *Chlorocardium*) gradually filters out slow growing individuals, thus causing a 'faster' trajectory (because only fast growing individuals reach a large size). This difference in mortality in the data is the result of only a few more recorded deaths in *Chlorocardium*, and should be interpreted with care. The standard deviation of the mean age produced by the trajectory method was 2-4 times smaller than the standard deviation of $\tau_i$, even though both are based on the same data (Table 9, Fig. 10).

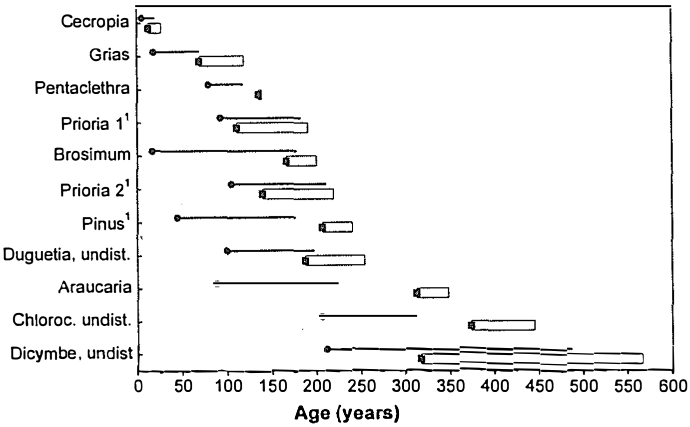


**Figure 8**

**Projected mean age at reaching the last size class (black squares) and at reaching the first reproductive class ($\tau_i$, black dots), and mean expected age at which these individuals die (right hand side of lines and bars) for the study species (undisturbed) and a number of other tree species. Standard errors are very large for all estimates (about equal to the means).**

**[1]The values for *Prioria* and *Pinus* are under-estimates because 'newborns' in these matrices were 1 cm and 2 cm dbh, respectively.**

### $^{14}$C determinations

For *Chlorocardium* we obtained a third type of age-estimate with $^{14}$C determination (Fig. 10b). Two of three large sized trees were aged within the range of the matrix-derived age estimates, and one sample, a tree of 92 cm dbh, appeared to be particularly young: 135 ± 37 years.

### Exploitation of *Chlorocardium*

Fig. 11 shows the estimated size-dependent growth rates for *Chlorocardium* over a 20 year period after logging, based on the measured values for exploited and undisturbed populations. These data were used to produce matrices for each year after logging. Data for early post-logging seedling dynamics had to be estimated, because *Chlorocardium* seedling dynamics in the exploited plot were already determined by light stress.

We first considered a number of recovery scenarios, where the populations were left to recover from a single exploitation event, and the amount of timber (trees in classes 13-14) was monitored (Fig. 12). All these scenarios projected *c.* 100 years of falling timber resources after an initial harvest of half of the available amount of timber (as was done in the exploited population). After this period, timber resources may fall further if nothing is done (Fig. 12a), or they may start to increase if seedling (class 3, 5 and 7) growth transitions are maintained at a high level (2-6 times the transition probability in the undisturbed population) for an extended period, *e.g.*, for a period of 10 years such as in Fig. 12a. This could probably be accomplished without liberation

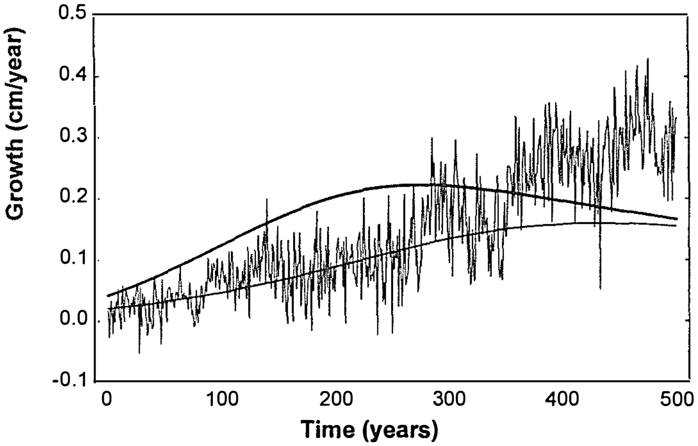
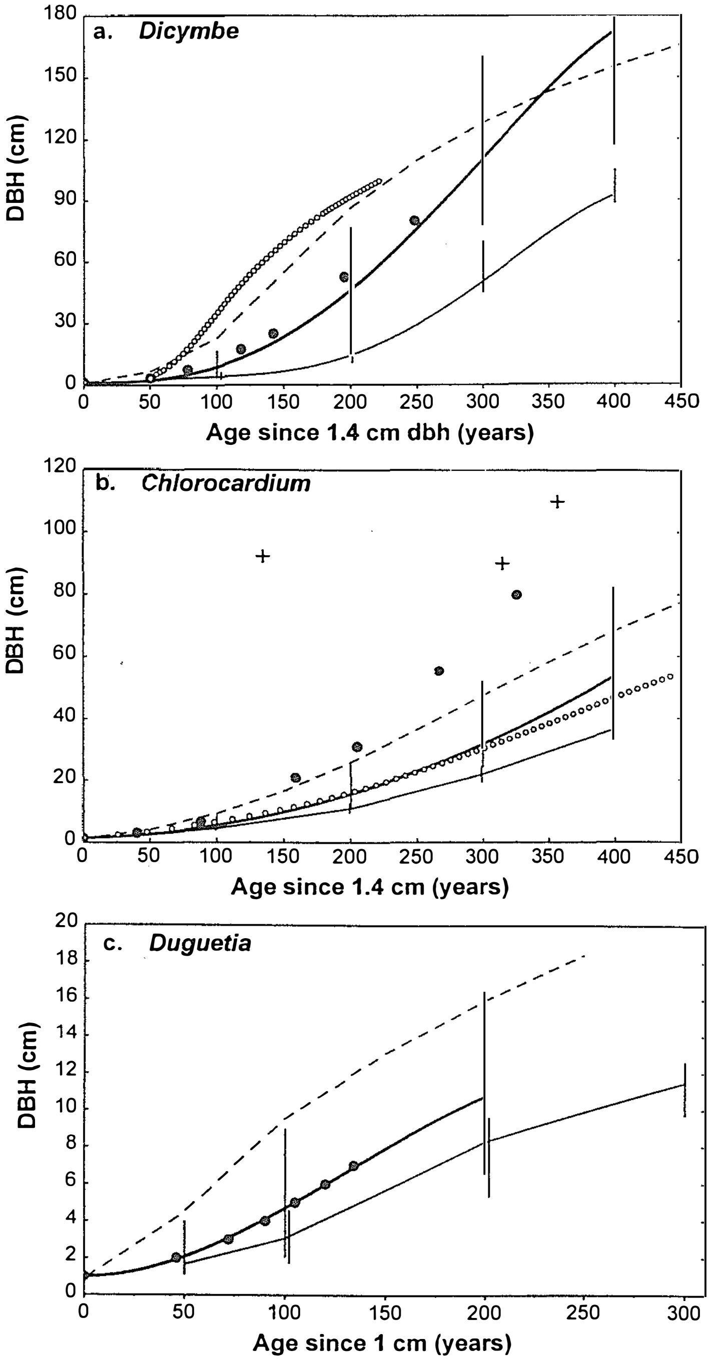


**Figure 9**
Comparison of the consequence for hypothetical life-time growth rates of three scenarios for growth projection: mean growth (lower line), mean + 1 s.d. (fast) growth (top line) and a randomly chosen auto-correlated scenario (ragged line, see methods). All lines refer to *Chlorocardium*. The final size that is projected for this tree if it would not die before age 500 would be 52.6, 86.2 and 72.9 cm dbh, respectively.

thinning for the first 4-5 years, followed by 1-2 liberation thinnings of seedlings until 10 years. The combined effect of increased seedling growth and liberation thinning of seedlings on future timber availability was larger than any other possible stimulating silvicultural measure, but their effect was projected to be maximal only after 250 years. Reduction of seedling mortality had less effect than increasing growth (data not shown). Reduction of logging damage to seedling classes (1-7) from 25% to 5% of the initial population increased future timber resources by *c.* 16% (Fig. 12b), even if seedlings and saplings were liberated as in Fig. 12a. Under the assumptions made the effect of reducing the harvest from 50 to 30% of the standing timber stock was small and mainly limited to the first 50 years after logging (Fig. 12c). We did not consider further reductions because this would affect early post-exploitation growth rates of the re-

