Regeneration in Natural and Logged Tropical Rain Forest

Modelling seed dispersal and regeneration of tropical trees in Guyana

L.H. van Ulft

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Regeneration in Natural and Logged Tropical Rain Forest

Modelling seed dispersal and regeneration of tropical trees in Guyana

Regeneratie in Natuurlijk en Gekapt Tropisch Regenwoud

Het modelleren van zaadverspreiding en regeneratie
van tropische bomen in Guyana

(met een samenvatting in het Nederlands)

Proefschrift

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Tropenbos International

The research reported in this thesis was carried out at study sites in the Mabura Hill area, central Guyana and was conducted within the framework of the Tropenbos-Guyana Programme.
The project (no. 895-10-022) was funded by the Netherlands Organisation for Scientific Research (NWO) within the framework of the priority programme ‘Biodiversity in Disturbed Ecosystems’ of ALW (Council for Earth and Life Sciences) and WOTRO (Netherlands Foundation for the Advancement of Tropical Research).

Voor Karina

Der beste, scharfsinnigste Schachspieler kann nur einige kleine Züge voraussehen; von einem französischen Schachspieler, der zehn Schachzüge vorausberechnen konnte, berichtete man wie von einem Weltwunder. Wie viele Schachzüge des Lebens aber sind uns denn bekannt?

F.M. Dostojewski – Idiot

Contents

Chapter 1

General introduction

Tropical rain forests are characterized by a high tree species diversity, although large differences exist between regions (*e.g.* Ek 1997, Gentry 1985, Phillips *et al.* 1994, ter Steege 2000, Whitmore 1975). Several mechanisms and theories have been proposed to explain the coexistence of so many species. Four important mechanisms or theories are recruitment limitation, niche differentiation, the Janzen-Connell hypothesis and the intermediate disturbance hypothesis. Regeneration (*i.e.* the development from seed to mature tree, see section 2) and gap dynamics (section 1) are crucial components of most, if not all, existing species diversity theories. For a better understanding of the regulation and maintenance of the high tree species diversity in tropical rain forests, and for an understanding of the ecological population dynamical processes in the tropical rain forest a much better understanding of the relation between tree regeneration and disturbance is necessary. This knowledge is urgently needed as the pressure on tropical forests imposed by anthropogenic disturbances, such as logging (section 3), has increased dramatically over the past decades, which may affect the tree populations and the species diversity.

Studying the response of tree regeneration to disturbance and subsequent shifts in the species composition is difficult: due to the longevity of trees, the response may be delayed for decades or possibly even centuries. Direct observation is therefore only possible in exceptional cases. An alternative approach, which is adopted in this thesis, is the use of computer models, based on ecological data, to simulate the long-term effects of disturbance on the species composition (section 4). This type of models is essential to evaluate the sustainability of current forest management in the context of timber certification. However, the earliest stages in the life of a tree (*i.e.* seed and small seedling stages) have so far received little attention in simulation models, in spite of their critical role in tree demography and maintenance the species diversity. This omission is expected to result in less accurate predictions of the impact of disturbances on the tropical rain forest.

In the present study, information on important processes in the earliest stages of regeneration will be presented for tropical rain forest tree species in Guyana (section 6). The collected information will be used to implement a new regeneration model in the individual-based, spatially explicit SYMFOR modelling framework. To facilitate interpretation of the model results, species will be classified into functional groups, *i.e.* groups of species with similar characteristics (section 5). The aim of the development of the model is to study the long-term changes of natural and anthropogenic disturbance on the diversity of the forest. The study was performed within the Tropenbos-Guyana Programme and the NWO priority programme Biodiversity in Disturbed Ecosystems (section 7).

1 Natural disturbance in tropical rain forests

Tropical forests are not as stable as once was thought. Continuously openings in the forest canopy, ‘gaps’, are created by falling branches and trees. Occasionally larger stretches of forest may be disturbed by rare events such as hurricanes, floods or fires. It has been estimated that around one or two percent of the area is affected by gap formation annually (Hartshorn 1990, van der Meer and Bongers 2001). Gap formation will change many aspects of the local microclimate and soil; however, the most obvious effect of gap creation is an increased light availability (Denslow 1987, van Dam 2001). Within gaps, the microclimate and soil conditions are highly heterogeneous (Canham *et al.* 1990, Orians 1982, van Dam 2001). Hence, disturbance enhances the availability of different environments, both between patches of different successional stages (from new gap to closed canopy) and within gaps. The gap versus non-gap dichotomy is an oversimplification of the actual situation (Lieberman *et al.* 1989), however, it is a useful and widely used concept to discuss disturbance and will be used as such in this chapter and in other parts of the thesis.

The intermediate disturbance hypothesis predicts that the highest species diversity will be found in areas with an intermediate level of disturbance (Connell 1978, Sheil and Burslem 2003). In forests with a higher disturbance regime, slow-growing species will not be able to reach maturity, hence favouring the fast-growing species. In forests with a lower disturbance regime the density of patches favourable for the successful regeneration of fast-growing species is too low and only the slow-growing species will survive. Either way, the species diversity will be lower than in forests with an intermediate level of disturbance where slower- and faster-growing species can coexist. The validity of the intermediate disturbance theory has received a lot of attention recently (*e.g.* Hubbell *et al.* 1999, Sheil and Burslem 2003, ter Steege and Hammond 2001).

2 Regeneration

The regeneration of a species encompasses the production and dispersal of seeds, their germination, and subsequently the growth of the juveniles until they reach maturity and start producing seeds themselves. At any moment in the regeneration process, an individual may die, for example following predation or due to adverse environmental conditions. The failure of a species to regenerate will ultimately result in its (local) extinction.

Probably the most widely accepted species diversity theory is the niche differentiation theory. According to this theory many species can coexist in an area because each species is specialized for recruitment, growth and mortality in a specific set of conditions (Brown and Jennings 1998, Denslow 1980, Grubb 1977, Poorter and Arets 2003). Few will doubt that this theory explains at least part of the high species diversity in tropical rain forests, as some species clearly are more adapted to a life in gaps and others to the forest understorey. However, there is a large group of generalist species, which do not show clear habitat specificity (Zagt and Werger 1998), and it seems unlikely that niche differentiation alone can lead to the coexistence of hundreds of tree species within a single hectare.

2.1 Seed production and dispersal

A tree starts its life as a seed. Species have developed a wide array of adaptations to assist the dispersal of their seeds, ranging from nutritious, colourful fruits to attract animal dispersers, to fruits that ‘explode’ and shoot the seeds several metres away. In tropical forests, the seeds of the majority of the species are dispersed by animals (Hammond *et al.* 1996, Hammond and Brown 1995). The enormous variety and the amount of photosynthetically gained energy spent on seed dispersal mechanisms suggest that dispersal is of critical importance to the fitness of the resulting seedling. Two advantages have been suggested in literature (Howe and Smallwood 1982). First, seed dispersal increases the probability that seeds encounter suitable sites for their establishment and subsequent development. Second, seed dispersal may help to escape from a higher probability of mortality below the parent tree.

The latter advantage of seed dispersal is captured by the Janzen-Connell hypothesis (Connell 1971, Janzen 1970). According to this hypothesis, the seed density will decrease with distance from the tree. However, due to species-specific predators and diseases, the seed and seedling mortality is expected to be highest near the parent tree. The multiplication of the seed shadow and seedling mortality then predicts that the seedling density will peak some distance away from the parent. The low recruitment probability under parent trees would prevent that one single species can dominate the forest and so enable the coexistence of species in the forest. Some evidence for this mechanism has been found, but mainly for attacks by invertebrate predators (Hammond and Brown 1998).

It is obvious that without seeds there would be no trees. Nevertheless, most studies on population dynamics in the past have ignored the seed stage, implicitly assuming seeds are always and everywhere available. Walking through the forest, however, it is immediately clear that this assumption does not hold and that the availability of seeds is generally limited. A species can be limited in its seed availability because parent trees are rare or clumped, have a low fecundity, fruit only rarely, or because seed dispersal is limited. The limited availability of seeds plays an important role in the recruitment limitation theory (Dalling *et al.* 2002, Hubbell and Foster 1986, Hurtt and Pacala 1995, Tilman 1994, 1999). If a species’ seed availability is limited, it fails to arrive at all sites, which are suitable for its germination, growth and survival, meaning that suitable sites will remain empty. Individuals of other, potentially less competitive species can then occupy these empty sites, since they do not have to compete with a stronger species. In this way, recruitment limitation can allow lesser competitive species to coexist among more competitive species.

Hence, it may be expected that seed production and dispersal play critical roles in a tree’s life and in maintaining the high species diversity. Proper descriptions of the seed production and dispersal are still scarce for tropical tree species and generally are restricted to case studies for single species, making the detection of general trends difficult. Inverse modelling seems a promising technique to approximate production and dispersal for many species (Clark *et al.* 1999, Dalling *et al.* 2002, Ribbens *et al.* 1994, van Rheenen *et al.* 2004b). This technique will be used in chapter 2 of the present thesis to estimate the seed production and dispersal for a number of species.

2.2 Post-dispersal seed fate

After the seed has been dispersed it has to germinate before it is killed or loses viability. It has been found that some species show an increased germination as light availability or gap size increases, while others show no response or are inhibited (Alvarez-Buylla and Martínez-Ramos 1990, Ellison *et al.* 1993, Kyereh *et al.* 1999, Ng 1978, Peña-Claros 2001, Raich and Gong 1990, Rose 2000, ter Steege *et al.* 1994, van Rheenen *et al.* 2004a). Partly the difference in response between species seems to be correlated to seed size. Generally, small-seeded species respond positively to an increased light availability. This response may be expected since species with small seeds have to rely on photosynthesis soon after germination, while large-seeded species can survive on their seed reserves for a long time. In the forest, however, not only light availability determines whether a seed will germinate. Other factors such as predation by mammals or insects, fungi or drought may kill the seed before it has been able to germinate (Blate *et al.* 1998, Hammond *et al.* 1999, Ng 1978, Notman and Gorchov 2001, Peña-Claros 2001, Zagt 1997a). The relation between seed size, gap size and the fate of seeds will be addressed in chapter 3 of this thesis.

2.3 Growth and mortality of juveniles

Many regeneration studies have investigated the growth and mortality of juvenile individuals in relation to the light availability or compared these two processes in the forest understorey and gaps. The results of most of these studies are consistent. Generally, juveniles grow faster and survive better in gaps or high-light environments than in undisturbed forest patches or low-light environments (*e.g.* Arets *et al.* 2003, Augspurger 1984, de Souza and Válio 2001, Denslow 1987, Howe 1990, Kobe 1999, Osunkoya *et al.* 1992, Peña-Claros 2001, Poorter 1998, Rose 2000, Sork 1987, ter Steege *et al.* 1994, van Rheenen *et al.* 2004a, Zagt 1997b, Zuidema 2000). Growth and mortality will not be explicitly addressed in this thesis, as these processes are studied in a partner project (Arets 2005). Growth and mortality data collected for the partner project will be used in the model development.

3 Logging

In many tropical countries, timber is extracted from the forest through selective logging. This will cause disturbance, usually heavy disturbance, to the forest. The number of harvested trees per hectare is generally low, but the damage to the remaining forest caused during the logging operation can be considerable (Johns 1988, Johns *et al.* 1996, van der Hout 1999). Logging gaps are generally larger than natural gaps, since only large, healthy trees are felled. An additional effect of logging is that the soil will be disturbed when the logs are removed from the forest by heavy extraction vehicles (‘skidders’), so creating ‘skid trails’. Thus, through selective logging, the frequency and intensity of disturbance will increase. Throughout the thesis, the term ‘undisturbed’ (forest or plot) will be used to refer to undisturbed by anthropogenic causes, while natural disturbance may have occurred.

Logging will affect the regeneration of tree species in several distinct ways. First, the creation of more and larger gaps will affect germination, juvenile growth and mortality. Although generally this may lead to faster growth and better chances of survival for juveniles, seed mortality of large-seeded species may increase, resulting in a lower germination success (ter Steege *et al.* 1994). Second, logging will have a large impact on the remaining population, since a large proportion of the reproducing trees is removed from the forest, especially for the harvested species, of which specifically the large, reproducing adults are felled. This will most likely result in a reduction in the seed availability and an altered distribution of those seeds over the forest. Third, logging can affect animal populations, which both disperse and consume seeds, through forest fragmentation and the opening of the forest to illegal hunting (Chiarello 1999). Finally, the extraction of the logs by skidders destroys much of the vegetation in loggings gaps and on skid trails, removing the ‘advance regeneration’ which forms the majority of the successful regeneration in natural gaps (Uhl *et al.* 1988). A detailed understanding of the regeneration processes and the way they are affected by disturbance would greatly assist in defining forest management strategies that promote a sustained extraction of timber in the future and at the same time minimize the effects on the species diversity.

4 Modelling

Tropical rain forest trees can live for centuries (Korning and Balslev 1994, Lieberman *et al.* 1985, Zuidema 2000) and populations of trees will react very slowly to changed circumstances. In the context of logging, this means that the effect of a reduction in regeneration that may be induced by logging may not be felt until years after the logging actually occurred. This phenomenon is known as ‘extinction debt’. A direct assessment of the long-term effects of logging or any other type of disturbance is currently only possible in a few exceptional cases, where forest inventories have been performed prior to a disturbance in the past (*e.g.* ter Steege *et al.* 2002). Although these studies are invaluable, they only provide a limited insight since generally only trees of ten centimetres diameter or more are included in the inventories (see datasets in Manokaran and Kochummen 1987, Phillips *et al.* 1994, Richards 1939, ter Steege *et al.* 2002). In addition, they are not flexible in the sense that only the effect of the disturbance that occurred in the past (for example logging without skidders and chainsaws) can be studied. Modelling is a alternative approach to study the long-term effects of disturbance.

In a simulation model the short-term data on recruitment, growth and mortality collected in the field can be used to predict the development of the forest after disturbances. During the last decade several simulation models were developed, which in principle may be suitable to study the long-term effects of disturbance on the species composition (*e.g.* Chave 1999, Köhler and Huth 1998, Liu and Ashton 1998, Phillips *et al.* 2003). However, none of these models includes a detailed description of all regeneration processes. Rather, several processes or stages in the regeneration are aggregated. This is a major limitation of these models as regeneration probably plays an important role in regulating the stand composition and maintaining the species diversity. In this thesis, the modelling framework SYMFOR (Phillips *et al.* 2003) will be adapted so that the regeneration can be explicitly modelled. For the calibration of the model the information on seed production, dispersal and germination collected for this study, as well as growth and mortality data for juveniles and trees collected by Arets (2005) will be used.

The aim of the development of this model is to study the long-term effects of natural and logging-related disturbance on the functional group diversity, and to evaluate forest management, such as the optimal length of logging cycles, harvest intensities, and the required number and distribution of remaining seed trees.

5 Classification of species

To facilitate the analysis of ecological processes and to discover general trends, tree species have often been classified into functional groups (*e.g.* Aubréville 1938, Lieberman *et al.* 1985, Phillips *et al.* 2002, van Steenis 1956). Generally, species have been classified based on similarities in their environmental requirements or on their abundance during different successional stages. Examples of these classifications are obligate gap vs. gap-independent species (Popma *et al.* 1992) and the well-known pioneer vs. climax (Swaine and Whitmore 1988), respectively. Most of these classifications are in fact rather similar. One problem of these classifications is that a small, rather distinct group of species can be classified as obligate gap or pioneer species and the other group still contains too many ecologically different species to serve the purpose of the classification. Therefore, sometimes an intermediate group is introduced, *e.g.* the gap-dependent species are placed between the obligate gap and gap-independent species, and the long-lived pioneers between the (short-lived) pioneer and climax species.

To assign a species to a functional group at least a basic knowledge of the species' ecology is needed. This information is lacking for the majority of the species in tropical rain forests. Therefore, a different approach is used in this study. Four species characteristics, which are considered effective proxies of a species' behaviour, are selected to classify species *a priori*. These are wood density, seed mass, adult stature and dispersal type. Information on these characteristics is available in literature for many species and missing information can be collected relatively easily. Wood density is included since it is related to maximum growth rate (Arets *et al.* 2003). Seed mass is related to an array of regeneration processes, such as seed production, seed dispersal, germination and emergence, initial seedling size and early seedling survival (Armstrong and Westoby 1993, Augspurger and Franson 1987, Boot 1996, Dalling and Hubbell 2002, de Souza and Válio 2001, Eriksson and Jakobsson 1999, Foster and Janson 1985, Rose 2000, Rose and Poorter 2003). The adult stature influences the environment of the adult tree and so the amount of resources available for reproduction and is related to seed production and dispersal distance (van Rheenen *et al.* 2004b). Also dispersal type has been found to be related to dispersal distance (Willson 1993). In addition, certain dispersal agents may carry the seeds specifically to sites suitable for the germination and survival of that species ('directed dispersal', Wenny 2001, Wenny and Levey 1998).

Throughout the thesis, classifications of species will be based on these four characteristics although in the first three chapters only a subset of the characteristics will be used. It should be realized, however, that any classification is only a tool and that in reality species rather cover a continuum of characteristics, responses or requirements (*e.g.* Whitmore 1989).

6 Guyana and study area

The fieldwork for this thesis was performed in Guyana. Guyana is situated on the northern coast of South America, bordered by Venezuela, Brazil and Surinam (figure 1). The country covers an area of 214,970 square kilometres and is inhabited by less than one million people, of which ninety percent live in the coastal region. Guyana has a tropical climate with average daily temperatures of 25-26°C and around 2700mm rainfall per year. Rainfall follows a bimodal pattern with most rain falling from May to July and a second rainy season in December and January (figure 2).

Approximately eighty percent of Guyana is still covered by more or less intact forest. Natural disturbances are mainly confined to falling branches and trees as large-scale disturbances, such as earthquakes and hurricanes, are very rare (Davis 1941, Hammond and Brown 1995).

Figure 1. Guyana’s position in South America (inset) and the location of the capital Georgetown, the Demerara Timbers Ltd. township Mabura Hill and the research areas in the Mabura Hill Forest Reserve (MHFR), West Pibiri and East Pibiri.

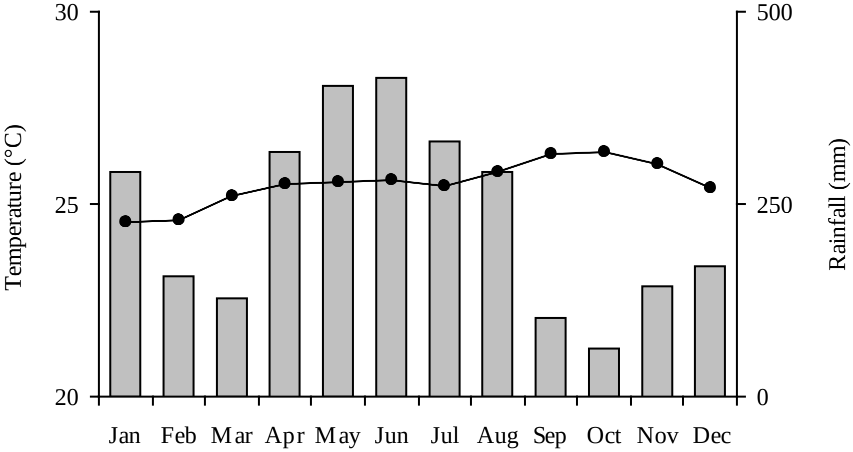

Figure 2. The monthly temperatures and rainfall in the Mabura Hill area. The values are averages for the period October 1991 to December 1993 in the Mabura Hill Forest Reserve and from 1996 to 2000 in Pibiri. The data are from Jetten (1994) and van Dam (2001).

For centuries selective logging has been practised at a very low intensity in Guyana. However, recently foreign logging companies have been attracted to Guyana and during the last decade the log production has increased dramatically. The Government of Guyana now has to make important decisions concerning the utilization, conservation and protection of the nation’s forest (ter Steege 1998). A detailed description of logging in Guyana is given by van der Hout (1999).

The actual data collection took place from June 1999 to December 2001 in the Mabura Hill area in central Guyana (5°13’N, 58°48’W, figure 1). The tropical rain forests of central Guyana display a high degree of monodominance and as such are low diversity forests when compared to forests in western and central Amazonia. Additionally, the forests contain many endemic species, of which *Chlorocardium rodiei*, is the best-known example (ter Steege 2000). The forests in central Guyana are characterized by tree species with a high wood density, large seeds and unassisted or rodent dispersal. The predominance of species with these characteristics is possibly related to the extremely low disturbance regime in the area, following the predictions of the intermediate disturbance hypothesis (Hammond and Brown 1995, ter Steege and Hammond 2001).