**Figure 10 ▶**
Age-size relations predicted by different scenarios for undisturbed populations of (a) *Dicymbe*; (b) *Chlorocardium* and (c) *Duguetia*. Drawn line: median and 5-95% range of projected growth curves based on the mean growth and random mortality (scenario 1). Broken line: individuals growing always 1 s.d. above mean growth (scenario 2). Bold line: the median and 5-95% range of *c.* 2500 projected growth curves based on the 'auto-correlated' scenario and random mortality (scenario 3). The crosses (*Chlorocardium*) are $^{14}C$ age determinations for three wood-samples. The large closed dots give the mean age of reaching size class $i$, $\tau_i$, calculated with matrix projection, plotted at the lower class limit, after subtraction of the estimated age at reaching the starting diameter for the simulations (*Chlorocardium* and *Dicymbe*: 1.4 cm, *Duguetia*: 1 cm). Standard deviations for $\tau_i$ were very large and are not plotted in the figure. The small open dots (*Chlorocardium* and *Dicymbe*) give the same, but calculated with a matrix consisting of 1 cm classes (see discussion). In *Duguetia*, less than 5 individuals were projected to survive 250 years in the auto-correlated scenario and older trees are omitted from the figure.


a. Dicymbe
DBH (cm)
0
30
60
90
120
150
180
0
50
100
150
200
250
300
350
400
450
Age since 1.4 cm dbh (years)
b. Chlorocardium
DBH (cm)
0
20
40
60
80
100
120
0
50
100
150
200
250
300
350
400
450
Age since 1.4 cm (years)
c. Duguetia
DBH (cm)
0
2
4
6
8
10
12
14
16
18
20
0
50
100
150
200
250
300
Age since 1 cm (years)

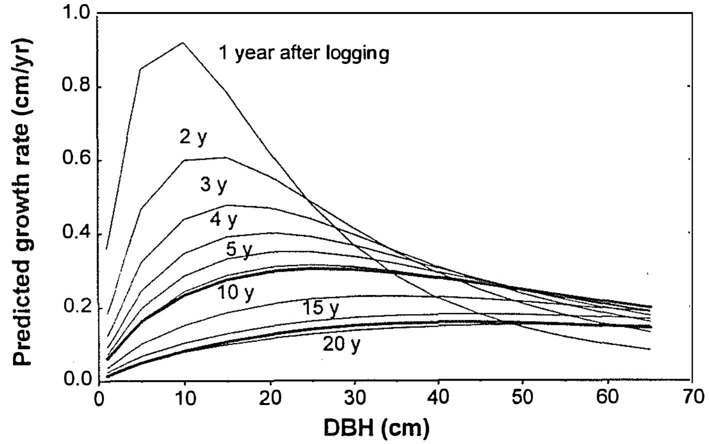


**Figure 11**
**Fitted Hossfeld IV equations describing hypothetical size-dependent growth of *Chlorocardium* between 1 and 20 years after logging. These lines are obtained from the equations for the undisturbed and exploited populations (bold lines).**

sidual population. A high density of large saplings and sub-adult trees, either naturally or stimulated by pre-logging silvicultural treatment strongly diminished the fall in timber availability *c.* 125 years after logging (20-40% more timber than in the standard scenario in populations with 2-3 times as many individuals of these classes; Fig. 12c).

Repeated logging increased the fraction of time that the population has a positive $\lambda_1$, and therefore the effect of repeated logging on *Chlorocardium* appeared to be better than a single logging operation. Increased seedling growth rates over 10 years (liberation) showed much faster recovery of timber resources than logging without liberation (Fig. 12d). Even with a logging cycle of 50 years and liberation of seedlings, it took 225 years to attain the same standing stock of timber as before the first exploitation. Liberation of larger saplings and pre-adults once every 7 year after logging had a strong projected effect, especially after repeated logging and liberation of seedlings had created a large seedling pool (Fig. 12e). The effect of liberation after logging was somewhat similar to the effect of liberation before logging (or logging populations rich in these individuals; Fig. 12c).

The response of exploited populations to repeated logging depended strongly on the assumptions we made for diameter growth rates in the first years after logging (Fig. 11). Especially the estimated growth rate in the first year following logging was very high (giving a $\lambda_1$ of the first year matrix of 1.08). If growth in the first year was assumed to be equal to second-year growth, this considerably reduced projected timber resources, especially on the long term (Fig. 12f). If we assumed the growth rates to be equal to our measured growth rates in the exploited population for 10 years after logging, and thereafter equal to the undisturbed population (*cf.* Fig. 2a), then projected timber resources fell back considerably (Fig 12f).

The response of *Dicymbe* to logging of *Chlorocardium* was very different from the response of *Chlorocardium* itself. Under all assumptions, the strong response of *Dicymbe* saplings as observed in the exploited plot (Table 4) led to high recruitment of adult trees. Unrestricted projection of *Dicymbe* population dynamics was illustrative of this strong response: the number of individuals in the classes 13-14 would exceed $2.10^6$ per hectare after 400 years, if Nature would allow that.

## Discussion

### *Chlorocardium* and *Dicymbe* compared

Although *Chlorocardium* and *Dicymbe* were co-dominant trees in the same stratum in the forest, they achieved this with clearly different life histories. *Dicymbe* had a higher average growth rate than *Chlorocardium* in most size classes (Table 4), although this was often not significant when tested on means. Higher seedling mortality in *Chlorocardium* seemed to be responsible for an under-representation of saplings and pre-adult trees when compared to *Dicymbe*, because after the seedling stage growth, mortality, and the response to increased light availability were quite similar between the species (Figs. 1, 3, 7). However, the averages (which were used for matrix modelling) for *Dicymbe* were almost always 'better' (in terms of a higher $\lambda_1$) than for *Chlorocardium*.

We identified one point in the life cycle where *Chlorocardium* performs 'better' than *Dicymbe*, and where it may partly compensate for its high seedling mortality. In very low light environments (in the undisturbed plot) *Chlorocardium* saplings grew significantly faster than *Dicymbe*, while the reverse was true with increasing light availability (Fig. 4). This is an important difference with seedling populations (class 2-7), where *Dicymbe* was demonstrated to grow faster (in height) than *Chlorocardium* over the entire light gradient found in the forest (Fig. 4; Chapter 6). This suggests that with increasing size (accompanied by a lower relative investment in leaves and higher investment in respiring tissues such as stems and branches, Boot 1994) the requirement for light increases more rapidly for *Dicymbe* than for *Chlorocardium* (*cf.* Grubb 1996), *i.e.*, *Dicymbe* needs gaps as a sapling in order to survive, whereas *Chlorocardium* is able to continue (very) slow growth in the understorey. This may be related to a different architecture of saplings of these species. Healthy *Dicymbe* saplings tend to be hardly branched and have relatively deep crowns with often few leaves, whereas *Chlorocardium* saplings are strongly branched and may have a high leaf area in shallow crowns. This distinction has been used by Kohyama (1987) to describe optimist (*in casu Dicymbe*) *vs.* pessimist (*Chlorocardium*) life histories. The 'critical' size class where *Dicymbe* starts to show increased light demand coincides with the point where we changed from height growth to diameter growth, so the effect might be considered a methodological artefact. This concern would have been real if *Dicymbe* dbh growth at low light were low but positive, but it is negative, which is a clear indication of poor performance. Note that this difference between the two species does not show in average growth per class, and therefore not in the matrices.

Another possible key to the abundance of *Chlorocardium* might be its long reproductive life compared to *Dicymbe*. Unfortunately, our estimates of total life expectancy of individuals in the largest size class appeared to be biased by the difficulty of properly estimating mortality rates of large trees. If $\tau$ instead of life expectancy is taken as an indication of total life span, it appears that the reproductive life of *Chlorocardium* is >60 years longer than of *Dicymbe* (Fig. 8, compare the left-hand side of the bars). A long life-span is one possible explanation for the fact that *Chlorocardium* is dominant as an adult in the canopy, but not as a seedling or as a treelet of the sub-canopy (classes 10 and 11) in many populations studied to date (ter Steege 1990). In that case the 'dip' in the population structure at juvenile size-classes, which is frequently considered a problem for the silviculture of *Chlorocardium* (ter Steege 1990) is not a consequence of a lack of juveniles, but rather of an accumulation of adults.

Higher observed growth rates of juveniles and adults of both canopy species in the exploited plot (Table 4) are a well-known response of trees to canopy opening, and is the basis of forest management (*e.g.*, de Graaf 1986, Jonkers 1987, Maître 1991, Primack & Lee 1991). *Dicymbe* increased sapling and pre-adult growth rates several fold (up a factor 10 in saplings of 1.4-6.6 cm), a similar increase as shown by the fast-growing pioneer species *Macaranga* (Primack & Lee 1991). *Chlorocardium* showed lower increases. *Chlorocardium* growth rates in the undisturbed plot were about the same as reported by ter Steege *et al.* (1995, 1996) for *Chlorocardium* in undisturbed forest. In exploited where competing trees are subsequently poisoned, *Chlorocardium* is capable of higher growth than reported for the exploited plot here (Prince 1973, ter Steege *et al.* 1995, 1996). For the exploited and undisturbed populations of *Duguetia*, the differences in average growth rate were small and not significant, possibly caused by the fact that most of the *Duguetia* population was below the secondary canopy. These results are in agreement with the observation that understorey species have a low growth rate (Lang & Knight 1983, Lieberman & Lieberman 1987, Welden *et al.* 1991, Favrichon 1994), although it should be noted that an increase in Dawkins index was correlated with higher growth rates in *Duguetia*, (less than in the other species; Fig. 3).

The growth stimulation in the exploited plot was limited to size classes in or above the canopy of the secondary vegetation. In the low light environment below the secondary canopy, *Dicymbe* (2-7) and *Duguetia* (1-4) seedling growth was not higher than in the undisturbed plot (*cf.* Table 4, Fig. 3), whereas mortality rates were similar or higher. For *Chlorocardium*, seedling growth was somewhat higher in the exploited plot in some size classes. This is explained by their higher leaf density (Chapter 7) and therefore only shows up in classes 5 and 7. This suggests that the growth stimulus caused by the opening of the canopy will last longer for the larger size classes, and that once individuals are 'overtaken' by the secondary canopy growth is slow and mortality is high. This was already demonstrated for *Chlorocardium* in this plot (Chapter 7).

As a general trend, the growth rates of individuals with the same Dawkins index were higher in the exploited plot than in the undisturbed plot (Fig. 3). This suggests that more factors than light contribute to the increased growth rates, such as a decreased below-ground competition or higher nutrient availability. The possibility that these differences were due to differences between plots can also not be excluded.

## Matrix models

Only *Dicymbe* showed an unequivocal response in terms of $\lambda_1$ to exploitation, while the $\lambda_1$ of *Chlorocardium* was only slightly higher. For both species, the juvenile classes (8-11) were the 'engine' for the increase population growth rate in logged populations: undisturbed population matrices which were given the vital rates of exploited populations in these classes gave $\lambda_1$ which were very close to the $\lambda_1$ of the exploited populations (data not shown). *Duguetia* suffered increased mortality rates over all size classes and therefore had a lower $\lambda_1$ in the exploited plot than in the undisturbed plot. The matrices for the exploited plot capture the demographic response of these populations during a short period, which is part of a longer process during which strong demographic changes take place. Inevitably the projected asymptotic behaviour of these matrices reflects the hypothetical demographic consequences of this short period. In reality tree growth rates are expected to decrease as the canopy closes and below- and aboveground competition increase, causing $\lambda_1$ to decline.

All populations except *Dicymbe* had $\lambda_1$ close to, and probably statistically indistinguishable from 1. This seems to be a general pattern for trees and palms (Table 8, Silvertown *et al.* 1993), and it is indeed hard to imagine how a non-invasive, long-lived tree species could accomplish a sustained population growth-rate larger than one under natural conditions. There are two major reasons for tree populations (of undisturbed forests) to have a $\lambda_1$ more than 1, maybe 2 percent points above or below unity. First, this may be caused by the difficulty to adequately estimate the parameters for the model, either because the observation period is short relative to the growth and survival rates. This problem may especially arise if vital rates are estimated from actual transitions. Clearly, estimates for mortality rates in classes with low mortality and few individuals are very vulnerable to this type of error.

Second, the population dynamics of such species may be characterised by fluctuations, or the species is in a period of demographic transition. This may be the case for species colonising an area, and this was evidently the reason for the extra-ordinarily high $\lambda_1$ for *Dicymbe* in the exploited area. This population growth rate can not be sustained over a long term, and is an artefact of measuring the population during a period of rapid expansion and temporally high growth rates. Comparable results could be obtained for populations in areas that are gradually changing (*cf.* Condit *et al.* (1996a), who describe the effect of a long-term drying trend and short term fluctuations in length of the dry season on tree populations on Barro Colorado Island, Panama). Similarly, the population dynamics of a species may be determined to an important extent by rare events that limit growth and survival: drought, flooding, plagues, hurricanes, *etc.* There is some evidence that the growth of natural *Dicymbe* populations is limited by drought, because a long dry season after the last measurement caused *c.* 30% of the *Dicymbe* seedlings (classes 7 and lower) to die, even though survival in *Chlorocardium* and *Duguetia* was hardly affected (R.J. Zagt, *personal observation*). The high $\lambda_1$ of undisturbed *Dicymbe* populations is possibly inflated by the absence of drought during the measuring period, and therefore simply does not adequately describe the population dynamics of this species.

Therefore, we expect that high or low $\lambda_1$ in tree species point to a partial description of the population dynamics of the species. Important differences in the population dynamics between species or populations may lead to rather limited differences in $\lambda_1$ (*cf.* Table 8); at the same time, it was demonstrated that uncertainties in the estimation of vital rates lead to rather wide confidence limits for $\lambda_1$ (Alvarez-Buylla & Slatkin 1993, Alvarez-Buylla 1994, Olmsted & Alvarez-Buylla 1995). To underscore that important differences in population dynamics may lead to small differences in $\lambda_1$, we calculated estimates for $\lambda_1$ under the assumption that they would go extinct due to failing reproduction (*i.e.*, birth matrix B has only zero entries), for all species (Table 8). These $\lambda_1$ are generally just below 1. They reflect the longevity of the species, and are for these species equal to the highest probability of stasis in the matrix.

Sensitivity and elasticity analysis showed that the demographic behaviour of the larger size classes in the study species (the two canopy species more than *Duguetia*) had a larger impact on $\lambda_1$ than the seedling size classes (Fig. 6). These species seem to follow a general pattern for trees, which often show the highest elasticity in the first reproductive stage or in a stage directly adjacent to this (Caswell 1989, Piñero *et al.* 1984). This pattern was present in 9 of 11 species listed in Table 8 (data not shown, the exceptions were *Cecropia* and *Pentaclethra*). A biological explanation might be that these stages contain individuals that just start to become reproductive, *i.e.*, they have not yet contributed to the future growth of the population, while at the same time they represent, statistically, the most 'expensive' individuals in the population in terms of number of seeds required to produce one individual in that stage. From the survivorship curve (Fig. 7) it can be deduced that from 18860 seeds (surviving till December) dispersed only one *Chlorocardium* individual is produced that begins flowering (aged 206 years, Table 9). For *Dicymbe* and *Duguetia* the corresponding figures were 63 and 17 (!). Peaks in sensitivity or elasticity can be expected where bottle-necks are present, either in the demography of the species or in the method to measure this. In our species this is visible in the size classes where the estimation method for vital rates changed from observed transitions to fitted transition parameters (class 8 in *Chlorocardium* and *Dicymbe*, class 5 in *Duguetia*, Fig. 6).

Silvertown *et al.* (1993) demonstrated that in trees for the larger size classes the elasticity of stasis was larger than the elasticity of growth, while for sensitivity the pattern was reversed (Fig. 6; Caswell 1989). The mathematical rationale for this pattern is more straightforward than a biological rationale. The change in $\lambda_1$ in response to absolute changes in the transition probabilities (sensitivity) is largest for those transitions which have the smallest value (and growth probabilities have usually a smaller value than probabilities of stasis). Similarly, a proportional change (elasticity) has more impact when it concerns a transition probability with a large absolute value: a change of 15% in a (generaly small) growth probability involves a smaller percentage of the individuals in a class than a change of 15% in a (generally large) stasis probability. A 'simple biological explanation' (Silvertown *et al.* 1993, also Caswell 1989) for the pattern

**Table 11**

**Comparison of estimates of age at maturity obtained with different methods. For the growth projections in mean and auto-correlated scenarios, the approximate age estimate of the median is given. For the growth projection estimates, τ at reaching the lower size for the analysis was added, giving somewhat biased estimates. Only undisturbed populations were used. 'Large matrix' indicates the estimate made with the matrix consisting of centimetre classes (*Chlorocardium* and *Dicymbe* only). See methods for descriptions of growth scenarios.**

| | | Matrix estimates | | Growth trajectory scenarios | | |
|---|---|---|---|---|---|---|
| Species | Size at maturity | τ | τ (large matrix) | Mean | Fast | Auto-correlated |
| *Dicymbe* | 24.9 | 211 | 160 | 310 | 170 | 220 |
| *Chlorocardium* | 20.9 | 206 | 280 | 350 | 225 | 280 |
| *Duguetia* | 3.0 | 100 | | 115 | 64 | 100 |

signalled above is not very simple, because biologically there is no difference between individuals that remain in the same size class, and individuals that grow into the next. Under the assumptions of matrix modelling, these individuals have the same probability of survival and the same growth rate.