There were two main research areas: the Mabura Hill Forest Reserve and the East Pibiri compartment of the Demerara Timbers Ltd. (DTL). The Mabura Hill Forest Reserve is a reserve covering an area of 2000 hectares, which has never been logged commercially. It encompasses the watershed of a creek and contains a wide variety of soil and forest types. The East Pibiri compartment has been logged by DTL in 1998. This site was selected since its forest composition appeared to match that in the reserve and because of its high degree of disturbance (figure 3). The soils in the two sites belong to the Ferralsols type (‘brown sand’), although the East Pibiri site appeared slightly loamier. In both areas, a square plot of nine

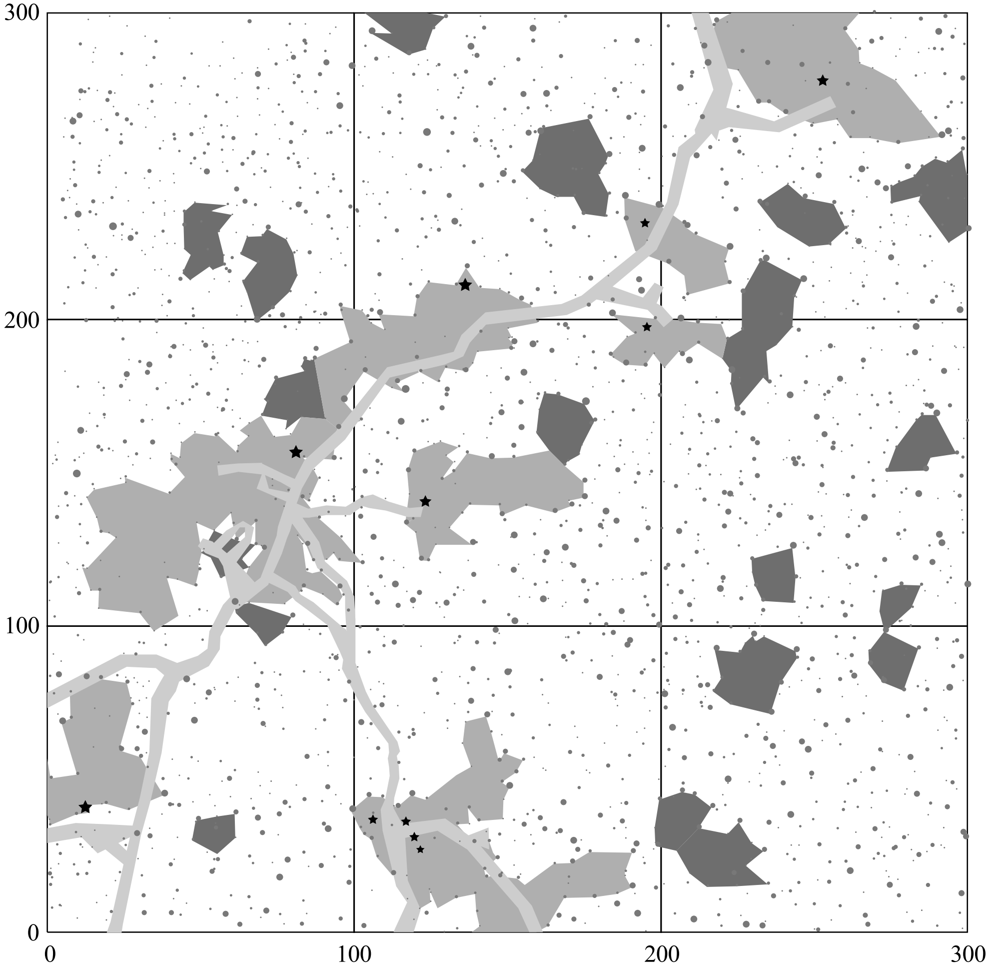

Figure 3. The nine-hectare plot in the East Pibiri compartment of the DTL concession in central Guyana. The area was logged in 1998. The figure shows all trees larger than 15cm diameter (dark grey circles, the larger the circle the larger the tree), the stumps of the felled trees (black stars), the skid trails (light shaded areas), the logging gaps (medium shaded areas) and the natural gaps (dark areas).

hectares was established, demarcated by plastic pegs. In both plots, all potential parent trees were mapped and identified. The identification was done by experienced 'tree spotters', of which some were trained during a biodiversity study in the same area (Ek 1997). In both plots sample quadrates of one square metre were laid out, following a random design in the reserve and a random stratified design in the East Pibiri plot, ensuring sufficient data for disturbed patches. In these quadrates, the seed and seedling distribution were monitored and the light availability was estimated. Additional data on the distribution of seeds around isolated trees were collected in both areas. In the East Pibiri area, two understorey sites and eight logging gaps were selected for a germination experiment. Data on the fruiting and flowering of species were collected throughout the area. The growth and mortality data of juveniles and trees were collected in the Pibiri research area in the West Pibiri compartment of the DTL concession (Arets 2005, van der Hout 1999).

7 Institutional setting

The present study was carried out within the Tropenbos-Guyana Programme and was funded by the Netherlands Organisation for Scientific Research (NWO) within the framework of the priority programme ‘Biodiversity in Disturbed Ecosystems’. Below a short description of these programmes is given. Detailed information can be obtained from their websites, www.tropenbos.nl and www.nwo.nl, respectively.

7.1 Tropenbos International

Tropenbos International is an intermediary organization that facilitates the development and implementation of research and capacity building programmes in tropical countries, particularly focussing on sustainable forest exploitation. Currently Tropenbos International is or has been operating and developing research sites in Colombia, Ghana, Guyana, Indonesia, Suriname and Vietnam in cooperation with research institutes, government agencies and other stakeholders (Tropenbos International. 2004).

The Tropenbos-Guyana Programme was established in 1989 based on an international agreement between the Netherlands and Guyana. In this programme, researchers from the University of Guyana, the Utrecht University, the Guyana Forestry Commission, and the National Agricultural Research Institute collaborated to study ecological and management aspects of the forests in Guyana and their use. The majority of the research has been carried out in the Demerara Timbers Ltd. concession in the Mabura Hill area and in the North West District. Since the start of the programme, many students and people involved in the utilization and management of the forest have been trained. After twelve years of research, and support to Guyanese research, policy and forest management organizations, the Tropenbos-Guyana Programme came to an end in December 2001. A Research Unit created under the Guyana Forestry Commission, continues to gather data, critical for the wise management of forests in Guyana.

7.2 Biodiversity in Disturbed Ecosystems

The priority programme ‘Biodiversity in Disturbed Ecosystems’ of ALW (Council for Earth and Life Sciences) and WOTRO (Netherlands Foundation for the Advancement of Tropical Research) started in 1995. The programme aims to define guidelines for the management, conservation and restoration of disturbed ecosystems. To this end, research is promoted that contributes to a better understanding of disturbance-related shifts in the species and genetic diversity, and to a better understanding of the dynamics in (disturbed) ecosystems. The programme encompasses 29 research projects carried out in ecosystems in Central and South America, Africa and South East Asia.

8 Thesis objectives and outline

8.1 Aims of the thesis

The importance of regeneration and disturbance in theories that attempt to explain the long-term species dynamics and the high species diversity in tropical rain forests indicates their partly proved, partly hypothesized importance in structuring the forests. The focus of the research in this thesis is on the earliest stages of regeneration, *i.e.* the seed and seedling stages, and the differential effect disturbance has on these stages. The growth and mortality of juveniles and larger individuals are studied in a partner project (Arets 2005). It is acknowledged that other processes than the ones studied in this thesis can have an effect on the regeneration. However, due to the limited time available for data collection only a few major processes could be studied. The selected processes are expected to respond strongly to disturbance (*i.e.* changes in light availability and distance).

The aims of the present study are:

1. To describe and understand the dynamics of the earliest stages of regeneration, *i.e.* from seed production to established seedlings, for a number of tropical rain forest tree species, differing in life history characteristics and response to disturbance.
2. To develop and use a simulation model to study the long-term effects of natural and logging-related disturbance on the functional group diversity, and to study the sustainability of forest management for future harvests and the functional group diversity.

8.2 Thesis outline

In chapter 2, the seed production and dispersal are estimated for a number of species using inverse modelling. Furthermore, the size at first reproduction is determined for many species. Potential effects of seed mass, dispersal type, adult stature and disturbance are discussed. In addition, the inverse modelling technique is evaluated. The estimated parameters will be used in the simulation model.

In chapter 3, the germination and seed mortality of eleven tree species is studied in relation to their seed mass and to gap size. It provides insight in the effect of disturbance on the germination success of species differing in seed mass.

In chapter 4, the distribution of seedlings with respect to adult trees, the estimated light availability and disturbance is evaluated for a number of species. The species are clustered into functional groups based on their wood density and seed mass. This chapter addresses the relative importance of vicinity to adults (seed dispersal), and light and disturbance (germination and survival) in shaping the spatial distribution of seedlings in relation to wood density and seed mass.

In chapter 5, the simulation model, aimed at evaluation of the long-term effects of disturbance on the forest composition and functional group diversity is described. This model includes the data and functions described in the second and third chapter and data collected in the Pibiri area by Arets (2005) and van der Hout (1999). The performance of the model is evaluated.

In the final chapter, the main conclusions of the previous chapters are summarized and discussed. The applicability of the obtained results to forest management will be evaluated.

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Chapter 2

Seed production and dispersal of tree species in the tropical rain forest of central Guyana

Abstract

According to the recruitment limitation theory, the limited availability of seeds can be crucial for the maintenance of the high tree species diversity in tropical rain forests. Factors that may affect the seed availability at a certain location are the minimum reproductive size, seed production and dispersal. These factors were described for eight tree species in relation to their seed mass, adult stature and dispersal type. In addition, the seed production and dispersal were compared for three species between a logged and an undisturbed area.

Analysis of 1421 observations of trees with flowers or fruits revealed that the minimum reproductive size increased with the maximum tree height. The seed production and dispersal were estimated from seed densities in two large plots and around isolated trees using ‘inverse modelling’. Subcanopy and canopy species produced fewer seeds than emergent species at a fixed reference size and small-seeded species produced more seeds than large-seeded species. Small-seeded species dispersed their seeds over longer distances than large-seeded species. The only wind-dispersed species that was included in this study dispersed its seeds over longer distances than the animal-dispersed species. In general, seeds were dispersed over short distances only and fifty percent of the seeds fell within 3.7 to 13.5m of the tree. Trees produced more seeds in the logged area than in the undisturbed area, while dispersal was not affected by logging. The final effect of logging on the seed availability is unsure: the individual seed production increased for the three studied species, but this increase may be counterbalanced by a reduction in the number of adult trees. Based on the results obtained in this study it may be expected that the study species may by limited in their regeneration by a limited availability of seeds, mainly because their seeds are poorly dispersed.

1 Introduction

It has been hypothesized that the limited availability of seeds may have a critical role in maintaining the high tree species diversity in topical rain forests. A species is said to be seed limited if it fails to arrive at all sites suitable for its establishment (Dalling *et al.* 1998, 2002, Eriksson and Ehrlén 1992, Muller-Landau *et al.* 2002, Nathan and Muller-Landau 2000, Sheil and Burslem 2003, Wang and Smith 2002). Because of seed limitation, the best competitor may be absent from a site suitable for its establishment, providing an opportunity for less competitive species to establish and persist at that site, thus slowing down competitive exclusion (Dalling *et al.* 2002, Hurtt and Pacala 1995, Tilman 1999). Despite the possible importance of seed limitation for the maintenance of the high tree species diversity in tropical rain forests, the processes that contribute to seed limitation have received little attention in population dynamical studies. The aim of this study was to describe the factors contributing to seed limitation for several common tree species occurring in the tropical rain forests of central Guyana.

An important aspect of seed limitation is the abundance of reproductive trees: an abundant species is less likely to be seed limited than a rare species. Determining the abundance of reproductive trees requires information on the minimum reproductive size, *i.e.* the size at which a species starts reproducing. These data are scarce for neotropical species (Guariguata and Pinard 1998). It seems likely that the minimum reproductive size increases with the maximum tree height attained. This expectation is supported by the study of van Rheenen *et al.* (2004) who found that Bolivian subcanopy tree species started reproducing at smaller sizes than taller tree species.

The second factor contributing to seed limitation is individual fecundity of the adult trees. The trade-off between seed mass and number is well known: given a certain amount of resources available for reproduction, the number of seeds decreases as seed mass increases (Greene and Johnson 1994, Harper *et al.* 1970, Smith and Fretwell 1974). Consequently, it may be expected that small-seeded species produce more seeds than large-seeded species at a given reproductive investment. The amount of energy available for reproduction will not be constant among species. Species that will have their crowns higher up in the canopy at maturity will be able to capture more light and gain more energy through photosynthesis. If this extra energy is (partly) invested in reproduction, it may be expected that seed production will be lowest for subcanopy and highest for emergent species.

Finally, the degree of seed limitation is determined by seed dispersal: a poorly dispersed species is more likely to be seed limited than a species that disperses its seeds over a large area. The range over which seeds are dispersed is affected by dispersal type and by seed mass. The difference in dispersal distance between wind- and animal-dispersed seeds is not clear, however, on average wind-dispersed seeds seem to travel further than animal-dispersed seeds (van Rheenen *et al.* 2004, Willson 1993). Generally, the dispersal distance of wind-dispersed seeds is expected to decrease with increasing seed mass (Augspurger 1986, Augspurger and Franson 1987). In Guyana, the majority of the tree species is dispersed by mammals or birds (Hammond *et al.* 1996, Hammond and Brown 1995). For animal-dispersed species the effect of seed mass on dispersal distance is less obvious and will depend on the abundance and effectiveness of species-specific dispersers. In this chapter, it is simply assumed that the effect of seed mass on dispersal distance is similar for all dispersal types and hence, that dispersal distance decreases with an increasing seed mass.

Logging will likely affect the degree of seed limitation in a number of ways. The fecundity of individual adult trees may increase, since the removal and killing of trees will increase the light availability for the remaining trees. The reduction in adult tree abundance will directly result in a reduction in the seed production in the forest, however this effect is outside the scope of the present study. Little is known about the effect of logging on seed dispersal (Guariguata and Pinard 1998) and for now it is assumed that logging will not have an effect on dispersal distance.

Summarizing, it is expected that 1) the minimum reproductive size increases with adult stature, 2) fecundity decreases with increasing seed mass, but increases with increasing adult stature, 3) dispersal distances are longer for wind-dispersed than for animal-dispersed species and decrease with increasing seed mass, 4) logging will increase individual fecundity, and 5) that logging has no effect on dispersal distance. The results will be discussed both from an ecological (the effect of seed mass, dispersal type, adult stature and logging) and a methodological point of view (accuracy of the estimated values and the influence of data collection). The descriptions of the minimum reproductive DBH, seed production and seed dispersal generated in this chapter will be implemented in the modelling framework SYMFOR to study the shifts in the forest composition following disturbance (chapter 5).

2 Methods

2.1 Data collection

2.1.1 Study area

The study was conducted in the Mabura Hill area in central Guyana, South America. The area has a tropical climate with average temperatures of 25.9°C and 2772mm precipitation annually, following a bimodal pattern with maxima in May-August and December-February (Jetten 1994, van Dam 2001). The area experiences low levels of disturbance and large-scale disturbances, such as hurricanes area very rare. The tropical rain forest of central Guyana is characterized by a predominance of hardwood species with large seeds and rodent or unassisted dispersal (Hammond and Brown 1995, ter Steege and Hammond 2001).

2.1.2 Minimum reproductive size

To obtain good estimates of the minimum reproductive DBH (the diameter at breast height, 1.30m above the ground, at which a species starts reproducing), phenological data were collected in the Mabura Hill area from 1999 to 2001. Of all trees with flowers and/or seeds, whether in research areas, surrounding forest or along the road, the observation date, species name and DBH were recorded. To exclude extremes, the minimum reproductive DBH was arbitrarily defined as the lower 10th-percentile of the observed size distribution of the reproductive trees of a species. To test the relation between minimum reproductive DBH and maximum tree height, a linear regression was performed. Data on maximum tree height were obtained from literature or from data collected by Arets (unpublished data). For this analysis only species with at least ten observations of flowering or fruiting trees were included.

2.1.3 Seed density in plots

In 1999 and 2000, two nine-hectare plots (300 · 300m) were established in forests of comparable soil type (Ferralsols: ‘brown sand’) and species composition: one in an undisturbed forest in the Mabura Hill Forest Reserve of the Tropenbos-Guyana Programme (5°13’N, 58°48’W) and one in a forest patch that was logged in 1998 in the East Pibiri compartment of the Demerara Timbers Ltd. concession (5°01’N, 58°34’W). In these plots, all potential parent trees ($n \approx 4400$ per plot) were identified and their stem diameter and position within the plot were measured. A potential parent tree was defined as a tree with a DBH of at least 15cm for the majority of the species. For species of which local field staff knew or suspected that they can reproduce at smaller sizes, all trees with a DBH of 5cm or more were included. Trees with seriously damaged crowns were excluded from the analysis.

In the undisturbed plot, 1694 sample quadrates of 1m^2 were randomly laid out. In the logged plot 498 quadrates were laid out in a stratified design focussing on logging gaps and skid trails. No quadrates were established in the outer 40m of the plot (the buffer zone) to reduce measuring seed inputs from outside the plot and hence, unknown trees. An initial count of seeds and fruits (henceforth the term seeds will be used to refer to both seeds and fruits) in the quadrates was conducted in April 2001 in the harvested plot and in May-June 2001 in the undisturbed plot. The seeds were marked for recognition. Three and six months after the initial count, the number of new seeds in the quadrates was counted and the number of seeds that entered each of the quadrates during the monitoring period of six months was calculated. Since only large seeds can be found on the forest floor and the number of seeds is generally low, seed counts were only conducted for a selection of common, large-seeded species. The species for which sufficient data (at least 100 seeds) were collected and their characteristics are shown in table 1. The seed fresh mass was measured for a large sample or derived from literature.

In the area of the undisturbed plot, Zagt and Werger (1997) collected similar data on the large-seeded species *Chlorocardium rodiei* and *Dicymbe altsonii* (table 1). Two plots of one hectare each were divided in a 5 by 5m grid. The number of fresh seeds of the two species (and recently germinated seedlings for *Dicymbe*) was counted once per year, shortly after the fruiting period, in quadrates of 1m^2 in the centre of each grid cell (*i.e.* 400 quadrates per plot). For *Chlorocardium,* seeds were counted during three consecutive years (1992–1994), while seed(ling)s of *Dicymbe* were counted only in 1993, the only year of the study in which it produced seeds (Zagt and Werger 1997). For *Chlorocardium* sometimes less than 100 seeds were counted. However, it was decided to include the data anyway, to evaluate the variation in the parameters between years.

Table 1. The species for which sufficient numbers of seeds were found and their characteristics. FM: fresh mass of fruit or seed (as dispersed) in grams, DT: dispersal type (m: monkey, r: rodent, v: bat, w: wind, u: unassisted), AS: adult stature (S: subcanopy, C: canopy, E: emergent). Species are ordered by fresh mass.

Scientific name	Family	FM	DT	AS
Sclerolobium guianense var. guianense[†]	Caesalpiniaceae	0.3	w	E
Oxandra asbeckii	Annonaceae	0.9	m	S
Licania heteromorpha var. perplexans	Chrysobalanaceae	4.1[a]	mrv	C
Parinari campestris[‡]	Chrysobalanaceae	10.6	mrv	E
Dicymbe altsonii	Caesalpiniaceae	14.3[b]	ru	C
Swartzia leiocalycina	Papilionaceae	21.6[a]	mrv	E
Catostemma fragrans	Bombacaceae	22.9	mr	C
Chlorocardium rodiei	Lauraceae	71.3	ru	C

[†] *Sclerolobium* fruits sometimes contained two seeds. These were regarded as separate fruits.
[‡] *Parinari* fruits can contain two seeds, however, this cannot be determined without opening the fruit.
FM: [a] From Hammond and Brown (1995) and [b] from Zagt (1997).

2.1.4 Seed density around isolated trees

Three isolated trees of *Parinari campestris* and *Sclerolobium guianense* and five isolated trees of *Catostemma fragrans* that had recently finished fruiting (*i.e.* had dropped most of their seeds) were selected (table 1). Around each tree, the number of seeds was counted in temporary 0.25m^2 quadrates along four perpendicular transects. Since north-easterly winds are prevalent in Guyana, the transects were laid out in north-easterly, north-westerly, south-easterly and south-westerly direction. For *Catostemma* and *Parinari* seeds were counted every 0.5m starting from the tree trunk. The length of the transect depended on the dispersal distance of the seeds. If no seed was found in ten subsequent quadrates, it was assumed that no more seeds would be found further away from the tree. For *Sclerolobium* seeds were counted every metre starting one metre from the tree trunk (centre of first quadrate at 1.25m). The length of the transect for *Sclerolobium* was 75 metres. However, one transect was not completed because it intersected a logging gap, where most likely the conditions for dispersal differed from those in the surrounding forest.

In 2000, *Swartzia leiocalycina* showed mast fruiting. Around five individuals of this species the number of seeds and recently established seedlings were counted in four directions. Transects for this species were only 10 metres long and seeds were counted every metre in a circle with a radius of 0.15m.

2.2 Seed shadow model

A model describing the seed shadow around a tree should consist of two components: 1) a component describing the fecundity or seed production of the tree as a function of its size and 2) a component describing the distribution of those seeds around the tree. In literature, several models that describe the production and dispersal of seeds or seedlings are available. The models of Chave (1999), Clark *et al.* (1998) and Ribbens *et al.* (1994) were used to derive the seed shadow model used in the present study.

Following the relation used by Ribbens *et al.* (1994), the number of seeds, *SP*, produced by tree *j*, is given by:

$$SP_j = SSP \cdot \left(\frac{D_j}{D_{\text{ref}}} \right)^{\beta} \tag{1}$$

where D_j is the diameter at breast height (1.30m) of tree *j* in centimetres, D_{ref} the reference DBH (*i.e.* approximately the average DBH of all parent trees). The reference DBH was set to 25.6cm. *SSP* (standard seed production) is the number of seeds produced by a tree with DBH = D_{ref} and β determines the rate at which seed production increases with DBH. In the models of Clark *et al.* (1998) and Ribbens *et al.* (1994), the seed production of a tree is assumed to be directly proportional to its basal area, *i.e.* β is taken as 2. This assumption is supported for temperate trees by the study of Greene and Johnson (1994), but only for diameters of less than approximately 35cm. In the present study, β is also assumed to equal 2, *i.e.* when a tree becomes twice as thick it produces four times as many seeds. This reduces the number of parameters that need to be estimated. Furthermore, during some initial analyses, β appeared to be very difficult to estimate, since β and *SSP* strongly depend on each other.

These SP_j seeds are distributed over a circular area around the tree, assuming radial symmetry. Generally, descriptions of the distribution of seeds around the tree, the second component of the seed shadow model, are based on a negative exponential function of distance. The probability density function, *i.e.* the proportion of SP_j seeds produced by tree *j* that arrives in a 1m^2 quadrate *q* centred at distance r_{qj} from the centre of tree *j*, is given by:

$$f = \frac{1}{N} \cdot \exp\left[-\left(\frac{r_{qj}}{\rho} \right)^{\theta} \right] \tag{2}$$

where r_{qj} is the distance of the centre of quadrate *q* to tree *j* in metres, ρ is a dispersion parameter in metres and θ is a dimensionless parameter that determines the shape of the function. *N* is a normalizing factor that ensures that the area under *f* equals 1. This normalizing factor *N* is obtained by arc-wise integration and integration over distance (0 to ∞) and takes the form:

$$N = \pi \cdot \rho^2 \cdot \frac{2}{\theta} \cdot \Gamma\left(\frac{2}{\theta} \right) \tag{3}$$

in which $\Gamma(x)$ is the gamma function (Arfken 1970). Since, ρ and θ strongly depend on each other, it was decided to set θ to 2, as do Chave (1999) and Clark *et al.* (1998). The normalizing factor *N* then reduces to:

$$N = \pi \cdot \rho^2 \tag{4}$$

and the probability density function, f, becomes a Gaussian distribution function. Ribbens *et al.* (1994) used $\theta = 3$, which gives a distribution that drops faster than a Gaussian distribution.

Assuming that the probability density function is not only influenced by distance, but also by the size of the tree's crown, it was decided to include the crown radius, $C_{\mathrm{R}j}$, following the approach of Chave (1999):

$$f = \frac{1}{\pi \cdot \left(\rho + C_{\mathrm{R}\,j}\right)^2} \cdot \exp\left[-\left(\frac{r_{qj}}{\rho + C_{\mathrm{R}\,j}}\right)^2\right] \tag{5}$$

However, since the crown radius was not measured, the linear relation:

$$C_{\mathrm{R}\,j} = a + b \cdot D_j \tag{6}$$

was assumed, to calculate the crown radius $C_{\mathrm{R}j}$ of tree j from its DBH (D_j) as suggested by Rollet (1973, as cited in Chave 1999). The species-specific parameters a and b in this equation were estimated from unpublished data collected by Arets (pers. comm.) in the same area.

Combining the formulas shown above, the following equation for the predicted seed density of seeds from tree j in a 1m^2 plot q centred at distance r_{qj} from the centre of tree j can be derived:

$$\hat{SD}_{qj} = SSP \cdot \left(\frac{D_j}{D_{\mathrm{ref}}}\right)^2 \cdot \frac{1}{\pi \cdot \left[\rho + \left(a + b \cdot D_j\right)\right]^2} \cdot \exp\left[-\left(\frac{r_{qj}}{\rho + \left(a + b \cdot D_j\right)}\right)^2\right] \tag{7}$$

2.3 Estimating the parameters *SSP* and ρ

2.3.1 Inverse modelling

The species-specific values of the seed production parameter *SSP* and the dispersion parameter ρ were estimated using inverse modelling. The procedure will be illustrated here for the two 9ha plots. For each of the quadrates, the distances to all parent trees of a species in the same plot were calculated. Using the equation for $\hat{SD}_{qj}$ as derived in the previous section (equation 7), the seed density each parent tree j is predicted to generate in the centre of quadrate q was calculated. Often, individual seed shadows will overlap and consequently, quadrates will receive seeds of several trees. Then, the seed density in the quadrate is calculated by summing the densities the quadrate receives of each of the surrounding trees, *i.e.* the predicted seed density in quadrate q, given T trees, is calculated as:

$$\hat{S}D_q = \sum_{j=1}^{T} \hat{S}D_{qj} = \sum_{j=1}^{T} SSP \cdot \left(\frac{D_j}{D_{\mathrm{ref}}} \right)^2 \cdot \frac{1}{\pi \cdot \left[\rho + \left(a + b \cdot D_j \right) \right]^2} \cdot \exp\left[-\left(\frac{r_{qj}}{\rho + \left(a + b \cdot D_j \right)} \right)^2 \right] \qquad (8)$$

The predicted seed density for a set of parameter values was calculated for all quadrates and translated to seed number by multiplying with the quadrate’s area. Subsequently, the agreement between the observed and predicted seed numbers was maximized. For this purpose, the coefficient describing the level of agreement between predicted and observed seed numbers, *i.e.* the scatter about the line of slope = 1 (predicted = observed), was used (Clark *et al.* 1998). Given Q quadrates this coefficient is defined as:

$$r^2 = 1 - \frac{\sum_{q=1}^{Q} \left(SD_q - \hat{S}D_q \right)^2}{\sum_{q=1}^{Q} \left(SD_q - SD_{avg} \right)^2} \qquad (9)$$

in which SD_q is the observed number of seeds in quadrate q, $\hat{S}D_q$ is the predicted number of seeds in quadrate q given this set of parameters and SD_{avg} is the average observed seed number in all quadrates. The combination of SSP and ρ, which gave the highest r^2, was then searched using a program written in C++. This was done by starting with 11 steps of 10000 (from 0 to 100000) for SSP and 11 steps of 10 (from 0 to 100) for ρ. For each combination of the two parameters, the agreement between predicted and observed seed numbers was calculated. The parameter set which gave the highest r^2 was then used to calculate 11 new SSP and ρ values, by dividing the step size of the previous run by two and then subtracting five times that new step size from the optimal value for that parameter to get a new starting value. If the optimal parameter value was either the lower or upper bound of the 11 values, the step size was multiplied by two. If the new starting value was negative, it was set to 0. This procedure was repeated until r^2 was not further improved, using a minimum step size of 1 for SSP and 0.01 for ρ.

Since the dispersion parameter ρ alone is difficult to interpret, the median dispersal distance (*MDD*), *i.e.* the radius within which 50% of the seeds fall was calculated and is also presented. The *MDD* depends both on ρ and the crown radius, but not on SSP, and is approximately $0.83 \cdot (\rho + C_{\mathrm{R}j})$. Furthermore, 99% of the seeds fall within circa $2.15 \cdot (\rho + C_{\mathrm{R}j})$.

2.3.2 Estimation from plot data

To minimize the input of seeds from unknown sources outside the plot, a buffer zone of 40m was used in which no quadrates were established, but all trees were mapped. However, in the model this would lead to a skewed seed input, *i.e.* quadrates at the edge of the buffer zone can receive seeds from trees up to 260m from one side and only from 40m from the other side. To prevent this skewed seed input in the model, it was decided to ‘allow’ only trees within 40.5 (width of buffer zone + 0.5m to the centre of the quadrate) of a quadrate to deposit seeds in that quadrate. Quadrates that were not within 40.5m of any parent tree for the species of interest were discarded from the analysis. Per species, parameter values were estimated for the logged and the undisturbed plots separately, and for the two plots combined, if data were available.

Zagt and Werger (1997) did not use a buffer zone during data collection. Therefore, a buffer zone that seemed appropriate after analyzing the data collected in the two 9ha plots and around isolated trees was used. Quadrates in this buffer zone and quadrates that were further away from any parent tree than the width of the buffer zone were discarded from the analysis. For *Chlorocardium*, data were available for three consecutive years. For this species, estimates of the optimal parameter values were made for each year separately.

2.3.3 Estimation isolated tree data

The isolated trees were regarded as being in separate plots, *i.e.* they could not deposit seeds in quadrates around the other trees. In contrast to the parameter estimation from the plot data, no maximum distance was set for the estimation from the isolated tree data, since there were no conspecifics in the vicinity, *i.e.* seed shadows did not overlap and quadrates could receive seeds from one tree only. However, in practice the maximum distance was more than 40.5 metres for *Sclerolobium* only. Per species, one optimal set of parameters was searched for all trees of that species combined.

2.3.4 Evaluating differences between species, plots and methods

The limited data availability does not permit thorough statistical testing of the hypotheses and interactions between factors could not be included. Nevertheless, simple exploratory tests were performed to obtain insight of the factors that contribute to seed limitation.

To enable a comparison between species, one parameter set per species was selected. Preference was given to parameter sets estimated from the two 9ha plots, since these were considered the best datasets. Seed production and dispersal were compared at D_{ref}. To study the effect of seed mass on seed production and dispersal, two linear regressions were performed with the $\log_{10}(SSP)$ and the estimated median dispersal distance as dependents and $\log_{10}$(mass) as independent.

Subsequently the data are presented for different datasets, to evaluate differences between plots, methods (9ha plots and individual trees) and years. These differences were assessed by calculating the level of agreement between predicted and observed seed numbers (r^2) for one dataset, using the parameters estimated from a different dataset. If r^2 is large, the datasets resemble each other. If r^2 is negative, the mean better describes the seed densities than the model, and the datasets are considered different.

In all cases, the parameter estimates are accompanied by the 95% confidence interval, derived from 2500 bootstrapped estimates using the percentile method (Caswell 2001). Parameter values were considered significantly different if the bootstrapped confidence intervals did not overlap.

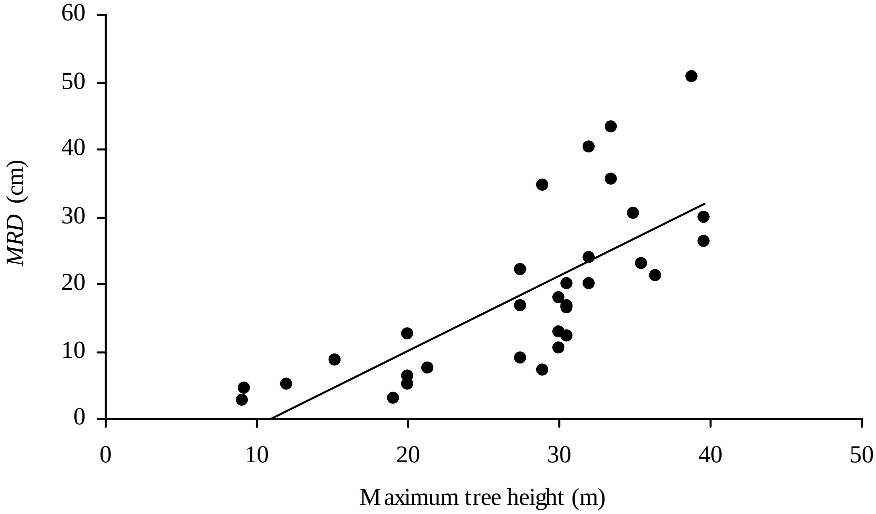

Figure 1. The relation between minimum reproductive diameter (*MRD*, in centimetres) and the maximum tree height (H_m, in metres). Each point represents one species with at least ten individuals. The equation is $MRD = 1.1 \cdot H_m - 11.9$.

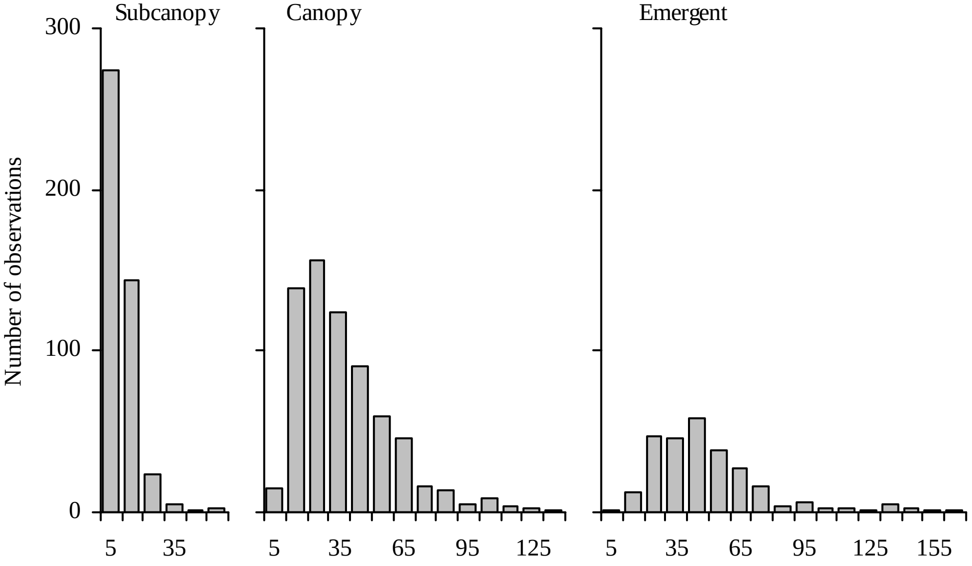

Figure 2. The number of observed trees with flowers and/or fruits for subcanopy, canopy and emergent species in 10cm DBH classes.

Table 2. The number of potential parent trees (*T*) and quadrates (*Q*) used to estimate the dispersal functions for each of the species in the logged plot (L), the undisturbed plot (U), around isolated trees (I) and/or by Zagt and Werger (1997, Z&W).

	L		U		I		Z&W	
Scientific name	*T*	*Q*	*T*	*Q*	*T*	*Q*	*T*	*Q*
Sclerolobium					3	885		
Oxandra	443	498	507	1694				
Licania	215	493						
Parinari	5	116	1	155	3	496		
Dicymbe							141	288
Swartzia					5	200		
Catostemma			106	1621	5	604		
Chlorocardium	82	394	235	1680			88	288

3 Results

In total, 1421 observations of trees with flowers and/or seeds were made (appendix A). 20 observations were discarded since the maximum tree height was not known. The smallest individual with fruits had a diameter of only 0.6cm. The minimum reproductive DBH (the 10th-percentile) increased with maximum tree height (figure 1, $n = 32$, $F_{1,30} = 34.97$, $R^2 = 0.538$, $p < 0.001$).

Since the number of observations per species was generally low, it was decided to define a minimum reproductive DBH for three adult stature groups rather than per species for the estimation of the seed production and dispersion parameters. Species were classified based on their maximum tree height (H_m) into subcanopy ($H_m < 25$m), canopy ($25 \geq H_m < 35$m) and emergent species ($H_m \geq 35$m). The minimum reproductive diameters were 4.1, 14.3 and 23.4cm for subcanopy, canopy and emergent species, respectively (figure 2). It should be realized, however, that the variation in minimum reproductive diameter is quite large between species within adult stature groups (appendix A). Since in the 9ha plots only trees of more than 5cm DBH for subcanopy and more than 15cm DBH for canopy species were included, their minimum reproductive diameters had to be increased to 5 and 15cm, respectively, for the estimation of the seed production and dispersion parameters. The effect on the estimated parameters for seed production and dispersal should be limited as small trees produce few seeds.

The minimum number of quadrates used to estimate the dispersal curves (quadrates within 40.5m of any conspecific adult tree) was 116 for *Parinari* in the logged plot, while for the very abundant subcanopy species *Oxandra*, with a total of 950 trees, all established quadrates in both the logged and the undisturbed plot were used (table 2). The number of seeds produced by a tree with an average DBH ($D_{ref} = 25.6$cm) ranged from 28 for *Chlorocardium* to 14301 for *Sclerolobium* (table 3). Although there was a trend towards a decreased seed production (*SSP*) with seed mass, the linear regression indicated that the slope did not deviate significantly from zero ($n = 8$, $F_{1,6} = 3.13$, $R^2 = 0.343$, $p = 0.127$). This seemed to be caused by the high seed production of *Swartzia*, which was mast fruiting that year. If this

Table 3. The datasets that were used to estimate the seed production parameter *SSP* and the dispersion parameter ρ, both with the 95% confidence interval, and the corresponding agreement between predicted and observed seed numbers. The crown radius (C_R in metres) and median dispersal distance (*MDD* in metres) are given for a tree with the reference diameter (D_{ref}). L: logged plot, U: undisturbed plot, Z&W: undisturbed plot of Zagt and Werger (1997), I: isolated trees.

Species	Data	*SSP*	ρ	r^2	C_R	*MDD*
Sclerolobium	I	14301 (12576;16023)	12.32 (10.24;14.42)	0.57	3.9	13.5
Oxandra	L,U	203 (154;263)	8.33 (6.16;9.74)	0.07	4.5	10.7
Licania	L	203 (147;265)	2.16 (1.27;3.26)	0.32	3.6	4.8
Parinari	L,U	627 (419;919)	1.70 (0.00;4.29)	0.56	2.8	3.7
Dicymbe†	Z&W	99 (83;280)	8.42 (3.71;30.36)	0.04	3.3	9.8
Swartzia	I	4615 (3775;5589)	2.06 (1.28;2.90)	0.43	3.0	4.2
Catostemma	U	47 (24;77)	2.48 (0.00;5.19)	0.05	2.8	4.4
Chlorocardium	L,U	28 (24;33)	2.23 (1.23;3.20)	0.12	3.3	4.6

† Based on the results from the 9ha plots, the width of the buffer zone was set to 22.5m for the data collected by Zagt and Werger (1997).

species was discarded from the analysis the regression was significant ($n = 7$, $F_{1,5} = 10.94$, $R^2 = 0.686$, $p = 0.021$). *SSP* values were higher for the three emergent species than for the subcanopy and canopy species. The canopy species did not consistently differ from the subcanopy species.

The estimated values for the dispersion parameter ρ, ranged from 1.70m for *Parinari* to 12.32m for *Sclerolobium*, which resulted in median dispersal distances (*MDD*) of 3.7m and 13.5m, respectively (table 3). Generally, ρ and dispersal distances were short (figure 3) and for five of the eight species, ρ was shorter than the crown radius at D_{ref}, resulting in *MDD*s only slightly longer than the crown radius. The median dispersal distance decreased with the logarithm of seed mass ($n = 8$, $F_{1,6} = 10.06$, $R^2 = 0.626$, $p = 0.019$). The only wind-dispersed species, *Sclerolobium*, did have the highest seed production and the longest median dispersal distance, however, for the remainder of the species differences between dispersal types did not show a clear pattern. The ρ and median dispersal distances of *Oxandra* (10.7m) and *Dicymbe* (9.8m) were long. The latter species had a very wide confidence interval for the dispersion parameter. The agreement between predicted and observed seed numbers (r^2) was reasonable for half of the species, but for the four abundant species for which the dataset from the undisturbed plot was used the r^2 was low (table 3). For all species the model predicted seed numbers that were lower than actually observed in quadrates with large seed numbers (figure 4). Additionally, the predicted seed numbers were too high in plots with few seeds for *Dicymbe*, *Swartzia* and, to a lesser degree, *Sclerolobium*.

Generally, the agreement between predicted and observed seed numbers was slightly better when parameters were estimated for the logged and undisturbed plot separately than for the two plots combined (tables 3 and 4). For the three species with sufficient data in both the logged and undisturbed plot, the seed production parameter was roughly two to seven times higher in the logged plot than in the undisturbed plot, though for *Parinari* the confidence intervals overlapped (table 4a). For *Oxandra*, the ρ- and *MDD*-values were larger in the

Table 4. The estimated values of the parameters *SSP* and ρ with 95% confidence intervals, the corresponding agreement between predicted and observed seed numbers and the median dispersal distance in metres, for species for which the parameters could be estimated from more than one dataset. Table a compares the results of the logged and the undisturbed plot, while table b compares the results from the isolated trees with the species' parameters as given in table 3. The last two columns give the level of agreement between predicted and observed seed numbers, using the parameters estimated from one dataset, to predict the seed numbers for another dataset. L(U) is the level of agreement in the logged plot using the parameters estimated for the undisturbed plot (L: logged, U: undisturbed, I: isolated trees, S: species). Coefficients < 0 indicate that the mean is a better predictor of seed number than the model.

a.	Logged				Undisturbed				r^2	
Species	*SSP*	ρ	r^2	*MDD*	*SSP*	ρ	r^2	*MDD*	L(U)	U(L)
Oxandra	558 (377;766)	8.82 (6.61;10.23)	0.23	10.7	81 (64;112)	1.44 (0.36;9.24)	0.02	5.0	0.01	< 0
Parinari	842 (554;1716)	0.72 (0.00;4.87)	0.62	2.9	484 (336;683)	1.60 (0.00;4.33)	0.63	3.6	0.47	< 0
Chlorocardium	101 (71;144)	2.38 (0.53;4.20)	0.40	4.7	22 (18;26)	2.79 (1.70;3.81)	0.09	5.1	0.10	< 0

b.	Isolated trees				Species				r^2	
Species	*SSP*	ρ	r^2	*MDD*	*SSP*	ρ	r^2	*MDD*	I(S)	S(I)
Parinari	432 (368;403)	1.39 (0.33;2.53)	0.26	3.5	627 (419;919)	1.70 (0.00;4.29)	0.56	3.7	0.15	0.50
Catostemma	383 (276;494)	1.02 (0.10;1.94)	0.22	3.2	47 (24;77)	2.48 (0.00;5.19)	0.05	4.4	< 0	< 0

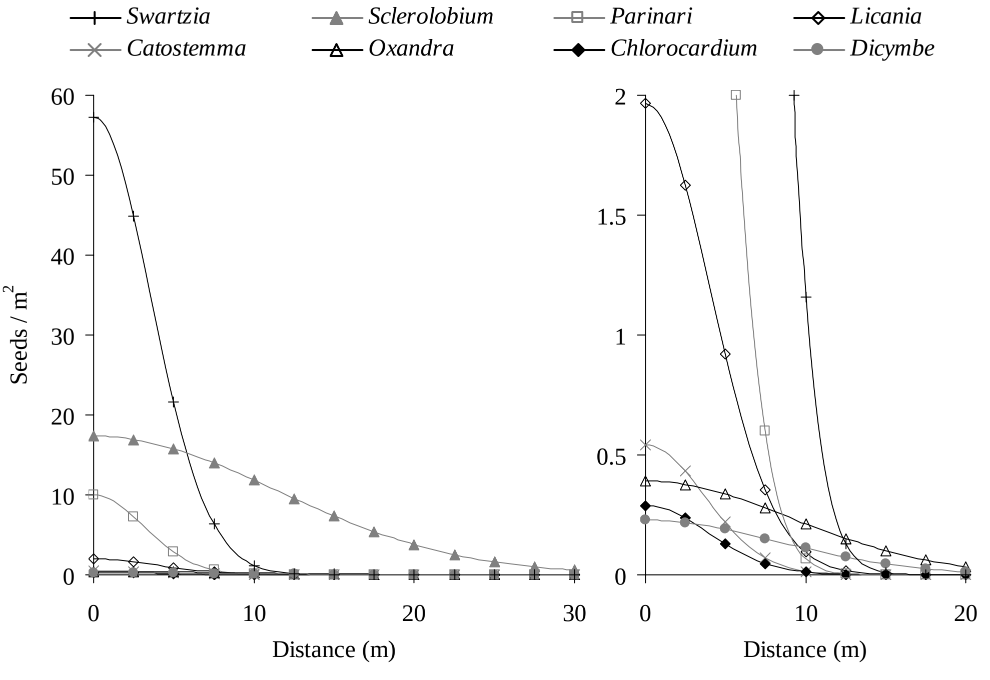

Figure 3. The estimated dispersal curves using the parameters given in table 3. The figure on the right is an enlargement of the lower-left part of the left figure. In the legend, species are ordered by seed density at distance 0.