In order to achieve biological relevance, the sensitivity and elasticity of matrix elements should be scaled to the biological variability (variance) of the matrix elements, the probability that such changes occur, and the correlation between matrix elements. The variability could be at the individual, spatial or temporal level. Individual, where it concerns differences between growth and survival probabilities within one population. Spatial, where populations are compared, and temporal, where the same population is compared at different moments in time. We could not perform such an analysis here, because we had no complete data on the variability at all these levels. Our growth definition necessarily precluded temporal variability, and variability in mortality rates is very difficult to study. Further, we had no replicates that could provide information about spatial variability.

## Age estimates

The population matrix method of age estimation suggests that the study species mature late (Table 11) and have a long life-span (Fig. 8). Both canopy species were estimated to start producing flowers after *c.* two centuries, *Duguetia* after one century. The mean maximum age was estimated to be more than 400 years for both canopy species, although in *Dicymbe* this seems to be an over-estimate, a consequence of a high estimated survival probability in the largest size class.

The method of growth trajectories yielded different age estimates, and depended strongly on the assumptions used. Trees growing at mean growth-rate were projected to take an extremely long time to reach maturity or maximum size, while only a few of them would survive to do so (Fig. 10, Table 10). It is often shown that growth is autocorrelated (Clark & Clark 1992, Swaine *et al.* 1987, Swaine 1989, Manokaran & Kochummen 1987) and it is suggested that only fast growing individuals contribute to mature size classes (*e.g.*, Prince 1973, Liu & Ashton 1995, O'Brien *et al.* 1995). This gave much accelerated growth trajectories. The median auto-correlated growth trajectory was surprisingly similar to the age-size relationship calculated with the matrix method for *Dicymbe* and *Duguetia*. The auto-correlated growth scenario was not based on real field data, but rather it was included to study the effect of cycles of suppression and release of trees on the size-age relationship. In one way it contains more realism than allowing just the fastest individuals to grow, as slow growing individuals are included, but rarely reach a large size. Only in *Chlorocardium* the matrix method yielded faster growth trajectories than the projection method. An independent control ($^{14}$C sampling) was partly compatible with matrix-derived growth trajectories for *Chlorocardium*, without being conclusive, because there were only three samples, and one of them gave a very low age estimate (Fig. 10b).

Age-size relationships based on growth projection have been published for quite a large number of species (Lieberman & Lieberman 1985b, 1987, Sarukhán *et al.* 1985, ter Steege 1990, Condit *et al.* 1993b, 1995b, O'Brien *et al.* 1995, Korning & Balslev 1994, van Groenendael *et al.* 1996). Comparison of the projected life-spans of the Guyanese species (mean growth data) with these published life-spans, and comparison of matrix-model estimates between those species that we had matrices for (Fig. 8), suggest that the study species have generally a longer life-span. We have no obvious explanation for this. Interestingly, 'Guyanese' species are well represented among the species with the highest life-span reported by Lieberman & Lieberman (1987): *Pentaclethra macroloba* and *Carapa guianensis* are both common species in or near the study plots. For *Prioria* (Condit *et al.* 1995b, O'Brien *et al.* 1995) and *Pentaclethra* (Lieberman & Lieberman 1985b, 1987) size-age relations are known from both the trajectory and matrix method, and they confirm the pattern of Fig. 10: the matrix-based estimates give faster growth trajectories than growth trajectories based on mean growth, but not as fast as the mean + 1SD growth trajectory (these data are only available for *Prioria*; matrix estimates are 'faster' than the fastest scenario of O'Brien *et al.* (1995), which seems different from Condit *et al.* (1995b)).

Prince (1973) calculated times of passage for *Chlorocardium* in exploited forest, based on 25% faster growth than the observed mean. A *Chlorocardium* of 7.4 cm dbh would take *c.* 96 years to grow from 7.7 to 47 cm dbh in untreated forest, while with treatment this would be achieved in *c.* 51 years. This is shorter than our own estimates (based on mean data): the difference between $\tau_{14}$ and $\tau_{11}$ (6.6-55.4 cm dbh) is 179 years in the undisturbed plot, and 116 years in the exploited (and untreated) plot. Fanshawe (1947) estimated that a *Chlorocardium* takes 136 years to reach 40 cm dbh (from 10 cm) in undisturbed (?) forest, and 120 years in treated forest. This compares well with our estimate for exploited forest (matrix method). Note that these relations require that post-logging growth rates be maintained over the entire period, and that silvicultural treatment is a prerequisite.

Discrepancies between age estimates obtained with the methods of Cochran & Ellner (1992) with transition matrices and growth projection *cf.* Lieberman and Lieberman (1985b) may be caused by the fact that matrices tend to be very 'forgiving' to

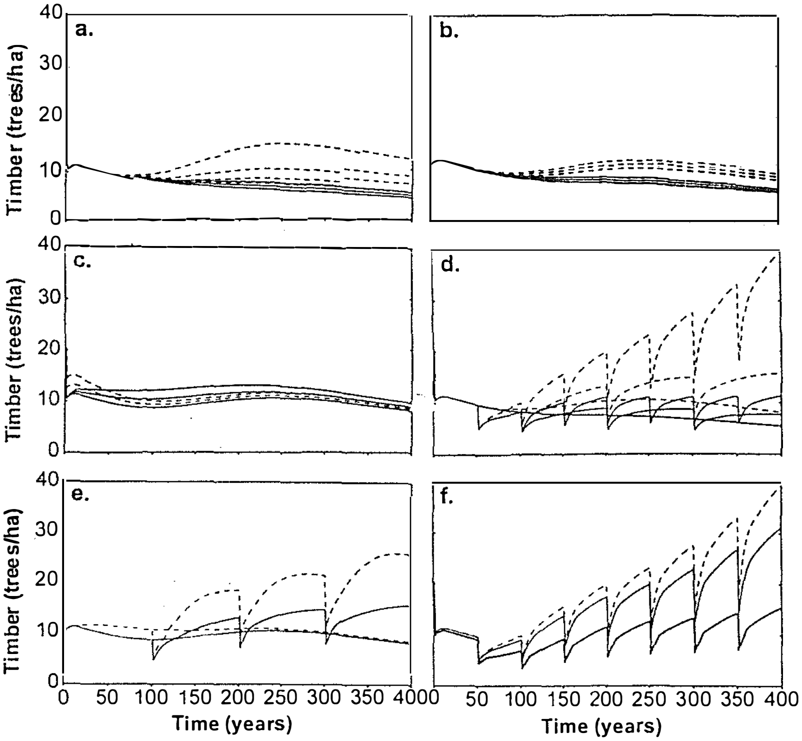


**Figure 12**

The projected effect of different management scenarios on the abundance of timber (*Chlorocardium* in size classes 13 and 14, 31-80 cm dbh) following logging. Diametrical growth rates vary *cf.* Fig. 11 over 20 years; seedlings grow fast (4 × normal) for 5 years, 5 years *cf.* exploited matrix and after 10 years *cf.* undisturbed matrix

a (seedling liberation) effect of increasing seedling growth rates ( × 1, × 2, × 4, × 6) during the first 5 years after logging (drawn lines) and seedling liberation: extending the period of increased seedling growth from 5 to 10 years (broken lines).

b (damage reduction and seedling liberation) effect of reducing the damage to seedlings and juveniles (class 1-11) from 75 to 85 to 95% surviving logging (drawn lines) and simultaneously extending increased seedling growth from 5 to 10 years (broken lines).

c (reduced logging intensity and increased juvenile density) effect of increasing juvenile density (class 10-11) before logging (× 1, × 2, × 3) (drawn lines) and reducing logging intensity (50, 40 and 30% of timber removed) (broken lines). Assumption: seedling growth x4 over 10 years (liberated).

d (increased logging intensity and seeding liberation) effect of increasing logging intensity (1 ×, 4 × and 8 × per 400 year) (drawn lines) and applying seedling liberation (seedling growth × 4 over 10 years) (broken lines).

e (juvenile and seedling liberation) effect of liberating juveniles (class 10-11) under two logging regimes (1 and 4 × per 400 years): 0 times during 20 years (drawn lines) and 3 times during 20 years (broken lines). Seedling liberation (seedling growth × 4 over 10 years) was simultaneously applied.

f effect of changing assumptions on one of the scenarios (as in 12d): logging intensity 8x in 400 years, seedling liberation. Assumptions: growth given by Fig. 11 (as in 12a-e, broken line); first year growth reduced and equal to second year growth (drawn line); 10 years growth as in exploited plot followed by 40 years growth as in undisturbed plot (bold line).