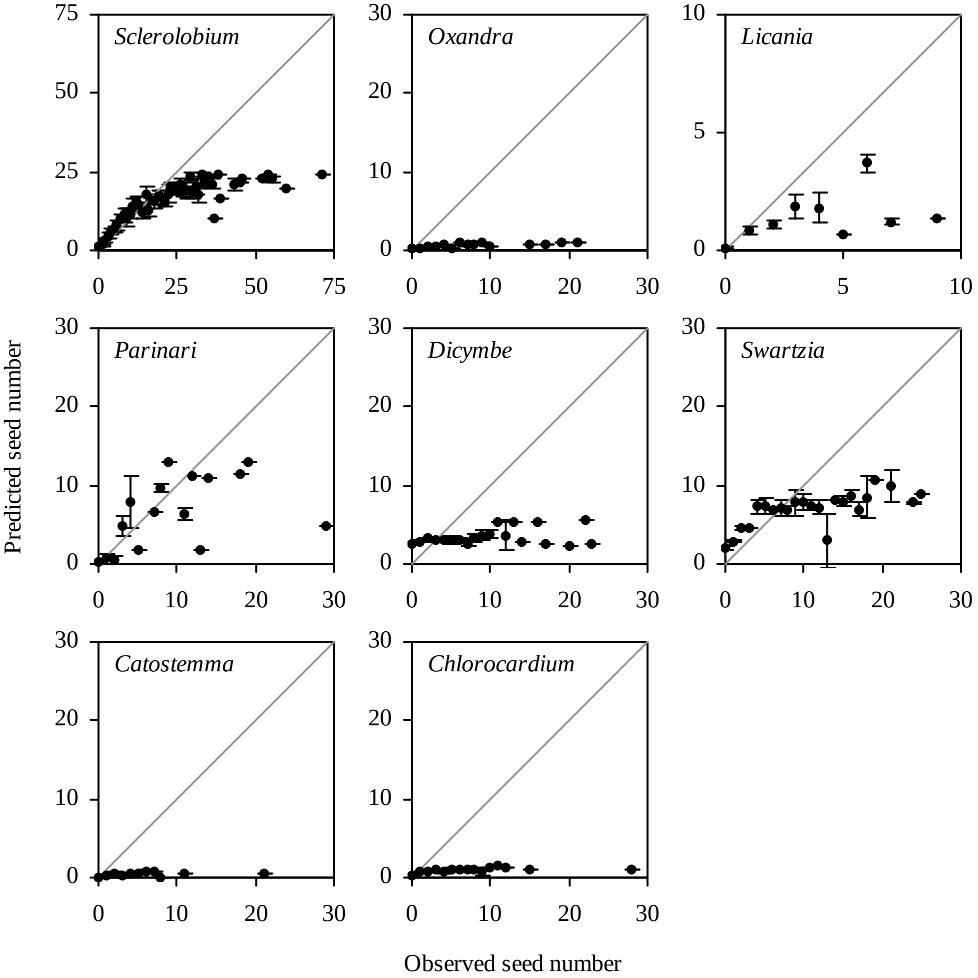

Figure 4. The average predicted seed number (± 1 · standard error) plotted against the observed seed number for each of the species using the parameter values given in table 3. The grey line represents the line y = x, *i.e.* the predicted seed number if the model were perfect ($r^2 = 1$). For *Sclerolobium* the seed number is given per 0.25m^2, for *Swartzia* per 0.07 m^2, for the remainder of the graphs the seed number is given per m^2. Note that the scale of the axes differs between graphs.

logged than in the undisturbed plot, while for *Parinari* and *Chlorocardium* ρ-values were somewhat smaller in the logged than the undisturbed plot, however, the confidence intervals overlapped for all three species. Using the parameters from the undisturbed plot to predict the seed densities in the logged plot, the resulting r^2-values were somewhat lower than the optimal parameters for the logged plot, but still positive (L(U) in table 4a). Remarkably, r^2-values for the undisturbed plot using the parameters from the logged plot gave were negative for all three species, meaning that the average seed density is a better predictor of observed densities than the model (U(L) in table 4a).

Table 5. The values of *SSP* and ρ with 95% confidence intervals, the agreement between predicted and observed seed numbers (r^2) and the median dispersal distance in metres, for *Chlorocardium* in the undisturbed plot of this study and the plots of Zagt and Werger (1997) in three consecutive years. The last four columns give the agreement between predicted and observed seed numbers, using the parameters estimated from one dataset, to predict the seed numbers for another dataset.

Dataset	*SSP*	ρ	r^2	*MDD*	r^2 (U)	r^2 (92)	r^2 (93)	r^2 (94)
Undisturbed 9ha	22 (18;26)	2.79 (1.70;3.81)	0.09	4.6		0.08	< 0	0.05
Z&W 92	20 (13;29)	4.48 (1.22;8.92)	0.10	6.5	0.09		< 0	0.07
Z&W 93	43 (32;55)	2.32 (0.60;3.91)	0.25	4.7	0.15	0.11		0.03
Z&W 94	12 (9;34)	2.99 (0.57;25.88)	0.09	5.3	< 0	0.02	< 0	

For *Parinari* the seed production parameter *SSP* was lower around isolated trees than in the 9ha plots, while *Catostemma* showed the opposite (table 4b). Although the ρ-values estimated for the isolated trees differed from those estimated from the 9ha plots, confidence intervals did overlap and ρ-values and dispersal distances were not considered significantly different. Interchanging parameters for these two species between the individual trees and the 9ha plots resulted in slightly lower r^2-values for *Parinari* and in negative r^2-values for *Catostemma*.

Also when comparing the estimates from the three consecutive years for *Chlorocardium* among each other and with the undisturbed 9ha plot, the variation in seed production, which ranged from 12 to 43, was larger than the variation in dispersal distance (table 5). The *SSP* in 1993 was higher than that in 1992 and the 9ha undisturbed plot of this study. Differences in ρ-values were not significant. Interchanging parameters gave r^2-values comparable to those with the optimal parameters. Exceptions were the dataset from 1994, which gave very low or negative r^2-values with the parameters from all other datasets, and the parameters from 1993, which gave negative r^2-values when used in combination with any of the other datasets.

Plotting the predicted against the observed seed numbers revealed that the model failed to predict sufficiently high seed numbers for (nearly) all datasets and that for a few datasets the predicted seed numbers in low density quadrates were somewhat high (figures not shown, but the trends are comparable to those in figure 4). Figure 5 shows the observed and predicted seed densities in the logged plot for *Chlorocardium*. Also here it can be seen that the peaks for the observed densities are higher than for the predicted densities. Furthermore, around some of the trees in the plot no seeds were found, while in the predicted figure, obviously, seeds are distributed around all trees.

4 Discussion

4.1 Evaluation of the ecological results

As was expected, the size at which a species starts reproducing increased with maximum tree height. If the relation holds for more species and areas, minimum reproductive diameters can be estimated for future studies and for timber species from the maximum height they attain. Data on maximum tree height can be collected relatively easily and are probably already

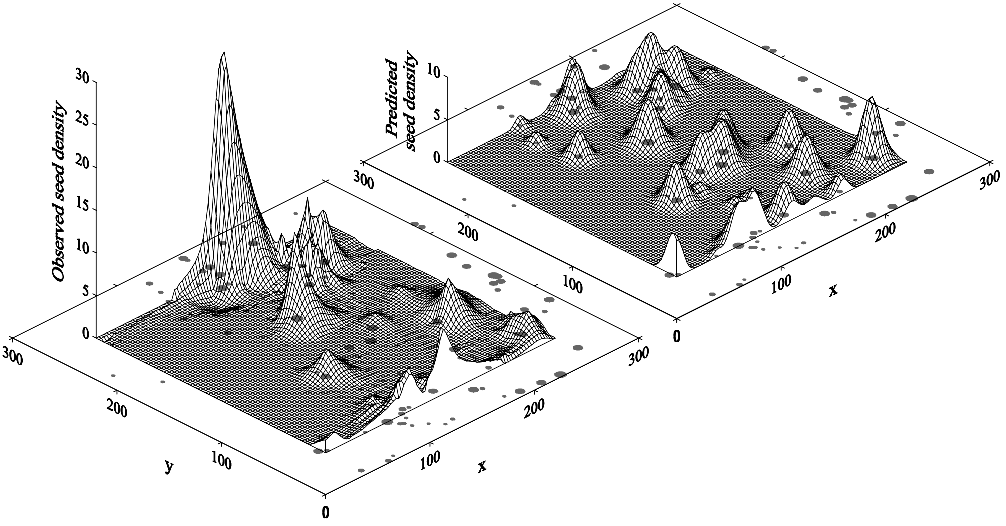

Figure 5. The observed (lower left, extrapolated from data using Kriging) and predicted (upper right, calculated every 2.5m) seed densities for *Chlorocardium* in the logged 9ha plot. The grey circles represent *Chlorocardium* trees larger than 15cm DBH and the size of the circle is related to the tree's DBH.

known for many species. The minimum reproductive diameters found in the present study are lower than those found in Bolivia by van Rheenen *et al*. (2004). They reported minimum reproductive sizes of 9cm for subcanopy, 40cm for canopy and 36cm for emergent species, however, they used a different definition (the DBH at which 50% of the trees reproduced). Additionally, in the present study part of observations was made along the roadside (approximately 100). Little is known about the effect of the environment on the minimum reproductive size. Future studies should try to collect information on this topic as logging may reduce the minimum reproductive size.

The trade-off between seed mass and seed number is well known and has been studied both theoretically (Smith and Fretwell 1974, Venable 1992) and empirically (*e.g.* Greene and Johnson 1994, Karrenberg and Suter 2003). Also in the present study, support for this trade-off was found. If all species were taken into account the relation between seed number and mass was not significant, although there was a trend for small-seeded species to produce more seeds than species with larger seeds. If *Swartzia* was discarded the relation did become significant. *Swartzia* was mast fruiting that year and the number of seeds produced was very high (a tree of D_{ref} produced 4615 fruits or roughly 100kg). Mast fruiting has been shown to be important for the reproductive success of species by satiating the seed predators (Jansen 2003), but is difficult to study since a comparison over many years will be needed to accurately describe mast fruiting and its effects on a species' regeneration. Also for species that do not clearly show mast fruiting data collection should span several years as *Chlorocardium* produced 2-3 times as many seeds in 1993 as in any of the other years. Year to year variation in seed production of tropical tree species is a well known phenomenon and can be extremely large (*e.g.* Schupp 1990, Sork 1987).

No difference in the standard seed production (*SSP*) was found between the subcanopy and canopy species, however, the *SSP* of subcanopy and canopy species was lower than for the emergent species. This result is partly confirming the hypothesis. Emergent species position their crown above the canopy, where light availability is highest. Note that the seed production at a constant DBH of 25.6cm was tested. The differences will be larger if the actual seed production of species is compared as the on average mature subcanopy trees will be smaller than mature emergent species. For example, the estimated number of seeds produced at their species-specific average DBH is 37 for *Oxandra* and 3980 for *Parinari*, or if expressed in weight an average *Parinari* tree will produce 1000 as much seed mass as an average *Oxandra* tree.

Generally, the estimated median dispersal distances were short and for the majority of the species the dispersal distances were only marginally longer than the crown radius. These distances are comparable to those reported by Dalling *et al.* (2002) for pioneer species in Panama. Half of the 14 species they studied had median dispersal distances of less than five metres, although four species had median dispersal distances of more than 20 metres. Additionally, Guariguata and Pinard (1998) cite a number of papers, which report short dispersal distances. Not only seed production, but also seed dispersal, *i.e.* the dispersion parameter ρ, was related to seed mass. As was expected based on the findings of Augspurger (1986) and Augspurger and Franson (1987) for wind-dispersed species, the dispersion parameter ρ decreased with seed mass. The role of dispersal type was not clear. The wind-dispersed species, *Sclerolobium*, dispersed its seeds furthest. This is consistent with Willson’s review paper (1993) and van Rheenen *et al*. (2004) who found that wind-dispersed species on average dispersed their seeds over longer distances than animal-dispersed seeds. No difference was found between the different groups of animal dispersal types. These short dispersal distances observed for the animal-dispersed species suggest that the majority of the seeds of these species were handled by animals in the parent tree and subsequently dropped or simply dropped from the crown, without being dispersed by animals.

Seed production was higher in the logged than in the undisturbed plot. This result was expected due to increased light availability in the logged plot. This result suggests that logging should increase seed availability, which may be true for non-timber species. Also for timber species the per capita seed production may increase, however, since the large, healthy trees are harvested the overall seed density may still decrease. Additionally, if harvest intensities are very high, reproductive trees may become isolated and the per capita seed production may decrease due to limited pollination (see Guariguata and Pinard 1998). The dispersal distance did not differ between the logged and undisturbed plot. All three species for which the comparison between logged and undisturbed plot could be made were animal-dispersed species. Guyana has a relatively intact fauna due to the low human population density in the interior and logging occurs in patches, leaving ample space for animals to survive. In addition, if the majority of the seeds are not handled by dispersers but simply fall from the crown then no difference between logged and harvested areas can be expected.

4.2 Limitations of the study and inverse modelling

Only eight species were included in this study, and the results obtained in this study may be specific for this set of species. Similarly, the result that trees produce more seeds in logged than in undisturbed areas is based on only three species and two plots and the results need to be confirmed for more species and replicate plots. The eight species used in the present study varied in seed mass, dispersal type and adult stature, which makes it difficult to study the effect of any of these characteristics separately. For example, the only wind-dispersed species was also the species with the lightest seeds. The relation between seed mass and dispersal type has been studied in the Guianas, Panama and Peru and it was found that generally wind- and bird-dispersed species had smaller seeds than species with mammal-dispersed seeds or unassisted seed dispersal (Hammond *et al.* 1996, Hammond and Brown 1995). This problem can be solved by including few species, which differ only in one characteristic, or by including many species and correcting for the interaction between characteristics. The data collection (counting seeds in sample quadrates or seed traps) is straightforward and it should be possible to collect data for many species in short periods of time, once the infrastructure is available.

The inverse modelling technique used to estimate the seed production and dispersal parameters performed well in some, but not all cases. A general problem that was observed was that the used model failed to predict seed densities as high as those observed in the field. This may be an effect of clustering caused by for example animal behaviour, tree architecture or obstacles. The used model assumes radial symmetry, no clustering and a continuously declining seed density with distance. These assumptions may be violated, especially for animal-dispersed species, which makes the current approach more suitable for wind-dispersed than for animal-dispersed species. Using a different model than the Gaussian seed shadow model used in this study may partly solve the problem (see Clark *et al.* 1999 for a comparison of models). In addition, it is possible to include asymmetric distributions and clustering, however, this will increase the model complexity and data requirements.

It should be possible to improve the method considerably by additional data collection. The data used here covered only short time periods. Future studies should use data that span several years to include annual variation in seed production and dispersal. Additionally, the sample quadrates should be monitored frequently during the fruiting periods, to prevent that the pattern resulting from primary dispersal is complicated by secondary dispersal by water, wind, gravity and animals. In addition, it was assumed that all trees larger than the minimum reproductive size produced seeds during the monitoring period, however probably not all trees fruit every year. In the model, seeds are distributed around trees that were not reproducing that year, and hence where no seeds were observed (figure 5). This will lead to an overestimation of seed densities around non-reproductive trees. This problem can be solved by monitoring the reproductive status of adult trees.

It has been argued that seed production and dispersal data collected around isolated individuals may not be representative of the species, due to differences in biotic and abiotic conditions (Ribbens *et al.* 1994). In this study no consistent difference was found for two species for which data were collected both around isolated trees and in plots. Dispersal distances did not differ significantly between the data collection techniques. Standard seed production estimates from the isolated tree dataset were lower for *Parinari* than in the plots but higher for *Catostemma*. *Parinari* is a relatively rare species, with less than one reproductive-sized adult per hectare, so basically also the trees inside the plot were isolated. More research is needed to clarify the difference between the two data collection methods and to test the hypothesis that seed production and dispersal of isolated trees differs from those of trees in dense populations.

4.3 Conclusions

The inverse modelling technique is not a very good method for detailed studies on the seed production and dispersal of tropical tree species. The variation explained by the model is often limited and may not be very suitable for animal-dispersed species. Nevertheless, since the data collection is simple and requires little labour, it is concluded that the method may be valuable to crudely estimate the distribution of seeds in dense populations of tropical tree species.

Factors that determine the degree of seed limitation were affected by seed mass, adult stature, dispersal type and logging. Generally, small species started to produce seeds at smaller sizes and produced less seeds than taller species. Small-seeded species produced more seeds than large-seeded species and dispersed those seeds over longer distances. The only wind-dispersed species dispersed its seeds over longer distances than the animal-dispersed species. Finally, trees produced more seeds in the logged area than in the undisturbed area. The results suggest that most of the studied species will be limited in their regeneration by a limited availability of seeds, mainly because most of their seeds fall within a few metres of the crown (see figure 5). The results obtained in this study should be combined with information on the spatial distribution of adult trees and of sites suitable for the establishment of species to obtain insight in the role of seed limitation on the successful regeneration of tropical tree species in undisturbed and logged forests.

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Appendix A. Information on the sizes of reproductive individuals for all species for which phenological data were collected. H_m: maximum height at maturity in metres, n: number of trees observed with flowers or fruits, the minimum, maximum and 10th, 50th and 90th percentiles of the sizes of these trees.

					Diameters (cm)				
Family	Species	Vernacular name	H_m	n	min	10%	50%	90%	max
Anacardiaceae	*Tapirira obtusa*	Duka	30	2	30				43
Annonaceae	*Anaxagorea dolichocarpa*	Kurihikoyoko	9	85	1	3	5	7	8
	Bocageopsis multiflora	Arara, fine leaf	29	3	12		16		22
	Duguetia neglecta	Yari Yari	9	73	2	5	6	8	11
	Duguetia yeshidan	Yeshidan	10	2	1				2
	Guatteria sp.	Arara, Smooth Skin	20	5	3		7		9
	Oxandra asbeckii	Karishiri	15	60	5	9	14	19	22
	Unonopsis glaucopetala	Arara, broad leaf	20	15	3	5	11	18	18
Apocynaceae	*Aspidosperma exselsum*	Yaruru	39	14	51	51	64	134	134
	Aspidosperma sp.	Shibadan	32	3	36		36		48
Bignoniaceae	*Jacaranda copaia*	Futui	30	6	26		50		52
	Tabebuia insignis	Cedar, white	27	3	31		40		76
	Tabebuia serratifolia	Hakia	29	2	12				25
Bombacaceae	*Catostemma commune*	Baromalli, swamp	38	1	47				
	Catostemma fragrans	Baromalli, sand	30	47	13	20	33	48	57
Burseraceae	*Protium decandrum*	Kurokai	27	3	36		57		70
	Protium guianense	Haiawa	10	1	17				
Caesalpiniaceae	*Aberema jupunba*	Huruasa	38	5	34		42		69
	Chamaecrista adiantifolia	Imirimiaballi	29	7	24		28		31
	Chamaecrista apoucouita	Apokaito	30	12	17	18	30	41	42
	Dicymbe altsonii	Wallaba, clump	32	26	32	40	66	114	121
	Eperua falcata	Wallaba, soft	36	150	12	21	39	60	87
	Eperua grandiflora	Wallaba, ituri	27	5	17		25		66
	Eperua rubiginosa	Watapa	27	55	13	22	44	64	85
	Hymenaea courbaril	Locust	42	2	55				119
	Mora excelsa	Mora	37	5	88		115		143
	Mora gonggrijpii	Morabukea	34	47	24	43	65	104	139
	Peltogyne venosa	Purpleheart	50	2	66				67
	Sclerolobium guianense	Kaditiri	40	10	25	26	57	94	95
	Vouacapoua macropetala	Sarebebeballi	26	4	11		23		35
Caryocaraceae	*Caryocar nuciferum*	Sawari	29	10	30	35	96	119	120
Cecropiaceae	*Cecropia obtusa*	Congo Pump, common	21	40	5	8	11	17	26
	Cecropia spp.	Congo Pump	21	7	8		10		18
Celastraceae	*Goupia glabra*	Kabukalli	40	19	26	30	48	137	143
Chrysobalanaceae	*Hirtella cf. caduca*	Fire Tree	20	2	3				11
	Licania alba	Kautaballi	27	31	8	17	25	47	50
	Licania cf. canescens	Marishiballi	30	28	8	17	28	48	51
	Licania cf. micrantha	Marishiballi, red	36	1	36				
	Licania heteromorpha var. *heteromorpha*	Buruburuli	30	1	34				
	Licania heteromorpha var. *perplexans*	Kairiballi	30	37	10	13	18	27	35
	Licania hypoleuca	Unikiakia	29	3	25		28		32
	Licania laxiflora or *L. persaudii*	Kauta	30	3	26		38		48
	Licania sp.	Konoko	30	1	18				
	Licania sp.	Mahaicaballi	36	4	25		32		43
	Parinari campestris	Burada	38	8	45		70		108
Combretaceae	*Terminalia amazonia*	Fukadi	43	3	60		72		126
	Terminalia dichotoma	Fukadi, swamp	43	1	30				
Dichapetalaceae	*Tapura guianensis*	Waiaballi	20	15	6	6	11	19	19
Eleocarpaceae	*Sloanea guianensis*	Aruadan	18	1	39				
Euphorbiaceae	*Aparisthmium cordatum*	Mababalli	15	2	16				20

					Diameters (cm)				
Family	Species	Vernacular name	H_m	*n*	min	10%	50%	90%	max
	Chaetocarpus schomburgkianus	Ruri	26	2	16				30
	Hevea pauciflora	Hatti	24	4	19		25		38
	Mabea spp.	Swizzle-stick	20	3	3		3		4
	Sandwithia guianensis	Unknown A	12	33	3	5	9	13	14
Flacourtiaceae	*Laetia procera*	Warakairo	37	2	42				57
Guttiferae	*Symphonia globulifera*	Manni	40	2	51				74
	Vismia cf. macrophylla	Bloodwood, broad leaf	26	3	9		12		19
Humiriaceae	*Humiria balsemifera*	Taurinero	32	2	44				61
Icacinaceae	*Emmotum fagifolium*	Manobodin	30	3	30		30		33
Lauraceae	*Aniba hypoglauca*	Silverballi, yellow	30	1	24				
	Aniba kappleri	Gale, ginger	20	1	26				
	Chlorocardium rodiei	Greenheart	34	13	33	36	65	85	86
	Ocotea puberula	Silverballi, kereti	34	3	24		28		48
Lecythidaceae	*Couratari guianensis*	Wadara	60	5	36		40		74
	Eschweilera coriacea or *E. decolorans*	Kakaralli, smooth leaf	32	41	18	20	35	52	65
	Eschweilera sagotiana	Kakaralli, Black	32	51	21	24	37	57	76
	Eschweilera wachenheimii	Kakaralli, fine leaf thick skin	30	8	17		24		30
	Lecythis confertiflora	Wirimiri	30	29	12	12	28	48	63
	Lecythis corrugata	Wina	30	10	16	16	28	62	64
	Lecythis holcogyne	Haudan	32	2	20				26
	Lecythis zabucajo	Monkey pot	32	6	28		42		62
Lissocarpaceae	*Lissocarpa guianensis*	Barabara, charcoal	25	5	10		15		52
Melastomataceae	*Bellucia grossularioides*	Sakwasepere	25	1	19				
	Miconia sp1.	Waraia, flaky bark	15	2	15				20
	Miconia spp.	Waraia	15	6	3		10		16
Meliaceae	*Carapa guianensis*	Crabwood	35	18	31	31	39	65	65
Mimosaceae	*Balizia pedicellaris*	Manariballi, red skin	27	3	52		58		65
	Enterolobium cyclocarpum	Devil's ear	40	1	75				
	Inga spp.	Warakosa	26	5	16		27		32
	Parkia nitida	Manariballi, black	40	3	62		90		104
	Parkia pendula	Hipanai	40	3	130		157		161
	Pentaclethra macroloba	Trysil	28	17	9	9	20	39	56
	Zygia racemosa	Tureli	37	1	10				
Myristicaceae	*Iryanthera sagotiana*	Kirikaua	27	5	20		27		30
	Virola surinamensis	Dalli, swamp	43	1	42				
Myrtaceae	*Eugenia patrisii*	Hicha	15	2	23				49
	Eugenia sp.	Turtle cherry	15	2	13				22
	Marlierea montana	Kwako	15	4	6		7		10
Olacaceae	*Chaunochiton kappleri*	Hiwaradan	30	2	20				29
	Maburea trinervis	Maburea	20	15	12	13	18	30	32
Papilionaceae	*Clathrotropis brachypetala*	Aromata	29	5	37		52		60
	Clathrotropis macrocarpa	Aromata, like	29	7	10		13		14
	Ormosia coccinea	Barakaro	34	2	56				74
	Ormosia coutinhoi	Korokororo	34	9	25		52		85
	Swartzia leiocalycina	Wamara	35	26	17	23	45	62	76
	Swartzia oblanceolata	Serebedan	30	68	8	10	16	24	44
	Swartzia sp.	Itikiboroballi, cauliflorous		10	10	10	11	18	18
	Swartzia spp.	Itikiboroballi	29	15	6	7	14	49	52
Rubiaceae	*Amaioua guianensis*	Komaramaraballi	15	1	16				
	Duroia eriophila	Komaramara	10	2	9				24
Sapindaceae	*Cupania cf. scrobiculata*	Kulishiri, white	10	3	8		10		12
	Cupania hirsuta	Kulishiri, black	15	2	5				7
	Cupania sp.	Kulishiri	15	3	10		21		22
Sapotaceae	*Chrysophyllum pomiferum*	Paripiballi	34	1	20				

Family	Species	Vernacular name	H_m	*n*	Diameters (cm) min	10%	50%	90%	max
	Chrysophyllum sanguinolentum	Barataballi	29	4	3		6		7
	Micropholis venulosa	Kudibiushi	26	2	30				42
	Pouteria guianensis	Asepoko	34	4	13		22		44
	Pouteria reticulata	Kokoritiballi, common	41	1	23				
Simaroubaceae	*Simaba multiflora*	Hachiballi	10	8	14		23		35
Sterculiaceae	*Sterculia rugosa*	Maho, rough Leaf	35	1	36				
unknown	unknown	Unknown		10	5	5	22	69	72
Violaceae	*Paypayrola guianensis* and *P. longifolia*	Adeboro	19	44	2	3	7	13	17
Vochysiaceae	*Vochysia surinamensis*	Iteballi	34	1	58				

Chapter 3

The effect of seed mass and gap size on seed fate of tropical rain forest tree species in Guyana

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Abstract

For eleven tree species, differing in seed mass, germination success (emergence success for two small-seeded species) and the causes of failure to germinate were studied in the forest understorey and in logging gaps in the tropical rain forests of Guyana. In the forest understorey, germination success increased with seed mass. However, as gap size increased the difference between smaller and larger seeded species diminished, because germination success of smaller seeded species increased slightly, while that of larger seeded species decreased dramatically. The negative effect of gap size on germination success of larger seeded species was caused by an increased risk of desiccation with gap size, which was a far more important seed mortality agent for larger than for smaller seeded species. Generally, seeds of smaller seeded species suffered more from insect predation and were removed at higher rates than larger seeded species. On the other hand, larger seeded species were eaten more by mammals than smaller seeded species. It is concluded that logging can result in shifts in the species composition in the tropical rain forests of Guyana, which are dominated by species with large seeds, since germination success of larger seeded species is dramatically reduced in large logging gaps.

1 Introduction

The tropical rain forests of central Guyana are characterized by a low species diversity and are dominated by shade-tolerant tree species with large seeds, high average wood density, and rodent or unassisted dispersal. Large-scale disturbances, such as earthquakes and hurricanes, are infrequent and disturbances are mainly confined to tree-fall gaps (Davis 1941, Hammond and Brown 1995). It has been hypothesized that this stability might explain the dominance of typical climax species in Guyana’s forests (Hammond and Brown 1995, ter Steege and Hammond 2001). The argument is as follows: typically, light-demanding or pioneer species have smaller seeds than shade-tolerant climax species (*e.g.* Foster and Janson 1985, Hammond and Brown 1995, Ng 1978, Raich and Gong 1990). Small seeds are an adaptation to increasing the likelihood of encountering a favourable site for establishment, while the internal energy reserves of large seeds decrease the risk of mortality after arrival at a particular site (Boot 1996, Dalling and Hubbell 2002, Hammond and Brown 1995, Ng 1978). Germination of many small-seeded species is triggered by temperature alterations and/or changes in the light environment, associated with gap formation (Bazzaz and Picket 1980, Denslow 1987, Pons 1992, Probert 1992, Vázquez-Yanes and Orozco-Segovia 1993, Vázquez-Yanes and Orozco-Segovia 1996), although low levels of germination have been observed in the dark forest understorey (Alvarez-Buylla and Martínez-Ramos 1990, de Souza and Válio 2001, Kyereh *et al.* 1999, Peña-Claros 2001). Stimulation of germination by factors related to high irradiance may be expected for small-seeded species, since their seedlings are dependent on photosynthesis for survival soon after germination. Large-seeded species, on the other hand, usually do not require an environmental trigger to germinate and their seeds germinate soon after dispersal (Bazzaz and Picket 1980, Denslow 1987, Ng 1978). In Guyana’s stable forests, the density of disturbed patches with high-light conditions, required for successful regeneration of small-seeded species, is too low for these species to occur in large quantities and large-seeded species dominate the forests (Hammond and Brown 1995, ter Steege and Hammond 2001).

During the last decades, however, conditions for regeneration may have changed, since selective logging has been practised on a large scale in Guyana. Although the average logging intensity is low, the area damaged by selective logging operations can be considerable (van der Hout 1999). Consequently, the density and size of disturbed patches in logged forest has increased and the chances for successful regeneration of small-seeded species may have increased. Predicting possible shifts in species composition following logging requires a better understanding of the effect of logging on all regeneration processes in relation to life history characteristics. In this study, germination success and causes of failure to germinate are investigated in relation to seed mass and gap size.

The number of seeds available for germination can be reduced by desiccation, predation or infection by fungal pathogens. Large-seeded species often require moist conditions for germination and their seeds lose viability when exposed to the low relative humidity and high insolation in gaps (ter Steege *et al.* 1994, Vázquez-Yanes and Orozco-Segovia 1993). Hence, it may be expected that the proportion of desiccated seeds increases both with seed mass and gap size. The moist conditions in the understorey, on the other hand, promote the growth of fungi and it has been found that the number of seedlings killed by fungi is higher in the understorey than in gaps (Augspurger 1983, 1984b, Forget 1997). Similarly, it may be expected that fungi kill more seeds in the understorey than in gaps.

Predation by insects and mammals is a very important agent of mortality (Crawley 1992). Probably the most important post-dispersal seed predators of small-seeded species are ants (Alvarez-Buylla and Martínez-Ramos 1990, Levey and Byrne 1993, Nepstad *et al.* 1996). Coleoptera, on the other hand, often infest seeds of large-seeded species (Hammond *et al.* 1999, Kitajima and Augspurger 1989, Terborgh *et al.* 1993). Levings (1983) found fewer ants in dry, sunny habitats. Furthermore, solar heating has been proposed as a technique for disinfecting seeds infested by larvae of Coleoptera (Chauhan and Ghaffar 2002, Chinwada and Giga 1996). Therefore, it is expected that the proportion of seeds removed and predated upon by both ants and Coleoptera larvae will decrease with gap size. Seeds of small-seeded species may be protected from mammal attacks by their small size, while mammals can attack large-seeded species at high rates (Hammond 1995, Hammond *et al.* 1999, Kitajima and Augspurger 1989, Terborgh *et al.* 1993). Rodents are the main mammalian post-dispersal seed predators (Forget 1989, Hammond *et al.* 1999, Nepstad *et al.* 1996, Sánchez-Cordero and Martínez-Gallardo 1998). Literature on attack rates by rodents in relation to gap size is contradictory (*e.g.* equal Hammond *et al.* 1999, higher Sánchez-Cordero and Martínez-Gallardo 1998, and lower rates in the understorey than in gaps Schupp *et al.* 1989, Schupp and Frost 1989). For now, it is assumed that predation and removal by mammals is not influenced by gap size.

In summary, it is expected that the germination success of smaller seeded species will increase with gap size since: 1) their germination is triggered by gap creation, 2) seed mortality caused by desiccation and mammal predation is not expected to be important for these species, and 3) the proportion of decaying seeds and seeds killed by insects is expected to decrease with gap size. For larger seeded species the relation between germination success and gap size is difficult to predict since: 1) their seeds do not require an environmental trigger for germination, 2) the proportion of desiccated seeds is expected to increase with gap size, and 3) the proportion of seeds killed by the remaining mortality causes is expected to decrease or remain constant with gap size. Since smaller seeded species remain dormant in the forest understorey, whereas larger seeded species germinate soon after dispersal and their seeds are adapted to survival in the understorey, it is expected that germination success will increase with seed mass in the forest understorey. However, as gap size increases the positive effect of seed mass is expected to decline, since the germination success of smaller seeded species will increase, while that of larger seeded species will decrease or remain constant.

2 Methods

2.1 Research area and study species

Guyana, situated in north-eastern South America, has a tropical climate with high annual rainfall (2772 mm) and average temperatures of 25.9°C (van Dam 2001). The study was conducted in the East Pibiri compartment of the Demerara Timbers Ltd. concession (5°01’N, 58°34’W), approximately 250 km south of Georgetown, Guyana’s capital.

Eleven common species that differ in seed mass were selected for the experiment (table 1, species will be referred to by their generic names in the remainder of the chapter). Fresh seeds, fruits, or infructescences of these species were collected below parent trees during their fruiting period. Since fruits of *Cecropia obtusa* could not be found in sufficient numbers, a mix of *Cecropia obtusa* and *Cecropia sciadophylla*, which have similar life history characteristics, was used. In the lab, seeds of *Jacaranda copaia* and *Goupia glabra* were removed from the multi-seeded fruits and fruits of *Cecropia* from the fruiting spikes. Henceforth, the term seed will be used to indicate both seeds and one-seeded fruits. Visually damaged or unripe seeds were discarded, except for *Cecropia* for which no selection could be made due to the small seed size. The dry mass of the seed reserve (embryo plus endosperm, oven dried at 70°C for at least four days) of a sample of 30 seeds per species (10 for *Pentaclethra*) was determined to the nearest milligram (Sartorius MC1 scales, model LC 620 S, Sartorius GmbH, Göttingen, Germany). Because the average fresh mass of these samples and of the sown seeds differed, it was decided to calculate a corrected seed reserve dry mass per species with:

Table 1. Tree species used in the experiment and their seed reserve dry mass (DM) in grams, the number of seeds used in the experiment (*n*) and the months in which the seeds were collected and sown (1 = January, 2 =: February, etc.). The classification in small-, intermediate- and large-seeded species is given as an indication, but is not used in the analyses.

Scientific name	Family	DM	*n*	Month
Small seeds				
Cecropia obtusa Trécul. & *Cecropia sciadophylla* Mart.	Cecropiaceae	0.00011 [a]	17970	4-9
Goupia glabra Aubl.	Celastraceae	0.0014 [b]	5945	10
Jacaranda copaia (Aubl.) D. Don	Bignoniaceae	0.0099	546	4-5
Intermediate seeds				
Sclerolobium guianense Benth.	Caesalpiniaceae	0.12	1199	4-5
Aspidosperma excelsum Benth.	Apocynaceae	0.22	1197	4-5
Parinari campestris Aubl.†	Chrysobalanaceae	0.46	1199	3-4
Oxandra asbeckii (Pulle) R.E. Fr.	Annonaceae	0.54	339	5-8
Large seeds				
Pentaclethra macroloba (Willd.) Kuntze	Mimosaceae	5.13	180	4-7
Catostemma fragrans Benth.	Bombacaceae	9.82	1199	7
Carapa guianensis Aubl.	Meliaceae	12.10	200	5-7
Chlorocardium rodiei (Schomb.) Rohwer, Richter & van der Werff	Lauraceae	33.51	1198	3-5

† Fruits of *Parinari* are two-locular, however the majority contained only one intact seed (personal observation).

DM: [a] *Cecropia*: dry mass of *C. obtusa* of embryo, endosperm and seed coat from Hammond and Brown (1995) and [b] *Goupia*: fresh mass from Rose (2000).

$$\mathrm{DM} = \frac{\mathrm{FM}_{\mathrm{Sown}}}{\mathrm{FM}_{\mathrm{Sample}}} \cdot \mathrm{RDM}_{\mathrm{Sample}} \qquad (1)$$

in which $\mathrm{FM}_{\mathrm{Sown}}$ and $\mathrm{FM}_{\mathrm{Sample}}$ are the average fresh mass of the sown seeds and of the sample, respectively, and $\mathrm{RDM}_{\mathrm{Sample}}$ is the average seed reserve dry mass of the sample. The corrected dry masses are shown in table 1. The seed masses of the small-seeded *Cecropia* and *Goupia* could not be determined with the available scales. For these species, seed masses available in literature were assumed.

2.2 Experimental design

In the East Pibiri compartment, hemispherical photographs were taken in 10 forest understorey sites and 30 logging gaps, using a Nikon Coolpix 950 digital camera with a FC-E8 8 mm fisheye converter (Nikon Corporation, Tokyo, Japan) during periods with overcast sky. The photographs were analysed using Winphot (ter Steege 1996) to determine the canopy openness (CO). Canopy openness is the percentage of sky hemisphere not covered by vegetation. Based on their canopy openness, two understorey sites, and eight logging gaps were selected, covering the range of canopy openness occurring in logged forests. In the selected logging gaps, all vegetation and coarse woody debris was removed to reduce heterogeneity of, and changes in, the light climate during the experiment resulting from growth of, or damage to, the vegetation. After clearing the sites, new hemispherical photographs were taken to determine the canopy openness more accurately. The values for canopy openness derived from these photographs were used in the analyses.

In the central 640 by 640cm of each site, 10 by 10cm cells were demarcated using string. The cells were labelled and per cell, one seed (five for *Goupia*, 15 for *Cecropia*) was laid to germinate. It was aimed to use 120 (600 for *Goupia*, 1800 for *Cecropia*) seeds per site per species, however, for four species, fewer seeds were found. The actual seed numbers per species are shown in table 1. Seeds were assigned randomly to cells, ensuring equal numbers in all sites, and pushed slightly into the soil. Their position was marked with a toothpick and for wind-dispersed species the toothpick was pushed through the wing to reduce the chance of being blown away. No treatments such as scarification, watering, or prevention of predation were applied and since seeds were collected and sown during the species' fruiting period, it is expected that they encountered similar climatic conditions as when dispersed naturally, although microsite conditions may differ.

From 19 March 2001, germination (protrusion of the radicle) and survival of seeds were monitored at four-weekly intervals. For each dead seed, the probable cause of mortality was scored in five categories: desiccation (cracked, hard, shrunk and wrinkled seeds), decay (soft, rotting seeds), predation by insects plus decay, predation by insects, and predation by mammals. Seeds were only recorded as being predated if remains of the seed were found. Seeds that had disappeared were recorded as being removed, however, the removal agent (wind, water or animals) could not be determined. By 5 December 2001, approximately nine months after the start of the experiment, most species showed little additional germination and mortality and it was decided to end the experiment. The seeds of the majority of the species were monitored over a period of four to nine months (see table 1). Seeds of *Goupia* and, to a lesser degree, *Cecropia,* were implanted at a late stage of the experiment and their seeds were monitored for relatively short periods. Seeds that had not germinated, nor died by the end of the experiment were recorded as dormant. It should be realized that seeds that were removed may have germinated elsewhere and that dormant seeds may have germinated after the end of the experiment. Germination and survival of *Cecropia* and *Goupia* could not be monitored, since their small seeds could not be seen. Therefore, germination was estimated by counting all seedlings of these species that emerged after their seeds were sown. Furthermore, mortality causes, removal and dormancy of these two species could not be determined.

2.3 Data analyses

Germination success was calculated as the proportion of sown seeds that germinated (emerged as seedlings for *Cecropia* and *Goupia*) per species per site at the end of the experiment. Similarly, for each of the remaining seed fates (*i.e.* the causes of mortality, removal and dormancy), the proportion of sown seeds experiencing that fate was calculated per species per site, excluding *Cecropia* and *Goupia*. To improve homoscedasticity and normality of the data, all proportions were angular transformed (Sokal and Rohlf 2001). To study the relationship between the proportion of sown seeds experiencing each of the seed fates, and dry mass and canopy openness, one forward stepwise multiple linear regression was done per seed fate. The regression analyses were carried out using SPSS for Windows (release 10).