trees with unrealistic life-histories. Matrix age estimates take into account a wide range of unrealistic pathways between seedlings and mature trees: it is possible to grow from the smallest to the largest size-class in 9 time-steps for *Chlorocardium,* but also to remain a seed for 20 years, grow in 10 years to class 10 and remain there for another 100 years. Although the probability of such a life-history is small, it affects the estimate of the tree age, and particularly the variance of tree ages at a certain size. We reduced the impact of unrealistically short life-histories by constructing adjusted matrices for *Chlorocardium* and *Dicymbe* (undisturbed), and determining the $\tau_i$. The seedling classes were identical to the normal matrix, but from 0.4 cm (*Dicymbe* 3.4 cm) all classes were 1 cm wide (which is more than the highest average growth rate). The $\lambda_1$ were identical (Enright *et al.* 1995), but there were profound effects on the age estimates (Fig. 10). In *Chlorocardium* it decreased the probabilities for, particularly, very fast life histories, and a much 'slower' growth trajectory was projected. In contrast, for *Dicymbe* the growth trajectory was much accelerated, probably because the species combined high survival and fast growth. High age estimates can be expected for such species if size classes are very wide, enabling individuals to remain long in a size class with a very low probability of death. With narrow size classes, individuals are forced to grow steadily through all size classes, which inevitably brings them in size classes with a higher probability of death. For both species, the variance of the estimate was reduced by a factor 2-3 in the very large matrix. Age-size relationships therefore seem to be very sensitive to the assumptions that are made, and it is hard to tell which approach is 'better' without independent validation methods such as radiocarbon dating (Worbes & Junk 1989) or tree-ring analysis (Mariaux 1967, Baas & Vetter 1989).

### Exploitation of *Chlorocardium*

We have shown above that matrix models provide clear insight in the consequence of demographic differences between species or populations. However, it was also clear that some of the results of matrix modelling depend strongly on the accuracy of the data and the size class width, and that mathematical and biological characteristics of matrices blend into each other. These considerations show that projections of population responses to exploitation need to be interpreted with care, particularly because in exploited forests the vital rates are subjected to continuing, drastic change. This causes a discrepancy between the requirement of tools for prediction of population responses to management, and the capacity of matrix models to provide no more than projections of this response, given the assumptions of the model (Caswell 1989, Boot & Gullison 1995). The use of matrix models for the management of trees should therefore be limited to the evaluation of 'What-if' scenarios, as we did with the management simulations. This could still produce insight in potentially valuable management options, but less so in quantitative aspects of forest management.

There are three starting points for assessing the consequences of exploitation for population dynamics: the effect on the population growth rate, sensitivity analysis, and simulation.

As *Chlorocardium* had a (slightly) negative population growth rate ($\lambda_1 < 1$) in the undisturbed forest and a slightly positive growth rate in the exploited forest, there is, in principle, a scope for sustainable logging. For *Chlorocardium*, the change in population growth rate gives the balance between, on one hand, the negative impacts of the removal of adults, damage to the residual stand (including seedlings and pre-adult trees), slow seedling growth rates in secondary vegetation and a reduced seed shadow, and, on the other hand, the positive impacts of increased illumination levels that stimulate the growth of the remaining individuals and, possibly, higher fecundity and earlier maturity of the trees. The maximum number of individuals that can be harvested from a growing population was defined by Usher (1966) as $N=(\lambda_1 -1) \times N_0$, where $N_0$ is the population size at $t=0$. This harvest should be equally distributed over all size classes. However, this method uses the asymptotic behaviour of the population, which may lead to problems if the population is not at equilibrium (which it is not, certainly not after exploitation). The transient behaviour of a population may be quite different from the asymptotic behaviour, and may show a temporal decline in the abundance of the size class which is being harvested, even when $\lambda_1 >1$.

Sensitivity and elasticity analysis are useful to select the size classes at which exploitation is directed (the least sensitive ones; *e.g.*, Peters 1991, 1996 for exploitation of fruits) or to determine which classes are targeted for silvicultural manipulation. For *Chlorocardium* this would mean that harvest is preferably taken from the size class >80 cm dbh, because this class contributes little to the population growth rate (Fig. 6c). This ecological consideration clashes with the foresters reality that a large part of the trees >80 cm dbh are hollow and have little commercial value (ter Steege 1990). The best compromise is to harvest the largest sound trees, because elasticity values monotonically decrease with increasing size. Furthermore, management should be concentrated on the pre-reproductive size classes, which have the highest elasticity values. Simulations showed that increasing the number of trees in these classes, either by choosing forests with a high proportion of these trees, or by adequately stimulating their growth prior to logging (as in the Tropical Shelterwood System, *cf.* Schmidt 1991), or by reducing logging damage to these trees, or by maintaining increased growth rates for these trees for a prolonged period after logging, gave substantially improved future timber resources on the medium term (Fig. 12).

The third starting point is simulation. This is often necessary for evaluating management options, because timber exploitation is not concerned with overall population growth rates, but with the amount of harvestable timber. Simulation reveals more clearly than population growth rates or sensitivity analysis the transient effects of logging. The most important transient effect that transpired from Fig. 12 is that timber resources were falling during *c.* 100 year following a logging operation as had been done in the exploited plot. The projections showed that this period could be reduced by rather intensive management of the residual *Chlorocardium* stand in the pre-reproductive size-classes. For the longer term availability of timber, the creation of a 'demic wave' (Sarukhán *et al.* 1985) through the management of seedling and sapling populations (classes 1-7) seemed of much greater importance than the management of pre-reproductive classes. The reason is that there are many more seedlings and saplings than pre-reproductive individuals. A management type that is successful in increasing growth rates (and to a lesser extent reducing mortality rates) of seedlings and saplings will eventually (after 150-250 years, compare Table 9) enhance timber resources more than management of pre-reproductives does.

All projections assumed that the growth and mortality rates are representative for the long-term growth and mortality of the species and that conditions in the future remain as they were during the measuring period. Moreover, in these matrices there were no regulatory mechanisms, such as competition or density-dependent growth and mortality, and for some simulations we assumed that the population response to future logging cycles would be the same as to the first logging, and that decreased logging would lead to the same stimulation of growth as in our exploited plot. None of these assumptions is completely upheld in the field, and therefore the actual response of populations to logging will be different than suggested by our projections. The most obvious deviation is caused by interaction between individuals within and between species. Although intra-specific density-dependent regulation of tropical tree species is only demonstrated for a few very common species (Condit *et al.* 1994), inter-specific density-dependent regulation is thought to determine growth and mortality in forests (*e.g.*, Kohyama 1992b). Density-dependent control and competition will certainly reduce the large increase that repeated logging is suggested to cause (Fig 12d-f). These peaks are the sole consequence of exposing the population to high light and increased growth rates for a longer period than in a situation of a single logging operation (Fig. 12a-c). Other species will similarly increase their growth rate, and the eventual effect on timber availability therefore depends on inter-specific competition between the species and density-dependent regulation. Our matrix model is not suitable to simulate these effects. Comparison of growth and mortality rates and $\lambda_1$ strongly suggest that *Dicymbe* (or other, similar species) is much better equipped to benefit from logging than is *Chlorocardium*, and that repeated logging cycles are not expected to decrease this advantage. This implies that the management of *Chlorocardium* is necessarily a very intensive one, because the species grows slowly and shows a less plastic response to canopy opening than other species (*cf.* Fig. 3).

In conclusion, exploitation of *Chlorocardium* in a polycyclic fashion based on natural regeneration seems not impossible. The species shows increased diametrical growth rates at increased light levels and a slightly positive population growth rate in the exploited plot. However, unassisted regrowth after harvest is certainly not sufficient to attain this goal. Substantial silvicultural intervention is required for two reasons. First, the rate of growth remains low, and without intervention, it will take a long time to produce a second crop for harvesting. Second, other species (exemplified by *Dicymbe* in this study) show much stronger responses to increased illumination levels and reduced competition, and without intervention, these species, and not *Chlorocardium*, will grow up to form the new canopy. The large difference in potential maximum growth rates between *Chlorocardium* and *Dicymbe* suggests that silvicultural intervention should be frequent and specific. While reducing harvesting losses to pre-reproductive individuals and stimulation of their growth after harvest increases the yield in the second harvest, the simulations suggest that for continued sustainability silvicultural intervention should also target seedlings and small saplings. Reduction of damage seems important to maintain populations of species which show a small or negative response to logging, as demonstrated here for *Duguetia*.