3 Results

1. *Henceforth, germination is used to refer to both emergence of* Cecropia *and* Goupia *seedlings and germination of the remaining species.*
2. *Although species were not classified into seed mass classes for the analyses, the terms small-, intermediate- and large-seeded species are used in the Results and Discussion sections to describe the relationships comprehensibly. For example, small-seeded species showed relation A with canopy openness and large-seeded species showed relation B is used to indicate that the fitted relation with canopy openness changed from A to B as seed mass increased from the smallest to the largest seed mass.*

The stepwise multiple regression with germination success (emergence for *Cecropia* and *Goupia*) as dependent variable was significant ($n = 110$, $F_{5,104} = 13.006$, $R^2 = 0.385$, $p < 0.001$) and germination depended on seed mass (species), canopy openness (gap size) and their interaction (table 2, model in caption). Germination success increased linearly with seed mass and the slope of this relation declined as canopy openness increased. Germination success of small-seeded species increased with canopy openness until intermediate canopy openness, while that of large-seeded species decreased with canopy openness (figure 1a).

Table 2. Coefficients estimated using stepwise multiple regression and the corresponding significance levels per seed fate. The used model was:

$$\text{arcsine}\sqrt{G} = a + b \cdot \log_{10}(\text{DM}) + c \cdot \text{CO} + d \cdot \text{CO}^2 + e \cdot \log_{10}(\text{DM}) \cdot \text{CO} + f \cdot \log_{10}(\text{DM}) \cdot \text{CO}^2$$

where G is the proportion of seeds that experienced the fate of interest, CO is the canopy openness, DM is the dry mass and a–f are the coefficients to be estimated. -: factor not included in model since $p \geq 0.05$; *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

	a.	*b.*	*c.*	*d.*	*e.*	*f.*
Seed fate	Constant	$\log_{10}$ DM	CO	CO^2	$\log_{10}$ DM · CO	$\log_{10}$ DM · CO^2
Germination	0.901 ***	0.314 ***	-0.049 ***	$8.77 \cdot 10^{-4}$ **	-0.024 ***	$4.84 \cdot 10^{-4}$ **
Desiccation	-	-	0.030 ***	$-5.84 \cdot 10^{-4}$ **	$4.99 \cdot 10^{-3}$ ***	-
Decay	-	-	-	-	-	-
Decay & insects	-	-	-	-	-	-
Insects	0.236 ***	-0.112 ***	-	-	-	-
Mammals	0.057 ***	0.061 ***	-	-	-	-
Removal	0.347 ***	-0.070 *	$7.98 \cdot 10^{-3}$ *	-	-	-
Dormancy	-	-	-	-	-	-

Mortality caused by desiccation (n = 90, $F_{3,86}$ = 14.966, R^2 = 0.343, p < 0.001, figure 1b), predation by insects (n = 90, $F_{1,88}$ = 26.595, R^2 = 0.232, p < 0.001, figure 1e), predation by mammals (n = 90, $F_{1,88}$ = 35.011, R^2 = 0.285, p < 0.001, figure 1f) and seed removal (n = 90, $F_{2,87}$ = 4.688, R^2 = 0.097, p = 0.012) were also influenced by seed mass and/or canopy openness, *i.e.* regressions for these seed fates were significant. For the remaining seed fates (decay, decay plus predation by insects, and dormancy, figures 1c, d and h, respectively), no significant models could be fitted, *i.e.* these fates were independent of seed mass and canopy openness. The proportion of seeds that died of desiccation increased linearly with seed mass, especially in sites with high canopy openness (table 2). The proportion of desiccated seeds increased with canopy openness and the highest proportion of desiccation was predicted at approximately 20% canopy openness for species with small seeds and in the largest gaps for species with large seeds (figure 1b). Desiccation was the only seed fate for which the constant was not significant, *i.e.* there was no desiccation in the understorey. The proportions of seeds killed by insects and by mammals both depended on seed mass only (figures. 1e, f and table 2). Mortality caused by insect predation decreased with seed mass, while mortality caused by mammals increased. Finally, seed removal decreased with seed mass, while it increased with canopy openness (figure 1g and table 2).

4 Discussion

In the forest understorey, germination success (seedling emergence for *Cecropia* and *G. glabra*) increased sharply with seed mass. As was expected, the slope of this relation declined as canopy openness increased and in gaps with intermediate canopy openness, germination success hardly increased with seed mass. The decreasing effect of seed mass with gap size was partly caused by an increase in germination from understorey to intermediate gaps of small-seeded species. However, far more important was the negative

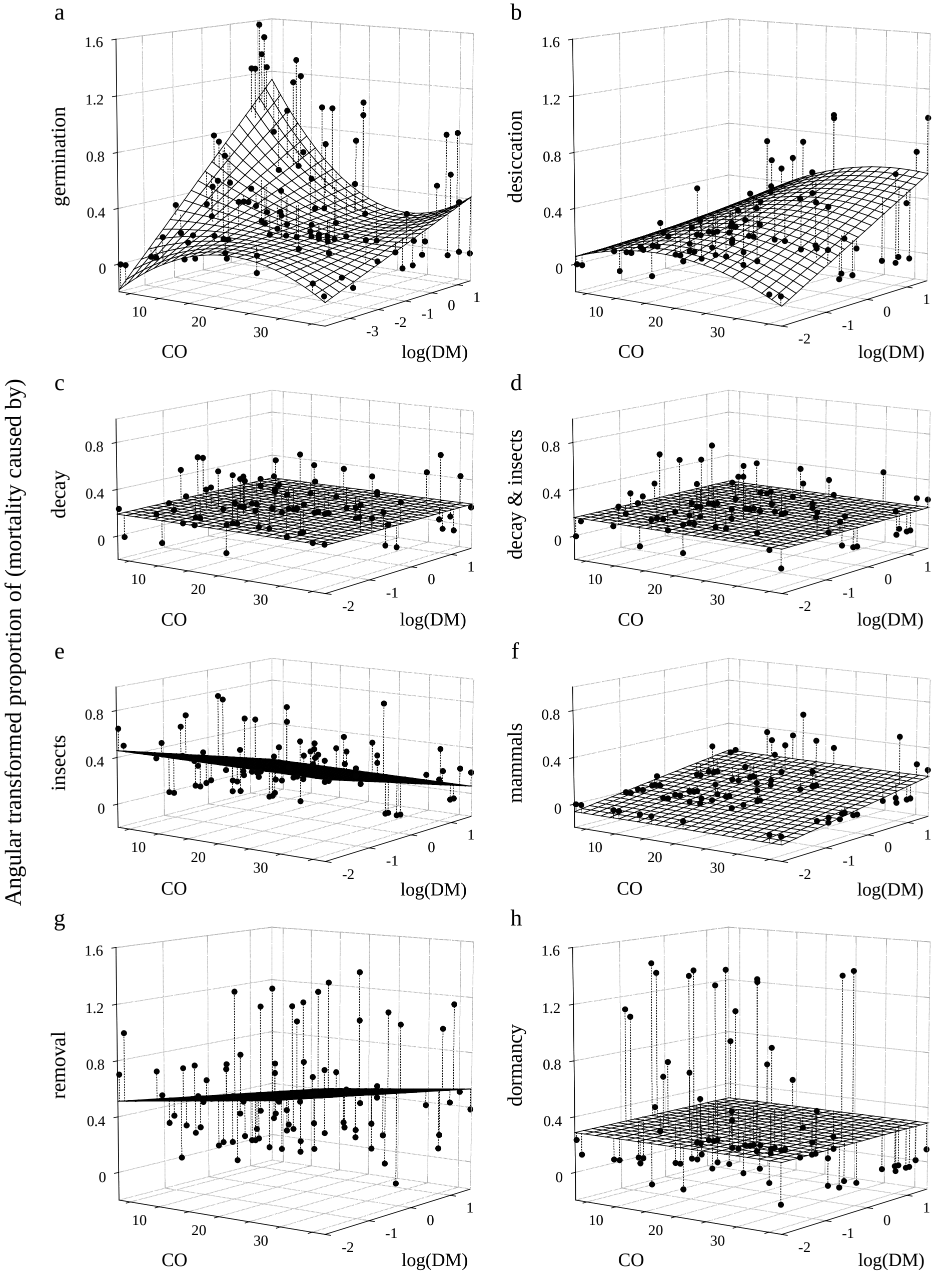

Figure 1. The angular transformed proportion of seeds per seed fate plotted against canopy openness (CO in %) and the logarithm of the seed reserve dry weight ($\log_{10}$(DM) in grams) and the corresponding fitted plane (see equation in table 2). Each point represents the average proportion for a seed fate for one species in one site. For seed fates for which no significant relation could be fitted (c, d and h) the plane represents the overall average proportion for that seed fate. Note that the minimum dry weight in the germination figure (a) is different. The angular transformed value of 0.0 = 0.0, ang(0.5) = 0.79, ang(1.0) = 1.57.

effect of gap size on the germination of intermediate- and large-seeded species. These results are supported by earlier studies. The positive germination response of small-seeded species to conditions associated with gap formation is well established in literature (*e.g.* Alvarez-Buylla and Martínez-Ramos 1990, Ellison *et al.* 1993, Raich and Gong 1990) and Raich and Gong (1990) and ter Steege *et al.* (1994) found that the germination of large-seeded species was reduced in large gaps. In the present study, the pattern reversed from intermediate to large gaps: germination of small-seeded species decreased while that of large-seeded species increased. Kyereh *et al.* (1999) also found that germination of some small-seeded, light-demanding species was reduced in extreme high-light environments. In addition, germination as defined in the present study, included up to four weeks survival and seeds, especially those of small-seeded species, may have germinated and died within a few days, without being recorded as germinated. Engelbrecht *et al.* (2001, as cited in Dalling and Hubbell 2002) found that mortality of recently germinated seedlings of pioneer species increased significantly in large gaps during short dry periods. The reduction in germination of small-seeded species in the largest gaps as found in the present study may therefore be caused by a reduction in early seedling survival, rather than by a reduction in actual germination. Finally, the reduction in germination success may be exaggerated by the quadratic regression model that was used. The increased germination success of the large-seeded species in the largest gaps cannot be explained and is most likely a regression artefact.

Desiccation hardly occurred in the forest understorey. However, as canopy openness increased, the proportion of seed mortality caused by desiccation increased sharply. Desiccation was rare in small-seeded species, while it was a very common cause of mortality for large-seeded species. This is in agreement with the expectations and studies cited in the review of Vázquez-Yanes and Orozco-Segovia (1993). The result that seeds of large-seeded species are more susceptible to desiccation than those of small-seeded species, since their seeds fail to imbibe properly in large gaps, implies that production of large seeds is less advantageous in heavily disturbed areas. On the other hand, the small seedlings of small-seeded species may be more vulnerable to desiccation than those of large-seeded species, since they fail to reach sufficient rooting depth with their limited seed reserves. It should be realized, however, that all existing vegetation and woody debris were removed in the logging gaps and that seeds were laid to germinate on the soil surface. Even in a recent logging gap, some vegetation will exist and logs can provide different microhabitats, which reduce the risk of desiccation. Furthermore, naturally dispersed seeds may be buried by for example ants or agoutis, which will reduce the risk of desiccation as suggested by the results of ter Steege *et al.* (1994), who found that germination success of buried *Chlorocardium rodiei* seeds was higher than that of unburied seeds. Finally, both biotic and abiotic conditions will change continuously during succession and the risk of desiccation will be reduced as soon as small-seeded species start to colonize a gap.

Many studies have reported a high risk of insect predation for small-seeded species (*e.g.* Alvarez-Buylla and Martínez-Ramos 1990, Levey and Byrne 1993, Nepstad *et al.* 1996, Peña-Claros 2001). The results obtained in this study are in agreement with these findings.

Predation by insects was an important mortality cause for small-seeded species. Furthermore, the proportion of seeds killed by insects decreased with seed mass as was expected. Possibly insect-mediated seed mortality decreased with seed mass because chances of survival after predation or infestation increase with seed mass, though this needs further investigation. Seed mortality resulting from predation by mammals increased with seed mass. However, seed losses to mammals were limited, even for the large-seeded species. Mammals are abundant in Guyana (personal observation) and therefore, the low proportion of seeds eaten by mammals does not seem to be related to low mammal densities. Again, this would need further investigation.

A large number of seeds disappeared, *i.e.* were removed. The proportion of seeds that was removed decreased with seed mass and increased with canopy openness. It is possible that seeds of small-seeded species were blown or washed away or carried away by insects and germinated outside the experimental area. In the gaps, it was observed that ants carried away the seeds of *Cecropia* shortly after they were sown. In addition, in one gap in which nearly all *Aspidosperma* seeds were missing, seeds showing signs of leaf-cutter ant activity were found (personal observations). Heavier seeds are less likely to be blown or washed away and these were probably eaten or cached by rodents. The final fate of removed seeds was not determined. This may have led to an underestimation of germination success and of the proportion of seeds that died because of insect or mammal predation. The opposite problem might have occurred when seeds that arrived in the experimental sites from surrounding vegetation were mistaken for sown seeds. Generally the arrival of naturally dispersed seeds in the gaps appeared to be very limited and since position, weight and entry date of each individual sown seed was known, the chance of confusion seems negligible for most of the species. For *Cecropia* and *Goupia* it is difficult to estimate the magnitude of the problem, since their seeds could not be recovered, although the number of seedlings of these seedlings that established outside the experimental areas in the same gaps was low.

In literature, the reported proportions of seeds eaten or removed by insects and/or mammals vary widely and it appears that variability in the rate of seed predation is the norm (Crawley 1992). This variability may explain why no relation with canopy openness was found for insect or mammal predation. Seed removal, however, did increase with canopy openness. The absence of a relation with canopy openness for insect and mammal predation suggests that predator abundance or activity was not affected by canopy openness. Therefore, the relation between seed removal and canopy openness may have to be attributed to a higher risk of being blown or washed away in gaps compared to the forest understorey, however, this requires detailed research on the fate of removed seeds. Furthermore, it should be realized that species were attacked by different groups of insects. Species with small and intermediate seeds seemed to be attacked mostly by ants, while large-seeded species were eaten mainly by termites and infested by Coleoptera (personal observations).

For three seed fates, decay, decay plus insect predation and dormancy, no significant model could be fitted. The proportion of dormant seeds was expected to decrease both with seed mass and canopy openness. There are two possible causes for the absence of a relation: 1) seeds of *Cecropia* and *Goupia*, which were most likely to show dormancy, could not be recovered due to their small size and 2) nearly all seeds of *Parinari*, a species with intermediate seed mass, remained dormant. Why no relation for decay and decay plus predation was found cannot be explained. Generally, variation between species was large (see figure 1), which may explain why for some seed fates no relations were found. Similar studies should be performed on a larger scale (more study species, sites and over longer periods, determine fate of small and removed seeds) to obtain more insight in the direct and indirect effects of seed mass on the regeneration of tropical tree species.

It can be concluded that germination success (emergence for *Cecropia* and *Goupia*) of small-seeded species is generally less than that of species with heavier seeds, because the seeds of small-seeded species are killed by insects or are removed. With increasing gap size, the risk of desiccation increases and the difference in germination success between species differing in seed mass becomes less due to desiccation of the seeds of large-seeded species, which implies that the production of large seeds is less advantageous in heavily disturbed areas than in the understorey. In the forests of Guyana, which are dominated by large-seeded species (Hammond and Brown 1995, ter Steege and Hammond 2001), this may lead to shifts in the species composition in logged forests, since the regeneration of large-seeded species may be inhibited in logged areas, while that of small-seeded species may increase. Guyana's most important timber species, *Chlorocardium*, may be especially vulnerable to disturbance. Populations of *Chlorocardium* are clumped (Zagt 1997) and due to its limited seed dispersal (chapter 2, Zagt and Werger 1997), *Chlorocardium* seeds have a high probability of dispersal into logging gaps. This, combined with the reduction of the number of seed trees due to logging and the reduced germination in logging gaps, can inhibit the regeneration of *Chlorocardium* severely in areas disturbed by logging. However, survival chances and growth rates of established seedlings are generally higher in gaps than in the forest understorey (*e.g.* Augspurger 1984a, Forget 1997, ter Steege *et al.* 1994). Therefore, it cannot be predicted if the reduction in germination success of large-seeded species will reduce regeneration in naturally regenerating logging gaps. Reduced impact logging techniques, aimed at minimizing gap size and total gap area (see van der Hout 1999), will limit the negative effect of logging on the germination of the large-seeded species.

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Chapter 4

The determinants of the spatial distribution of tree seedlings in the tropical rain forest of central Guyana

Abstract

The spatial distribution of seedlings of several tree species was analysed in the tropical rain forest of central Guyana. Species were classified into three functional groups, pioneer, long-lived pioneer and climax species, to evaluate overall trends. For nearly all species seedling abundance showed some degree of positive spatial autocorrelation (clumping) over distances of approximately 10 to 25 metres. Seedlings of pioneer species were more strongly clumped than those of long-lived pioneer and climax species. Pioneer seedlings were clumped at locations with intermediate to high light availability and at locations that were recently disturbed by logging, but not at short distances from conspecific adult trees. Seedlings of long-lived pioneer and climax species, on the other hand, were on average distributed randomly with respect to light availability and disturbance history, but often showed a strong clumping around adult trees, although the variation within groups was large. Also the adult trees of the majority of the species were clumped, but on a larger spatial scale than the seedlings. It is concluded that pioneer species are limited in their recruitment, because the conditions required for their germination and seedling survival are rare, while long-lived pioneer and climax species are limited in their recruitment because they can disperse their seeds over short distances only.

1 Introduction

Seedlings of tropical tree species are not distributed randomly in space, but rather exhibit some degree of clumping (*e.g.* Alvarez-Buylla and Martínez-Ramos 1992, Forget *et al.* 1999, Hubbell *et al.* 1999, Itoh *et al.* 1997, Kitajima and Augspurger 1989, Nicotra *et al.* 1999). The current spatial distribution is the result of regeneration processes that took place in the past. Analysing the distribution of seedlings can reveal information on the species-specific constraints on successful regeneration.

Clumping of seedlings (on a scale of metres to hectares) may be expected for any species with either limited dispersal or specific regeneration requirements. If seed dispersal is the limiting factor for the regeneration of a species, then it may be expected that seedlings of this species will be clumped around adult trees. If the adult trees themselves are also clumped, then the clumping of seedlings may be even stronger. On the other hand, if a species can disperse its seeds over large areas or has a persistent soil seed bank, but requires specific conditions for its germination or survival, then it may be expected that seedlings of this species will be clumped at sites where these conditions are met. A low light availability is one factor that can limit the germination and survival in the tropical rain forest. If a species requires relatively high light intensities for its regeneration it may be expected that seedlings of this species will be clumped in high-light environments. A second factor, to which light availability is often related, is the disturbance history of a patch. In new gaps, whether created naturally or during logging, the light availability is higher than in undisturbed understorey patches and the soil can be disturbed (Denslow 1987, van Dam 2001). Some species may specifically need the perturbation of the soil in combination with a high light availability for successful regeneration. Seedlings of these species may be expected to be clumped in disturbed patches.

It has been proposed that recruitment limitation may play an important role in maintaining the species diversity in tropical rain forests (Eriksson and Ehrlén 1992, Hubbell and Foster 1986, Hurtt and Pacala 1995, Muller-Landau *et al.* 2002, Tilman 1999). The former type of recruitment limitation describe above, when seeds are dispersed over short distances, will contribute to ‘seed limitation’. In the presence of seed limitation, the best competitor may be absent from an available site, enabling any other species that happens to arrive at the site to occupy the site. The other type of recruitment limitation has been termed site limitation (or establishment limitation). In the presence of site limitation, species can coexist because they occupy different regeneration niches. Hence, studying the spatial distribution of seedlings will contribute to a better understanding of the maintenance of the high tree species diversity in tropical rain forests.

In this study, the spatial distribution of seedlings is evaluated with respect to the distance to conspecific adults, light availability and disturbance history, for tree species belonging to different functional groups (*i.e.* groups of species with similar characteristics). The importance of proximity to adults and the availability of suitable sites for successful regeneration in shaping the spatial distribution of seedlings may be expected to differ between species belonging to different functional groups. According to the classical classification of Swaine and Whitmore (1988), tree species can be divided into pioneer and climax species. The small seeds of pioneer species are widely dispersed and available in the soil seed bank. Pioneer seeds only germinate in high-light environments and their seedlings cannot survive in the shade. Climax species, on the other hand, generally have large, poorly dispersed seeds and their seedlings can survive in the shade for long periods.

It is expected that seedlings of all species are clumped. However, based on the characteristics of the functional groups, it is hypothesized that the spatial distribution of pioneer seedlings is predominantly determined by light availability and recent logging-related disturbance, while that of climax species is mainly determined by the distribution of adult trees. Since the majority of the species in tropical rain forests are climax species a third group, the long-lived pioneers, is placed in between the pioneers and the climax species. The distribution of seedlings of long-lived pioneers is expected to be determined by the availability of suitable microsites, but less than pioneer species, and by the proximity of adults, but less than for climax species. This idea is tested in the tropical rain forest of central Guyana.

2 Methods

2.1 Functional groups

Data on wood density and seed mass available in literature were used to classify a large number of tree species occurring in Guyana into functional groups. Seed mass has been shown to be correlated with several regeneration processes such as dispersal, germination, initial seed size and survival (chapters 2 and 3, Augspurger and Franson 1987, Boot 1996, Dalling and Hubbell 2002, Rose and Poorter 2003), while wood density is related to a species' maximum growth rate (Arets *et al.* 2003) and can be used as an indicator of disturbance sensitivity (ter Steege and Hammond 2001) and shade tolerance (Augspurger 1984). Typically, pioneer species tend to have small seeds and a low wood density, while climax species tend to have large seeds and hard wood (Foster and Janson 1985, Hammond and Brown 1995, Ng 1978, Raich and Gong 1990, Rose and Poorter 2003, ter Steege and Hammond 2001).

The main sources that were used to collect information on seed mass and wood density were Hammond and Brown (1995) and ter Steege (2000). Additional information was obtained from CTFT (1989), Fanshawe (1961), Favrichon (1994) and Gérard *et al.* (1996). Since wood density and seed mass are continuous and no obvious segregation existed, a *K*-means cluster analysis was performed with these two characteristics (seed mass in logarithmic classes) to define groups based on wood density and seed mass in SPSS 8.0 for Windows. This resulted in three groups: a group with low wood densities (< 0.8 g·cm^{-3}) and low seed masses (< 0.1g), a group with low wood densities and high seed masses, and a group with high wood densities and a high seed masses. Henceforth these functional groups will be referred to as pioneer, long-lived pioneer and climax species, respectively.

2.2 Field data collection

The field data for this study were collected in the tropical rain forests around the township of Demerara Timbers Ltd., Mabura Hill, approximately 250km south of Georgetown, the capital of Guyana. The area has average temperatures of 25.9°C and an annual rainfall of 2772mm with maxima in May-August and December-February (Jetten 1994, van Dam 2001). The forests of central Guyana have low species diversity and are dominated by tree species with high wood density, large seeds and rodent or unassisted seed dispersal (Hammond and Brown 1995, ter Steege and Hammond 2001).

In the Mabura Hill Forest Reserve a plot of nine hectares was established (5°13'N, 58°48'W). The area has never been logged commercially. A second plot was established in the East Pibiri compartment of the Demerara Timbers Ltd. concession (5°01'N, 58°34'W), which was logged in 1998. The plots will be referred to as the undisturbed and the logged plot, respectively. They will not be used to examine differences between logged and undisturbed forests, but rather to get a larger dataset. Both plots were situated on brown sand (Ferralsols). All potential parent trees in the plots were identified and their position and size were measured. A parent tree was defined as a tree with a DBH (diameter at breast height, 1.30m above the ground) larger than a certain threshold. These thresholds were 5cm for subcanopy tree species (*i.e.* species that reach a maximum height of less than 25m), 15cm for canopy species (maximum height between 25 and 35m) and 23.4cm for emergent species (maximum height of 35m or more). These minimum reproductive sizes were derived in chapter 2 of this thesis.

In the undisturbed plot, 1694 square quadrates of 1m^2 were established following a random design. In the logged plot, all logging gaps and skid trails were mapped. Based on this map 150 1m^2 quadrates were established at random positions in undisturbed patches, 148 in logging gaps, 150 on skid trails and 50 quadrates on skid trails in logging gaps. During the fieldwork, the disturbance status of the forest patches in which the quadrates were placed was re-evaluated and quadrates were classified as being in undisturbed patches, natural gaps (vegetation less than 2m high), on skid trails, in logging gaps or on skid trails in logging gaps. This classification was used to evaluate the spatial distribution with respect to disturbance. The outer forty metres of the plots were used as a buffer zone where no quadrates were established, but the adult trees were measured.

Between 12 June and 4 October 2000 the number of seedlings per tree species in the quadrates was determined. In principle a seedling was defined as any individual between 10 and 110cm height. However, in the logging gaps some seedlings that were approximately 30cm in height when establishment of the quadrates was started had grown above the upper limit when establishment of the quadrates was finished. Therefore, it was decided to include larger individuals if it seemed likely that they had established after gap formation. Individuals less than 10cm were excluded, since it is difficult to identify very small individuals to species.

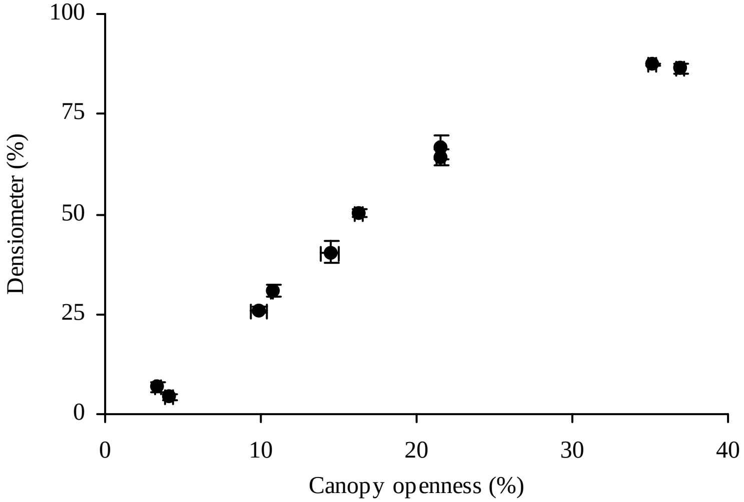

Figure 1. The relation between densiometer values and canopy openness as measured in two understorey and eight logging gaps. Each point represents the average of five values (± 1 · standard error, SE) in one of the sites.

At the end of the fieldwork period (2001) the light climate in each of the quadrates was determined at one metre height using a densiometer (Model C (Concave), Robert E. Lemmon, Forest Densiometers, Bartlesville, OK, USA). This is a concave mirror with which the overhead vegetation cover can be estimated. The relation between densiometer value and canopy openness (percentage of sky hemisphere not covered by vegetation) as determined using hemispherical canopy pictures was evaluated at some test locations and densiometer value appeared a good predictor of canopy openness (figure 1).

2.3 Data analyses

For all analyses concerning the spatial distribution of seedlings only species with at least 50 seedlings in one of the plots were included. If a species had more than 50 seedlings in both plots, these two combinations of species and plot were analysed separately, since distances between quadrates in different plots cannot be calculated. Henceforth, these combinations of species and plot will simply be referred to as species. Moran's *I* statistic of autocorrelation (During and Lloret 1996, Upton and Fingleton 1985) was calculated to determine the degree of clumping of seedling densities. Moran's *I* can be calculated for any distance class *d* using:

$$I_d = \frac{n}{S_0} \cdot \frac{\sum_{i=1}^{n} \sum_{j \neq i} W_{ij} \left(x_i - x_{avg}\right)\left(x_j - x_{avg}\right)}{\sum_{i=1}^{n} \left(x_i - x_{avg}\right)^2} \qquad (1)$$

where n is the number of quadrates, x_i and x_j are the seedling densities in quadrates i and j, and x_{avg} is the average seedling density over all quadrates. W_{ij} is an element of the weight matrix at distance *d, i.e.* 1 if quadrate *j* is within distance *d* of quadrate *i,* and 0 if it is not. S_0 is the sum of all the weights W_{ij}, *i.e.* twice the number of neighbouring quadrates. Although the upper and lower bounds of Moran's *I* are not fixed it rarely takes on a value outside the range (-1,1). Under complete randomness the expected value of Moran's *I* is close to zero (a very small negative number). Positive values indicate clumping of seedlings, while negative values indicate segregation of seedlings.

Moran's *I* was calculated for each species using distance classes of five metres and plotted in correlograms. Additionally, 95% confidence intervals were constructed from 1000 Monte Carlo simulations to evaluate deviations from randomness for each distance class. For the Monte Carlo simulations seedling densities were redistributed randomly, rather than individual seedlings, since the latter randomization would result in an overestimation of the degree of clumping. Average correlograms were constructed for each of the functional groups.

To evaluate the effect of distance to conspecific adults, light and disturbance an approach similar to that described by Hamill and Wright (1986) was used. The technique will be described for distance to adults only since it is essentially the same for all factors. For each species the distance to the nearest adult was calculated for all quadrates. For each distance class of ten metres the proportion of seedlings in that class was calculated. Subsequently, the expected proportion of seedlings in each of the distance classes is calculated assuming a random distribution of seedlings. This means that the expected proportion of seedlings in a distance class is equal to the proportion of quadrates in that class. If a quadrate is closer to the plot edge than to the nearest adult it is possible that a closer tree is outside the plot, which may result in an overestimation of the observed distribution and underestimation of the expected distribution at larger distances from adult trees. A way to deal with this problem is to discard all quadrates for which the nearest tree is further away than the plot edge. However, this will result in an overestimation of the expected distribution close to adult trees, if seedlings are clumped around adult trees. Under the assumption that effects of adult trees are strongest close to adults, it was decided not to discard these quadrates. Consequently an uncertainty is introduced at distances more than 40m from the nearest tree.

For each of the species, graphs were constructed with the difference between observed and expected proportions of seedlings as a function of distance. The difference between observed and expected proportion was used, since the expected values differ between species, depending on the distribution of the quadrates around adult trees. Average graphs were constructed for each of the functional group. Additionally, significance of differences between observed and expected seedling numbers were tested for each of the species using G-tests with Williams' correction or a correction for continuity if the number of seedlings was less than 200. If the expected seedling number in a distance class was less than five, it was grouped with an adjacent class. Because multiple tests were performed a Bonferroni correction was applied. If a G-test was significant then it was subjectively decided whether for that species seedlings were clumped around adult trees or avoided those. The effect of densiometer value was evaluated using the same approach, but with a class width of five

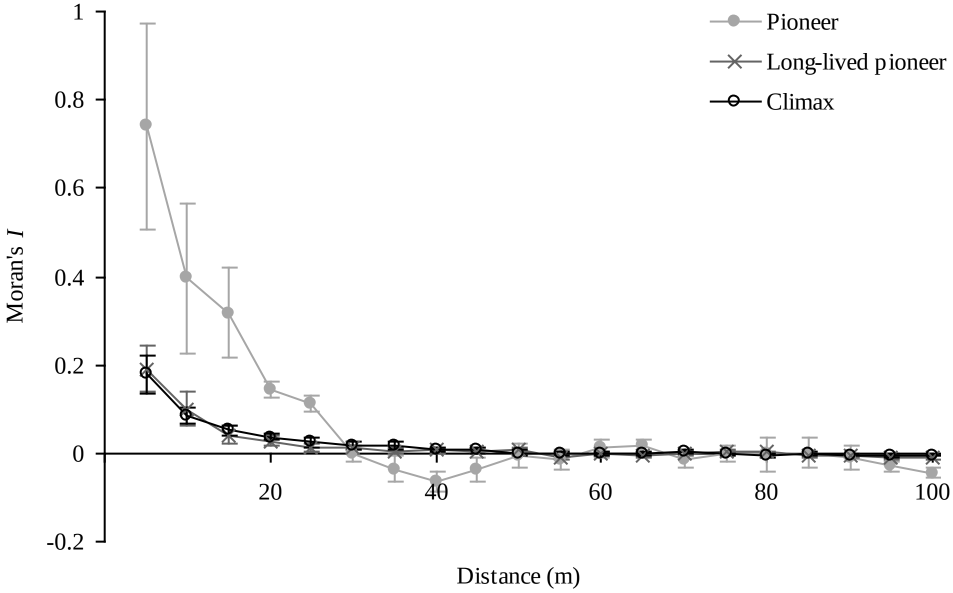

Figure 2. The average Moran's *I*, a measure for spatial autocorrelation, (± 1SE) against distance for the three functional groups.

percent. Based on the G-tests it was decided if a species had more seedlings low-light or high-light environments, or it was distributed randomly with respect to light. For the effect of disturbance only the data from the logged plot were used, since only in this plot logging related disturbance was present and the number of quadrates in natural gaps in the undisturbed plot was very low (31 out of the 1694 quadrates).

The spatial distribution of adult trees was analysed using Ripley's *K* function (*e.g.* Goreaud and Pélissier 1999, Itoh *et al.* 2003, Ripley 1977, Wiegand and Moloney 2004), which is given for distance class *d* by:

$$K_d = \frac{A}{n^2}\sum_{i=1}^{n}\sum_{j\neq i} k_{ij} \tag{2}$$

Herein *A* is the size of the plot and *n* is the number of trees. $k_{ij} = 1$ if the distance between trees *i* and *j* is less than or equal to distance *d*, else $k_{ij} = 0$. The edge correction as described by Goreaud and Pélissier (1999) was used. The Ripley's *K* statistic was transformed to the *L*-statistic using:

$$L_d = \sqrt{\frac{K_d}{\pi}} - d \tag{3}$$

The *L*-statistic has the advantage that it is easier to interpret, since it is 0 if trees are distributed randomly. The *L*-statistic was calculated for each species-plot combination with

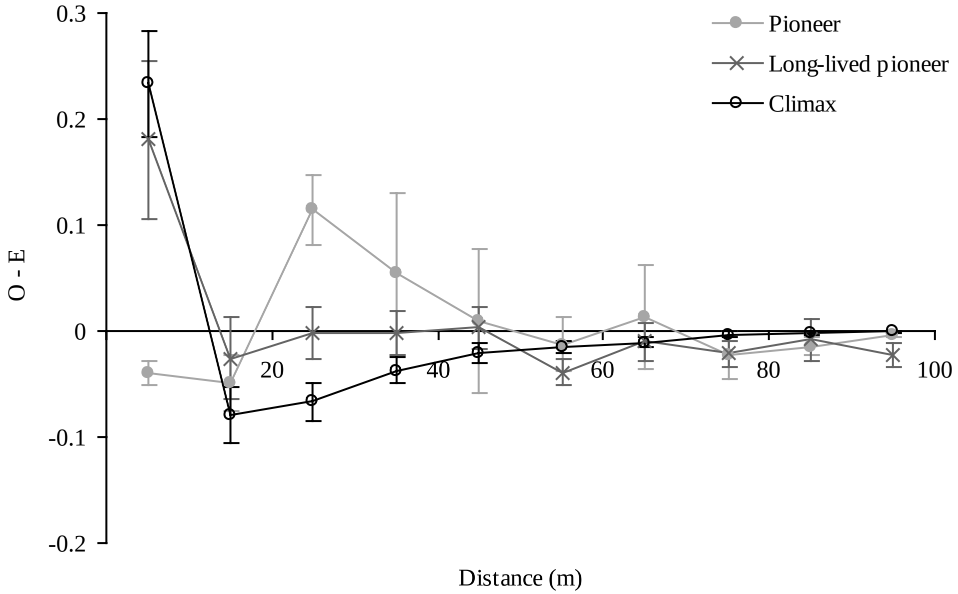

Figure 3. The average of the proportion of seedlings observed minus the proportion of seedlings expected in each 10m-distance class (± 1SE) against the distance to the nearest conspecific adult for the three functional groups. A positive value indicates that more seedlings were found in that class than expected assuming a random distribution of seedlings with respect to distance to the nearest adult and a negative value indicates fewer seedlings were observed than expected.

at least ten individuals. The species that were used were not the same as those used as for the seedling analyses, although for nearly all species with 50 seedlings more than ten adults were present. Average graphs with the *L*-statistic against the lag distance were constructed.

3 Results

For only two out of the 33 combinations of species and plot the value of Moran’s *I* did not exceed the 95% confidence interval at any distance up to 100 metres. For four additional species Moran’s *I* deviated slightly at a few distance classes but without a clear pattern. On average, seedlings of pioneer species (3 species) showed stronger autocorrelation than seedlings of long-lived pioneers and climax species (10 and 20 species, respectively, figure 2). Pioneer species showed strong positive spatial autocorrelation of seedlings at distances up

Table 1. The number of species per functional group for each type of distribution around adult trees. - = relatively more seedlings close to nearest conspecific adult, ns = no significant difference between observed and expected distributions, + = more seedlings at intermediate or large distances.

Functional group	-	ns	+
Pioneer	0	0	3
Long-lived pioneer	5	5	0
Climax	13	7	0

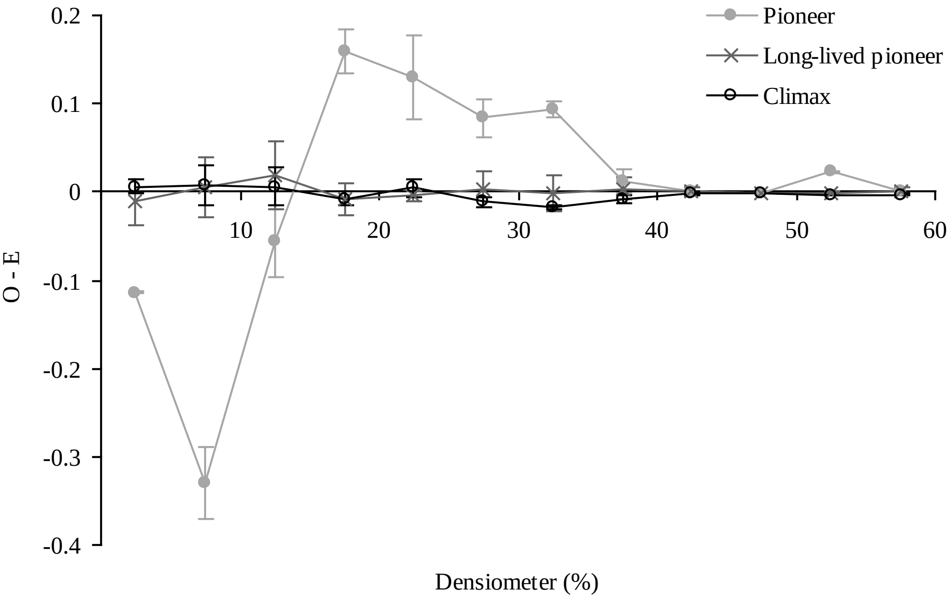

Figure 4. The average difference between the observed and expected proportion of seedlings (± 1SE) against the densiometer value for each of the functional groups. Points indicate class middles.

to 25 metres. Beyond 30m the pioneers showed some negative autocorrelation before returning to randomness. On average, the long-lived pioneers and climax species both showed weak positive autocorrelation over approximately 15m, however within these groups many species were randomly distributed.

For all three pioneer species more seedlings were found at intermediate to large distances than was expected based on a random distribution (figure 3 and table 1). None of the long-lived pioneers and climax species showed this trend. Half of the long-lived pioneer species and 65% of the climax species had more seedlings close to the tree than was expected.

All pioneer species had more seedlings than expected in quadrates with intermediate (between 15 and 35%) densiometer values (figure 4 and table 2). The majority of the long-lived pioneer and climax species did not respond strongly to light: a few species had more seedlings in low-light quadrates and one long-lived pioneer and one climax species had more

Table 2. The number of species per functional group for each type of distribution over the densiometer value classes. - = relatively more seedlings in quadrates with low densiometer values, ns = difference between observed and expected distributions not significant, + = more seedlings in quadrates with intermediate or high values.

Functional group	-	ns	+
Pioneer	0	0	3
Long-lived pioneer	2	7	1
Climax	4	15	1

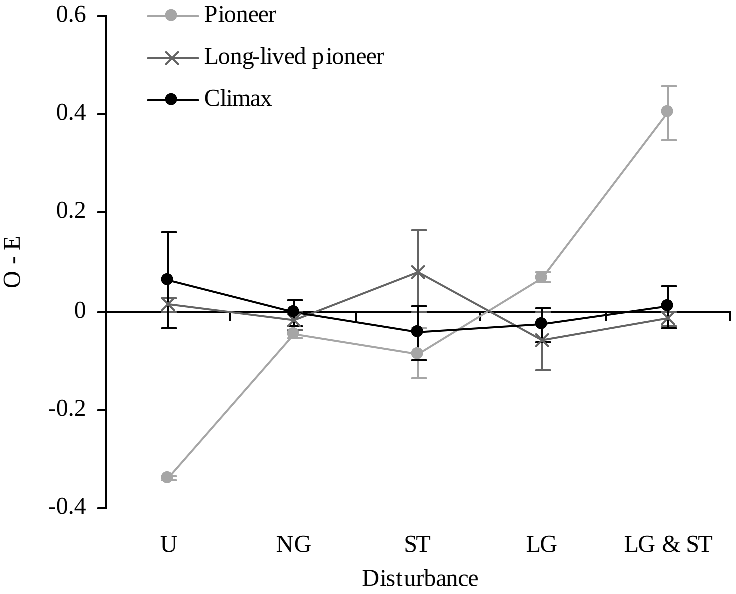

Figure 5. The average difference between the observed and expected proportion of seedlings (± 1SE) in the five disturbance types for each functional group. Disturbance types (shown in this order): U = undisturbed, NG = natural gap, ST = skid trail, LG = logging gap, LG & ST = skid trail in a logging gap.

seedlings in intermediate light quadrates than expected from a random distribution. In the undisturbed plot, the observed and expected proportions did not differ significantly for any of the species.

For all species except two climax species the observed and expected proportions of seedlings per disturbance type differed significantly. The three pioneer species had fewer seedlings than expected in the understorey quadrates and more in the logging gaps and especially in skid trails in logging gaps found (figure 5). The long-lived pioneer and climax species all showed different distributions over the disturbance types. Some species were in excess in undisturbed patches, some were found mainly on skid trails, some showed the same distribution pattern as the pioneers and some did not shown a clear distribution pattern (results not shown). On average this resulted in a random distribution over the disturbance types for long-lived pioneers and climax species.