The conclusion that sustainable exploitation of *Chlorocardium* is possible is based on the demographic response of the species on first time logging, but does not consider the effects of logging on nutrient dynamics, hydrology or biodiversity. These aspects were studied by Jetten (1994), Raaimakers (1995), Brouwer (1996) and Ek (*in prep.*) at Mabura Hill. These studies reached similar conclusions: sustainable exploitation is possible under stringent conditions, which mainly concern the limitation of damage (ter Steege *et al.* 1996)

Although for tropical trees validation has never been attempted, matrix models can be a useful to understand the demographic life history of species, especially when they are used as a tool of comparative study. However, as in all models, certain assumptions and restrictions apply, and the results of matrix modelling should be critically scrutinised for their biological implications. This restricts the usefulness of matrix models as a blanket tool for assessing the demographic consequences of timber exploitation. Still, it is probably the preferable approach to modelling in situations where data availability is limiting, and it shows clearly the long-term demographic consequences of manipulation of the vital rates.

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## Appendix A

Matrix population models for *Prioria copaifera* and *Pinus palustris.* All classes are based on dbh.

*Prioria* 1, period 1982-1985 (source Condit *et al.* (1993), Table 1).

| *class* | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 1-2 | 0.920 | 0 | 0 | 0 | 0 | 0 | 0.235 | 0.235 |
| 2-3 | 0.061 | 0.901 | 0 | 0 | 0 | 0 | 0 | 0 |
| 3-4 | 0 | 0.091 | 0.861 | 0 | 0 | 0 | 0 | 0 |
| 4-8 | 0 | 0 | 0.132 | 0.948 | 0 | 0 | 0 | 0 |
| 8-16 | 0 | 0 | 0 | 0.050 | 0.961 | 0 | 0 | 0 |
| 16-32 | 0 | 0 | 0 | 0 | 0.037 | 0.942 | 0 | 0 |
| 32-64 | 0 | 0 | 0 | 0 | 0 | 0.054 | 0.945 | 0 |
| >64 | 0 | 0 | 0 | 0 | 0 | 0 | 0.050 | 0.988 |

*Prioria* 2, period 1985-1990 (source Condit *et al.* (1993), Table 1).

| *class* | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 1-2 | 0.928 | 0 | 0 | 0 | 0 | 0 | 0.235 | 0.235 |
| 2-3 | 0.060 | 0.915 | 0 | 0 | 0 | 0 | 0 | 0 |
| 3-4 | 0 | 0.075 | 0.860 | 0 | 0 | 0 | 0 | 0 |
| 4-8 | 0 | 0 | 0.132 | 0.955 | 0 | 0 | 0 | 0 |
| 8-16 | 0 | 0 | 0 | 0.039 | 0.959 | 0 | 0 | 0 |
| 16-32 | 0 | 0 | 0 | 0 | 0.037 | 0.960 | 0 | 0 |
| 32-64 | 0 | 0 | 0 | 0 | 0 | 0.038 | 0.971 | 0 |
| >64 | 0 | 0 | 0 | 0 | 0 | 0 | 0.026 | 0.988 |

*Pinus* (source Platt *et al.* (1988), fertility calculated from Fig. 4).

| *class* | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 2-10 | 0.756 | 0 | 0.076 | 0.149 | 0.155 | 0.332 | 0.179 | 0.055 |
| 10-20 | 0.082 | 0.834 | 0 | 0 | 0 | 0 | 0 | 0 |
| 20-30 | 0 | 0.138 | 0.865 | 0 | 0 | 0 | 0 | 0 |
| 30-40 | 0 | 0 | 0.127 | 0.834 | 0 | 0 | 0 | 0 |
| 40-50 | 0 | 0 | 0 | 0.152 | 0.899 | 0 | 0 | 0 |
| 50-60 | 0 | 0 | 0 | 0 | 0.077 | 0.875 | 0 | 0 |
| 60-70 | 0 | 0 | 0 | 0 | 0 | 0.084 | 0.891 | 0 |
| 70-80 | 0 | 0 | 0 | 0 | 0 | 0 | 0.054 | 0.882 |

# Summary and conclusions

In this study the population dynamics of three tree species of the rain forest of Guyana were compared, two canopy species and one understorey species. Although all three were late successional species, there were large differences between them, also between the two canopy species. There were differences in size-dependent growth and survival rates, in reproductive characteristics such as yearly seed production, in population structure and in life-span. *Chlorocardium rodiei* was characterised by a protracted germination, high seedling mortality and a long life-span. The seedling mortality of *Dicymbe altsonii* was very low, while at the same time the number of saplings was very much higher than in *Chlorocardium*. *Dicymbe* reproduced via massive, bi-annual seed production, but was also capable of retaining its canopy position by means of stem sprouts. *Duguetia neglecta* was a slow growing species with low mortality throughout its life cycle. This correlated with a relatively 'flat' population structure. The yearly reproductive output per individual seemed to be very low compared to both other species. This is possibly because the species flowers and fruits in understorey environments, and generally not in high-light environments, as with both canopy species. *Dicymbe* responded strongly to increased light conditions, such as found in gaps. This response had two aspects, an individual aspect and a population aspect. Individuals showed a strong increase in growth rate with increased light, but in addition the abundance of the 'responsive population' (seedlings and small saplings) was generally much higher than in *Chlorocardium*. Both factors probably contributed strongly to the apparent success of *Dicymbe* in the exploited plot. The increase with increasing light of the diametrical growth rate in *Chlorocardium*, and to some extent also *Duguetia*, was not unlike the increase observed in *Dicymbe*, but contrary to *Dicymbe* these two invest much biomass in the growth of branches, rather than height growth of the main shoot. This gives *Dicymbe* an extra advantage in high-light environments.

In this Chapter a short summary is given of the main results of the study. After that, two questions which formed the basis of the study and which are relevant for the management of *Chlorocardium* and *Chlorocardium*-rich forest are addressed: how is *Chlorocardium* maintaining itself in the community, and how should it be managed?

In **Chapter 2** two main groups of hypotheses explaining species diversity in tropical rain forests were compared and evaluated. Equilibrium theories suggest that species differ in their regeneration requirements and partition the available space over resource gradients. Non-equilibrium theories propose that most species have similar resource requirements and emphasise chance as the major factor determining the species composition of tropical rain forests. It is argued that the choice of large sized trees (>1 cm diameter, but often >10 cm diameter) for evaluation of these hypotheses strongly under-estimates the potential for differentiation between species, because of problems associated with measuring growth and survival in large trees. Therefore any functional explanation of the composition of a forest community should encompass all the stages of the life cycle, not only the larger ones.

The roles of chance and inter-specific differences in determining regeneration are not constant during the forest cycle. The importance of growth and survival in the understorey is stressed: processes occurring before gap formation partly determine the result of interspecific competition after a gap has formed. Nevertheless, owing to a higher availability of resources, species-specific differences in growth are more pronounced in the gap phase than in the understorey, whereas the contribution of chance factors to regeneration is most pronounced during the pre-gap phase. Four mechanisms were proposed by which species with similar regeneration requirements can maintain themselves in the community. These are based on differences in competitive ability (*e.g.*, growth rate), the abundance of seedlings and their spatial distribution.

In **Chapter** 3 the demography of flowers was described for *Dicymbe altsonii*, a dominant tree of the canopy in central Guyana. This species produces large numbers of flowers once every two years. It was shown that losses of flowers and developing fruits were much larger, in absolute and in relative terms, than losses in any later stage of the life cycle of *Dicymbe*. Only 4% of the flowers produced a pod, while survival among just germinated seedlings in the following few months was 61%. Comparison of amounts and nutrient contents of leaf litter and reproductive litter (flowers and fruits) indicated that the latter signifies a high investment in nutrients for the parent tree. This was calculated for phosphorus. It was shown that reproductive trees grow significantly slower than non-reproductive trees during flowering years.

This Chapter and Chapters 6 and 8 illustrate the changing demographic constraints that act on a cohort of *Dicymbe* individuals. The number of flowers and developing fruits is constrained by the availability of resources to the mother and by the need to produce flowers for other purposes than seeds (*i.e.* for the production of pollen or to attract pollinators). Developing pods are predated by monkeys and birds. Germinating seedlings are killed by insects (ants) and fungi. Larger seedlings are nearly insensitive for these attacks, but may be killed by falling branches and trees. Suppression due to low light levels reduces the number of seedlings, and this may even be more important for saplings of 1-10 cm. Large trees finally may die because they are hit by falling trees or because of, wind, heavy rain or lightning.

**Chapter** 4 highlights an unusual feature among tropical trees: vegetative reproduction by means of stem sprouts in *Dicymbe.* These sprouts may grow out before or after the death of the parent to become reproductive individuals. The number and size distribution of sprout populations were compared between two *Dicymbe* populations, on contrasting soil types (white and brown sands). The number and total basal area of sprouts per tree was positively related to parent size and the occurrence of damage in the crown, and there were significant differences in these aspects between the two populations that were compared. In contrast to the parents, the population size distributions of the sprouts were characterised by a high abundance of mainly small sprouts in the brown sand population, and by a low abundance, but large size of sprouts in the white sand population. This difference was attributed to differences in the light climate between the forest types. Trees that originated from sprouts constituted *c.* 8-10% of the total number of trees >10 cm dbh in both forest types. Sprouts may increase the probability that *Dicymbe* retains a canopy site after the death of the mother, while saplings are more suitable for the occupation of new sites.

In **Chapter 5** the survival and germination were studied for three seed cohorts of *Chlorocardium rodiei*, a very large-seeded species. Seed fall occurred over a period of six months in each year, and was variable in amount and phenology. Median time till germination was about one year, and germination was still continuing after 3 years. The survivorship of seeds was higher than of rooted or germinated (leafy) individuals, and was negatively correlated with rainfall per three-month period. Rooting had no clear relation with the amount of rain. The timing of rooting was related to survivorship as a rooted individual: individuals that rooted early had a higher survivorship than individuals that rooted late. This seemed to be simply a correlate of age, and not related to other factors that potentially affect germination.

The evidence was considered whether this variable germination behaviour could be interpreted as a mechanism of risk spreading. A model showed that large variation in phenology and in rainfall led to only limited variation in germination success.

In **Chapters 6 and 7** the ecological correlates of seedling growth and survival were studied for *Dicymbe*, *Chlorocardium* and *Duguetia neglecta.* Seedling growth was mainly affected by light availability and seedling size, expressed as height, leaf density or rank in the local height hierarchy. There was no clear trade-off between high-light growth and low-light survival, and the species were not differentially distributed over the light gradient in the forest. Seedling height and the number of leaves explained as much of the variation in growth as light did. *Chlorocardium* responded to logging with increased seedling growth, but it was soon overgrown by faster growing species. Four to seven years after logging it was still maintaining itself below the secondary canopy, but most seedlings were suffering heavy leaf losses. It was concluded that intensive management of the secondary vegetation was required in order to maintain *Chlorocardium* in the exploited forest.

In **Chapter 8**, population models were derived for the three species in undisturbed and exploited forest. *Chlorocardium* and *Duguetia* had approximately stable population sizes in either plot, while *Dicymbe* was increasing in the undisturbed plot and very strongly increasing in the exploited plot. All species had higher growth rates with increasing light availability, but *Dicymbe* benefitted most from the higher light availability in the exploited plot. Projected age-size relationships indicated that the study species belonged to the longest-living species among a group of tropical tree species. *Chlorocardium* was expected to become reproductive after about 200 years. Simulation indicated that sustainable management of *Chlorocardium* is possible but not easy.

## How is *Chlorocardium* retained in the community?

Analysis of seedling growth and survival revealed no obvious way by which *Chlorocardium* would be able to maintain itself in the community. In the forests studied, *Dicymbe* is arguably its main competitor for canopy sites. *Dicymbe* produces waves of rather large seedlings that carpet the forest (Chapter 3), while *Chlorocardium*, with a much larger seed (Chapter 6, Table 1), produces similar-sized seedlings, which emerge over a period of many months. Seedling growth in *Chlorocardium* was always less than seedling growth of *Dicymbe*, independent of the naturally occurring light environment, while its survival in shade was lower, not higher than *Dicymbe*'s. Thus the often found negative relation between high-light growth and low-light survival (*e.g.* Hubbell & Foster 1992), a mechanism for coexistence of two species, did not apply for these species. However, for larger-sized individuals this mechanism appeared to be present (Chapter 8, Fig. 6): the difference in growth between the two species was not only dependent on light, but also on the size of the individual. *Chlorocardium* grew faster than *Dicymbe* at very low light levels, but only above a certain size threshold (*c.* 0.5 cm dbh).

Based on the evidence, I propose the following mechanism by which *Chlorocardium* maintains itself in the community (a slight modification of the mechanism given in Chapter 2, as the 'type 2' strategy). *Chlorocardium* is not a competitive species and will not secure a canopy site on the basis of fast growth in gaps, at the expense of similar sized competitors. Instead, *Chlorocardium* individuals will only be successful in capturing canopy sites when they occupy an advantageous site within a gap (with an increased access to light, nutrient or water resources compared to close neighbours), in combination with an advantage of size compared to close neighbours. The first condition is inevitably met in some gaps, at some times, for any species: it is a chance occurrence. Chance recruitment as a strategy is not likely to be successful for species with irregular, scarce reproduction, but a species may capitalise on chance by being common. *Chlorocardium* is locally very common as a seedling, achieved by abundant yearly reproduction and by concentrating seedlings in space (limited dispersal). An alternative strategy could be directed dispersal, by which dispersers transport seeds selectively to favourable sites. This mechanism is proposed for large seeded species (and *Chlorocardium*) by Hammond *et al.* (*in prep.*); and Forget *unpublished manuscript*. In addition, this can be achieved by being very long-lived, so that once a canopy position is secured, it is kept for a very long time, and many cohorts of seedlings can be produced. *Chlorocardium* is very long-lived, but the evidence supporting that it has a much longer reproductive life than *Dicymbe* is not yet very strong (see discussion in Chapter 8).

In addition, *Chlorocardium* is capitalising on size once it is advanced to the sapling status. The evidence from Chapter 8 indicates that *Chlorocardium* saplings may continue to grow slowly in the deep understorey, where other, faster growing species (exemplified by *Dicymbe*) do not grow or even die. In this way *Chlorocardium* may gradually accrue a large size, which may be of advantage at the moment that a gap is formed above it. With a larger size it is more likely to be successful in the gap, even when it is growing together with potentially faster growing but smaller individuals. It would be interesting to know whether forests exist where *Chlorocardium* is rare (1-2 adults per ha) and maintaining itself. The mechanism described here more or less implies that the species needs to be common as an adult and, at least locally, as a seedling.

In Chapter 2 it was pronounced that species characterised by such a strategy have a bimodal population size distribution. High seedling mortality and slow growth would limit their relative abundance as saplings and pre-reproductive individuals. Individuals that are successful in reaching the canopy remain there very long and produce an accumulation of adults. The bimodal population size distribution is a well-known feature of *Chlorocardium* (ter Steege 1990). Other authors have pointed out that the bimodal population size distributions could also be a transient effect, the consequence of rare establishment conditions (Aubréville 1938, Bongers *et al.* 1988, Poorter *et al.* 1996). However, the evidence presented in this thesis suggests that if this is caused by large regeneration waves, these are certainly not due to large-scale disturbance. An alternative, non-transient (equilibrium) explanation for a bimodal distribution is that there are large differences in growth or mortality rate between large saplings and adults. Caswell (1989) formally derived a (matrix-model) formula describing such a situation: $w_j > w_{j-1}$ if $G_{j-1} > \lambda - P_j$ ($w_j$ is the number of individuals in class *j*, G and P are the probabilities of growth and stasis, respectively, $\lambda$ is the population growth rate; certain other conditions apply). This formula explains that a peak in the population size distribution occurs if the probability of entering a class is larger than the probability of leaving it (by growth or by death). The data do not support the possibility of large differences in demographic rates between juveniles and adults (Chapter 8), at least not when all individuals from different light environments are pooled in one size class.

## Exploitation

Exploitation affects the population structure and the demographic rates of the species (Chapter 8). The population structure of *Chlorocardium* was affected in a planned fashion, but in addition to that, changes in the population structure occurred as a result of unintended, logging-related damage. There were very few juveniles (1-20 cm dbh) in the exploited population, and in Chapter 8 it was suggested that this was due to logging damage. The same phenomenon was observed in other logging areas (and destroyed juveniles were sighted there, personal observation), and no undisturbed forests have been described without juveniles. Similarly, damage may explain the low number of small *Duguetia* individuals in the exploited plot.

Growth was increased for all species, although *Duguetia* showed a less strong response to light than both other species. Individuals of the subcanopy (1-20 cm) responded strongly to increased light. For seedlings this was not as clear, but this may have been caused by a lack of seedlings with high crown illumination in the exploited plot. Growth in the exploited plot was stimulated by light, but possibly also by other factors, such as reduced root competition or increased nutrient availability caused by decaying organic matter (*cf.* Brouwer 1996).

Mortality was increased for seedlings in the exploited plot, although for *Chlorocardium* mortality was low (compared to the undisturbed plot) before and during the study period (<7 years after logging). It is expected that mortality is going to increase for seedlings of this species, given the high leaf loss rates that were observed. The sample sizes for larger trees were too small to detect differences in mortality. Therefore, a possible increased mortality of saplings and small trees in the exploited plot, caused by falling debris and the fall of damaged trees could not be shown, although this is often suggested to occur in exploited forest. *Dicymbe* saplings belonging to the secondary canopy had a slightly increased mortality (Table 4, Chapter 8), possibly associated with thinning of the secondary canopy. This higher mortality was observed in the same classes as those in which growth was negative under the low light conditions in the undisturbed plot (Fig. 6, Chapter 8).

No clear differences in reproduction could be demonstrated, except for a reduced seed shadow of *Chlorocardium.*

Population modelling indicated that these differences meant an increased population growth rate for *Chlorocardium* in the exploited plot, and therefore sustainable management is, in principle, possible. However, the benefits of management were not expected to become apparent within 50-100 years after logging, as a result of the lack of large juvenile individuals. From the foregoing it should be remembered that *Chlorocardium* is not successful in a community because it is competitive, but because it is able to grow slowly to an advanced size class, after which it may be successful in some gaps thanks to this large size. Therefore, a management strategy that creates environments where competition is determined by differences in growth rates (large gaps with seedling or sapling vegetations that are homogeneous in size) is not expected to be successful for *Chlorocardium*, unless competitors such as *Dicymbe* are removed often. Instead, management that enables *Chlorocardium* individuals to secure a high position in the local size hierarchy is expected to be more successful, can be less intensive but requires long rotation times. This form of management requires more skills than the first mentioned form, because it requires silvicultural decisions to be taken at an individual level.

With simulation it was shown that stimulation of abundance and growth of large juveniles (6-20 cm dbh) had positive and comparatively rapid effects on the abundance of timber in the population. In many populations such large juveniles are rare, and therefore the benefits of specific management of these individuals are relatively low. *Chlorocardium* seedlings are common in most populations, and they were shown to be remarkably persistent to deep shade once they had been able to accumulate a large size (Chapter 7). Therefore silviculture of seedlings may have higher potential benefits than silviculture of large juveniles (Chapter 8), but it will take a longer time to become important in terms of timber production, and involves higher costs. *Dicymbe* (or other similar species) is expected to respond better and faster than *Chlorocardium* to most forms of treatment.

The present management of *Chlorocardium* populations is limited to the harvest of individuals above the cutting limit (*c.* 30 cm), while harvest damage reduction (planned skidding, directional felling) is employed at some concessions. The results of this study show clearly that this is not sufficient for the sustainable management of *Chlorocardium.* The need for post-logging investment in the residual forest is paramount. *Chlorocardium* is not a species that lends itself to cheap and simple forestry, but it needs intensive attention. The high costs involved for this management can only be earned back if silvicultural management is augmented with other measures. These measures range from improving timber recovery in the forest and at the sawmill, extending the range of species that is utilised, optimising the legal framework in which forestry is operating in Guyana, to a more realistic valuation by customers of this unique timber resource.

# Samenvatting

Tropisch regenwouden staan om verschillende redenen onder sterke belangstelling. De biologische verscheidenheid en de bijzondere complexiteit van de relaties tussen planten en dieren in het regenwoud hebben altijd tot de verbeelding van wetenschappers gesproken. Daarnaast is er gedurende het afgelopen decennium een toenemende publieke belangstelling voor het regenwoud, aan de ene kant doordat er grootschalige aantasting van het bos plaatsvindt en aan de andere kant doordat het regenwoud door televisie en toenemende reislust een stuk dichterbij is komen te staan.

Voor veel tropische landen is het tropische regenwoud een belangrijke natuurlijke hulpbron en een van de weinige mogelijkheiden om economische groei te bewerkstelligen. In sommige landen, zoals Maleisië en Indonesië is houtexploitatie uit tropisch regenwoud al vele decennia een belangrijke bron van inkomsten; andere landen beginnen zich nog maar net de mogelijkheden van het tropisch regenwoud als economische hulpbron te realiseren. Eén van die landen is Guyana, aan de noord-oost kust van het Zuid-Amerikaanse continent. Kleinschalige commerciële exploitatie van regenwoudprodukten (met name van Letterhout, *Piratinera guianensis*, het rubber-achige balata van de *Manilkara bidentata* boom en Groenhart (*Chlorocardium rodiei*) balken voor havenwerken) vindt daar al gedurende enkele eeuwen plaats, maar pas in de tachtiger en negentiger jaren van de twintigste eeuw begon daar de grootschalige en systematische bosexploitatie. Het Guyanese regenwoud ontkomt aan sommige van de belangrijkste problemen, die andere tropische regenwoudgebieden kenmerken: de bevolkingsdruk in het bos is laag en er is weinig zwerflandbouw. Aan de andere kant is de exploitatie van het bos onzorgvuldig en levert het relatief weinig op. De houtkap concentreert zich op slechts enkele soorten en ondanks de gemiddeld lage kapintensiteit, is het gebruik van het bos niet duurzaam. Er vindt op vele plaatsen in de kapcyclus veel verspilling plaats. Hoewel bossen 87% van het landoppervlak beslaan, vertegenwoordigt hout maar 2% van de exportinkomsten, levert het werkgelegenheid op voor niet meer dan 20.000 mensen en zijn de baten voor de overheid in de vorm van belastingen slechts zo'n 1 miljoen Amerikaanse dollar per jaar.

Het Tropenbos Programma in Guyana is opgezet om aan een aantal van die problemen tegemoet te komen. De doelstelling van het programma is om kennis van het tropische regenbos in Guyana te verwerven en deze in te zetten om een duurzaam systeem van regenwoud gebruik te bewerkstelligen. Hierbij wordt gebruik gemaakt van een multi-disciplinaire benadering, waarbij in deelonderzoeken water- en nutrientenstromen, plantengroei, populatie dynamiek en biodiversiteit in ongestoorde situaties, alsmede in stituaties waarbij houtkap heeft plaatsgevonden, worden bestudeerd. Voorts worden de effecten van verschillende intensiteiten van experimentele houtkap op de bijgroei van de resterende bosopstand bestudeerd. Het voorliggende onderzoek betreft een studie naar de populatiedynamiek van tropische boomsoorten in relatie tot verstoring veroorzaakt door commerciële houtkap. Hierbij wordt onderzoek verricht naar de toe- en afname van boompopulaties, naar factoren die hiervoor verantwoordelijk zijn en naar manieren om deze aantalsveranderingen ten behoeve van het beheer van het bos voor houtproduktie te sturen.

De doelstellingen van dit onderzoek waren:

1 het beschrijven en verklaren van de populatiedynamiek (groei, overleving en reproductie) van tropische boomsoorten, met name in verband met de beschikbaarheid van licht;
2 het verklaren van de gevolgen van houtkap op de demografie van deze soorten en
3 het opstellen van een populatiemodel dat gebruikt kan worden om de gevolgen van houtkap voor deze soorten te beoordelen.

Het onderzoek wordt gerechtvaardigd door de noodzaak een duurzaam bosbouwsysteem op te zetten, niet alleen ter ontwikkeling van de Guyanese economie, maar ook om het bos een maatschappelijke functie te geven en daarmee het behoud van de ecologische bosfuncties te waarborgen.

Er werden drie modelsoorten gekozen om dit onderzoek aan uit te voeren: *Chlorocardium rodiei* (Lauraceae, Greenheart), de tot voor kort voornaamste commerciële houtsoort van Guyana; *Dicymbe altsonii* (Caesalpiniaceae, Clump Wallaba), een niet commerciële soort, die samen met *Chlorocardium* het leeuwendeel van de kroonlaag van veel bossen in Centraal Guyana uitmaakt; en *Duguetia neglecta* (Annonaceae, Yarri yarri), een zeer algemene ondergroei soort. Al deze soorten zijn in meerdere of mindere mate schaduwtolerant en kunnen dus aanzienlijke delen van hun leven in de schaduw doorbrengen. Daarnaast hebben tenminste *Chlorocardium* en *Dicymbe* gedurende een aantal levensfasen een verhoogde lichtbeschikbaarheid nodig om naar een plek in de kroonlaag toe te kunnen groeien. Deze soorten werden verondersteld representatief te zijn voor de verschillende strategieën waarmee boomsoorten zich handhaven in het bos.

Het onderzoek werd uitgevoerd op de Tropenbos onderzoekslocatie nabij Mabura Hill in Centraal Guyana en vond grotendeels plaats in 2-4 ha grote permanente proefvlakken, waarin alle individuen van de onderzoekssoorten gelokaliseerd en gemerkt waren. Eén proefvlak bevond zich in ongestoord bos, terwijl een ander geplaatst werd in een bos dat in 1988 geëxploiteerd was. De gemerkte populaties werden tussen 1991 en 1995 jaarlijks opgenomen: de hoogte- en diametergroei werden gemeten en sterfte en aanwas werden bepaald. Andere aspecten, met name wat betreft kieming en zaai-