Generally, trees were clumped over large distances (figure 6). Only for two pioneer species sufficient trees were present in the area. One of these showed a strong clumping over large distances, the other pioneer species was less clumped and over shorter distances, hence the large error bars. On average pioneer species seemed to be more clumped than the long-lived pioneer and climax species. Again, long-lived pioneers and climax species showed similar patterns. The variation within these groups was large.

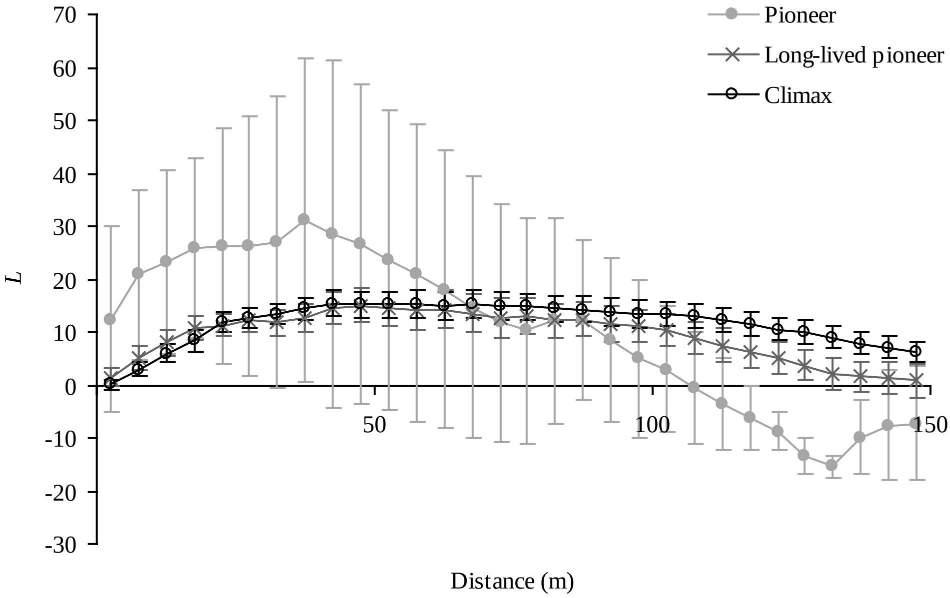

Figure 6. The average *L*-statistic (transformation of Ripley's *K*) for adult trees (± 1SE) against distance in classes of five metres for the three functional groups. Positive values indicate clustering of adult trees, 0 means spatial randomness.

4 Discussion

As was expected, seedling abundance was spatially autocorrelated for nearly all species. On average, seedlings of pioneer species were clumped more strongly than those of long-lived pioneers and climax species. Long-lived pioneers and climax species showed similar degrees of clumping.

It was expected that long-lived pioneers and especially climax species would be clumped around parent trees. Approximately half of the long-lived pioneer and two thirds of the climax species had more seedlings close to adult trees than expected under a random distribution. Climax species showed slightly stronger clumping than long-lived pioneers. For all pioneer species the observed distributions around adult trees differed significantly from the expected distribution. Unlike species from the other functional groups, pioneer species had more seedlings than expected some distance away from adult trees, rather than close to the tree. The clumping of seedlings around adult trees of long-lived pioneer and climax species, and the distances over which this clumping occurred are in keeping with a number of studies conducted in tropical forests, which all report clumping of seedlings in the vicinity of adult trees (*e.g.* Forget 1989, 1992, Itoh *et al.* 1997, Kitajima and Augspurger 1989, Zagt and Werger 1997). This clumping of seedlings around adult trees is explained by the fact that the seeds of many tropical tree species are dispersed over short distances, resulting in clumped distributions of seeds around the adult trees (chapter 2, Dalling *et al.* 2002, Forget

1989, 1992, Guariguata and Pinard 1998, Howe *et al.* 1985, van Rheenen *et al.* 2004, Willson 1993, Zagt and Werger 1997).

Clumping of adult trees was observed for two thirds of the species. Clumping of adult trees did not differ between long-lived pioneers and climax species. Because only two pioneer species had sufficient trees for the analysis, which showed a very different clumping pattern, conclusions about differences in degree of clumping between pioneers and the other functional groups cannot be made. It was argued that clumping of adult trees could strengthen the clumping of seedlings, if seeds are dispersed over limited distances and seedlings are clumped around adult trees. However, the clumping of trees occurred at a much larger spatial scale (often more than 100m) than the clumping of seedlings (less than 25m) and it seems unlikely that the clumping of adult trees can explain the clumping of seedlings at the studied spatial scale.

Pioneer seedlings were expected to be clumped at high-light sites, while a weaker and no clumping were expected for long-lived pioneer and climax species, respectively. The three pioneer species, one long-lived pioneer species and, to a lesser extent, one climax species had less seedlings in dark quadrates and more seedlings in quadrates with intermediate light levels than was expected under a random distribution. Approximately a quarter of the long-lived pioneer and climax species had more seedlings in dark quadrates than expected and for the majority of the species in these functional groups seedlings were distributed randomly with respect to light. These results can largely be explained by differences in germination behaviour and seedling survival. Seeds of many pioneer species require a trigger related to gap formation to germinate (Bazzaz and Picket 1980, Denslow 1987, Pons 1992, Probert 1992, Swaine and Whitmore 1988, Vázquez-Yanes and Orozco-Segovia 1993, 1996) and their germination is enhanced by increased light levels (chapter 3, Alvarez-Buylla and Martínez-Ramos 1990, Ellison *et al.* 1993, Raich and Gong 1990). Additionally, small-seeded pioneer seedlings require high light levels to survive (Rose and Poorter 2003, and references therein). The combination of increased germination and survival in high-light environments of pioneers explains the clumping of pioneer seedlings in quadrates with higher light levels. The large-seeded long-lived pioneer and climax species, on the other hand, are able to germinate and survive in low-light environments (chapter 3, Ng 1978, Raich and Gong 1990, Rose and Poorter 2003), which explains why they do not show a strong response to light. The finding that some long-lived pioneer and climax species had more seedlings in darker quadrates than expected is counterintuitive, but may be explained by the fact that the light climate in a quadrate is determined by the trees surrounding it. If seedlings are strongly clumped around adult trees, the majority of the seedlings will grow in the shade of the parent tree. This may have been the case for some, but not all of the species that favoured dark sites, since not in all of these species seedlings were clumped around adults.

For nearly all of the species that were studied the seedlings were not randomly distributed over patches with different disturbance regimes. Almost half of the long-lived pioneer and climax species were more abundant in the understorey than expected and less in all logging

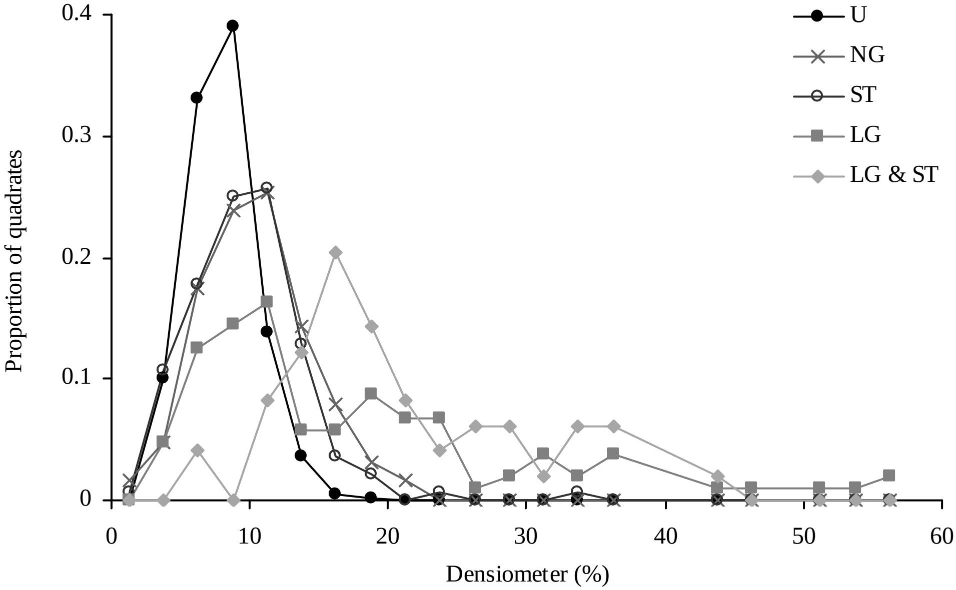

Figure 7. The proportion of quadrates in each of the densiometer classes for five disturbance types (see figure 5).

related disturbance types. The negative response to disturbance of some long-lived pioneer and climax species may be caused by a reduction in the seed survival and germination in high-light environments (chapter 3, Raich and Gong 1990). One long-lived pioneer and a climax species had disproportionate large numbers of seedlings on skid trails. The pioneer species and the remainder of the long-lived pioneer and climax species were found more in logging gaps and on skid trails in logging gaps. On average, this resulted in a strong bias towards logging gaps and skid trails in logging gaps for pioneer species and the absence of an effect of disturbance for long-lived pioneers and climax species.

An important limitation of this study is that the interaction between distance to adults, light and disturbance could not be evaluated with the current dataset. The distance to trees influences the light availability at a site. In addition, light availability differs between patches with different disturbance histories. In this study the understorey quadrates were darkest, followed by natural gaps and skid trails, then logging gaps and the patches on skid trails in logging gaps had the highest light levels (figure 7). Furthermore, logging in Guyana is concentrated in patches where *Chlorocardium rodiei*, the main timber species, is abundant, meaning that logging-related disturbance is not randomly distributed over the plot. These interactions may explain some of the obtained results and the variation within functional groups. For example, the clumped distribution at 20 to 50m from parent trees may have partly been caused by a clustering of disturbed patches at these distances from the parent trees. A second problem was the limited data availability for the pioneer species. Pioneer species only occur at low densities in the forest of central Guyana, which is dominated by climax species (Arets *et al.* 2003, ter Steege and Hammond 2001).

The spatial distribution with respect to the studied factors was very similar for long-lived pioneers and climax species. The long-lived pioneers as defined in the study had smaller seeds than pioneer species and a lower wood density than the climax species. The fact that the spatial distribution of long-lived pioneers resembled that of the climax species and not that of the pioneer species suggests that the processes studied here are more related to seed mass than to wood density. Overall the results support the classical dichotomy of pioneer and climax species.

The results obtained in this study partly support the hypothesis proposed in the introduction. Seedlings of the majority of the species showed some degree of clumping. The spatial distribution of pioneer seedlings was mostly determined by light availability and disturbance history, while seedlings of long-lived pioneer and climax species were generally clumped around conspecific adult trees. The role of disturbance in shaping the spatial distribution of long-lived pioneer and climax species differed between species and may depend on interactions between the studied factors or on species characteristics not evaluated in this study. It is concluded that the recruitment of pioneer species is limited by the availability of microsites that are suitable for their germination and survival, *i.e.* site limited, while the recruitment of long-lived pioneer and climax species is limited by the inability to disperse their large seeds over long distances, *i.e.* ‘seed limited’.

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Chapter 5

The explicit modelling of tree regeneration within the SYMFOR framework for the tropical rain forest in central Guyana

With Eric J.M.M. Arets, Paul D. Phillips, Paul R. van Gardingen and Peter van der Hout

Abstract

Regeneration processes are rarely modelled explicitly in simulation models of tree growth and yield in tropical rain forests. This omission possibly leads to an underestimation of the effects of anthropogenic and natural disturbance on the species diversity. In this chapter, the implementation of a new recruitment module in the SYMFOR modelling framework is described. This module explicitly simulates the seed production and dispersal, germination, establishment and juvenile growth and mortality. The functions were calibrated using data from permanent sample plots and experiments collected in the tropical rain forest of central Guyana. Tree species were classified into 15 functional groups (groups of species with similar characteristics) to facilitate the interpretation of the model results. The performance of the model was evaluated by running a series of test simulations, by analysing the sensitivity of the model to a number of processes and by a comparison with field data.

Simulations of undisturbed forest revealed that the model did not predict a constant functional group composition. Part of this instability in the model results can be explained by small differences in regeneration processes between the first ten years of the simulations and field data. Generally, annual recruitment was higher, and juveniles grew faster and survived better in the simulations than in the field, which partly explained the rapidly increasing number of juveniles observed for some of the functional groups. However, shifts in the number of individuals in the field suggest that the forest patches from where the data were collected may also not maintain a constant composition. This may also explain part of the composition shifts in the simulations.

The model did respond to logging as was expected. If logging was applied only once, at the start of a simulation, the functional group composition hardly differed from that in the simulations without logging. However, in simulations with a 25-year logging cycle, approximating the harvesting intensity in Guyana, logging rapidly converted the stand into a secondary forest, with low yields per logging event. This clearly demonstrates the applicability and necessity of simulation models to evaluate current forest management.

Nevertheless, based on the instability in the undisturbed forest simulations, it was decided that the model within SYMFOR described in this chapter cannot be used to study ecological species diversity theories and to evaluate forest management without some substantial improvements. The lack of long-term data describing the regeneration processes and rare events currently prevents further improvements and development of the model.

1 Introduction

Tropical rain forests worldwide are threatened by anthropogenic influences. A detailed understanding of the maintenance of species diversity in these complex ecosystems and the impact of anthropogenic influences is required to design management approaches that preserve the species diversity in these forests. Simulation models are considered excellent tools for this purpose as relatively short-term data can be used to evaluate long-term forest dynamics. From an ecological point of view, species diversity theories, such as the intermediate disturbance theory (Connell 1978) and recruitment limitation (Hurtt and Pacala 1995), may be tested, while governments and logging companies can use simulation models to define and evaluate forest management.

Several simulation models for tropical forests have been developed during the last decades (*e.g.* Köhler and Huth 1998, Liu and Ashton 1998, Phillips *et al.* 2003). Generally, regeneration processes are underrepresented in existing models. Often recruitment is modelled as the creation of trees with stem diameters of five or ten centimetres, reflecting a focus on larger individuals in forest inventories and growth and yield studies. This aggregation of processes for individuals smaller than a specified diameter into one recruitment function has two major limitations. First, it neglects the history of the stand and juvenile demography. The recruitment probability estimated from field data will be attributed to the situation at the time the data were collected, while in reality it is the result of events that occurred during the decennia or centuries before the data were collected and, hence, are unknown. Similarly, in simulations the recruitment mainly depends on the situation in the forest at the time the recruitment occurs and not on events in the past. This will likely result in less accurate predictions of the responses of tree populations to disturbances, compared to predictions based on a model in which all regeneration processes are simulated explicitly. Second, recruitment is often modelled completely independent of position and even number of conspecific adult trees in the stand, implicitly assuming that seeds are always and everywhere available. This assumption will lead to more stable model results and an overestimation of the regeneration in simulations with reduced adult densities.

Guyana, situated in northern South America, is still largely covered by intact forest (ter Steege 2000), although selective logging takes places in large areas. The species diversity in Guyana’s forests is low compared to other neotropical forests, but Guyana’s forest flora contains many endemics (ter Steege 2000). The Government of Guyana is committed to preserve the country’s species diversity. The Guyana Forestry Commission has a vital role to play, as it is responsible for the management and utilization of the nation’s forests. In 2001 a model in the SYMFOR modelling framework was calibrated for forests in central Guyana and made available to the Guyana Forestry Commission as a tool to evaluate forest management (Phillips *et al.* 2002b). However, SYMFOR did not include explicit modelling of recruitment processes and may underestimate the consequences of logging on the species composition and future harvests. In this chapter the implementation of a new recruitment module, which explicitly addresses several regeneration processes (*i.e.* seed production and dispersal, germination, establishment, and juvenile growth and mortality) is described, and the performance of this new module will be evaluated. It is expected to provide better estimates of the long-term changes in the tree species diversity following disturbances.

2 Model description

2.1 General

SYMFOR was originally developed by the University of Edinburgh and the Indonesian Ministry of Forestry as a tool to assist in defining forest management policies using Permanent Sample Plot (PSP) data from dipterocarp forests in East Kalimantan, Indonesia (Phillips *et al.* 2003). Later it was adjusted and calibrated for forests in Guyana (Phillips *et al.* 2002a, 2002b), Ecuador and Brazil (Phillips *et al.* 2004). SYMFOR is a spatially explicit, individual-based modelling framework that includes both ecological and forest management models. The ecological models describe the recruitment, growth and mortality of tree species, while the forest management models describe logging processes and silvicultural treatments.

For the present study, adjustments were made to all ecological models. For the growth and mortality models, changes were restricted to implementation of new functions, while for the recruitment model the structure was also changed. In previous SYMFOR models, seedling and saplings were not modelled explicitly. Recruitment was modelled as the creation of trees of five or ten centimetres DBH (diameter at breast height, 1.30m above the ground), depending on the expected growth rate at a location and the species of the tree. It was ensured that trees would not recruit at recently disturbed locations. Using this approach, recruitment of new trees does not depend on adult tree distribution, number or presence, except in contributing to a competition index that influences the expected growth rate. This is a major limitation of the original version, since trees can recruit anywhere in the plot, even if seed dispersal is limited. In addition, a reduction in adult tree abundance and consequently seed availability, for example caused by logging, will not result in a reduction of recruitment, but rather in an increased recruitment because competition decreases. Therefore, it was decided to explicitly represent seedlings and saplings in SYMFOR and to simulate seed production and dispersal, germination and growth and mortality of seedling and saplings. Since modelling individual seeds, seedlings and saplings would be impractical due to their sheer numbers, a cohort modelling approach was used.

Each of the ecological processes is discussed below. Some general conventions apply throughout this chapter. Probabilities and random numbers are always within the range 0 to 1, inclusive. The abbreviations and symbols are summarized in appendix A. Although tree size is continuous in SYMFOR, functions or parameters differ between size classes. Throughout the chapter, the term juveniles will be used to indicate individuals with a DBH of less than five centimetres and trees are individuals with a DBH of five centimetres or more. The juveniles will be subdivided into seedlings (DBH less than 2cm) and saplings (DBH at least 2cm and less than 5cm), while trees will be subdivided into poles (DBH at least 5cm and less than 20cm) and large trees (DBH at least 20cm). The forest management models will not be treated here since these were not changed. The management models and general structure of SYMFOR are described in detail by Phillips and van Gardingen (2001, 2003) and on the homepage of SYMFOR (www.symfor.org).

2.2 Species groups

SYMFOR uses species groups to facilitate implementation of the model and interpretation of the results. An additional advantage of species groups is that rare species, for which insufficient data are collected to calibrate models for individual species, can be included in SYMFOR as contributors to the species group they belong to. SYMFOR uses two different types of species groups: functional or ecological groups, which determine the behaviour in the ecological models, and utility groups, which are used for the forest management component. The classifications are described in section 3.1.

2.3 Model flow

At the start of a simulation, PSP data are read in by SYMFOR. The most important data elements are the dimensions of the plot and the DBH, position and functional and utility group of each tree in the plot. Since data on smaller trees, saplings and seedlings are generally available only for sub-samples of the PSPs, these data are not read in at the start of the run. Individuals in these size classes are created using an algorithm based on the numbers and size distribution observed in the field. This initialization algorithm is explained in section 2.10. SYMFOR works with time steps of one year. During the simulation, SYMFOR loops through the following processes each year in the order specified below. The items in italics are model objects.

1. Harvesting (management): if harvesting is selected and it is a harvest year, then harvesting is simulated, *i.e.* tree selection, felling, damage to other trees and creation of *skidtrail*s. Harvested trees become *felledtree* objects.
2. Thinning (management): if selected and it is a correct year, then selective thinning of trees is performed.
3. Strip clearing (management): if selected and it is a correct year, then strip clearing and replanting are performed.
4. Tree growth (ecological): the diameter increment of each *livetree* object, *i.e.* individual living tree, is calculated.
5. Tree natural mortality (ecological): for each *livetree* it is decided if it dies that year. If it dies, the *livetree* becomes a *fallentree*, which either falls down or dies standing. If a

fallentree falls over it may damage and kill surrounding smaller *livetree*s, which then become *smashedtree*s.

6. Recruitment (ecological): the simulated area is divided into *gridsquare*s.
   a. Seedling creation: calculation of seed production, dispersal, germination and establishment. Per *gridsquare* and functional group, one new *cohort* may be created.
   b. Juvenile development: for each *cohort* created previously, the mortality resulting from fallen trees and skidding is calculated. Subsequently, its growth and natural mortality are calculated.
   c. *Livetree* creation: if a *cohort* reaches a certain diameter, its individuals become individual *livetree*s.
7. At the end of each time step, the age of objects is updated and simulation results can be stored.

2.4 Plot wrapping

All spatially explicit models have to deal with edge effects. Without a proper solution for edge effects trees at the border of the simulated plot would for instance experience less competition for light from neighbouring trees than trees in the centre of the plot. SYMFOR uses a common solution to this problem: plot wrapping. This means that the plot is simulated as a torus and hence that each plot border is connected to the opposite border (*i.e.* east to west and north to south). In practice this means, for instance, that in a plot of $100 \cdot 100$m a tree at position (1,1) can shade a tree at position (99,99) or that seeds that are dispersed outside the plot will enter the plot on the opposite side. All spatial processes, *e.g.* seed dispersal and competition indices, use plot wrapping.

2.5 Juvenile cohort creation

A juvenile cohort is defined here as a group of juveniles (DBH < 5cm) of one functional group that are located within the same grid square and have the same age. The terms seedling cohort and sapling cohort will be used to indicate juvenile cohorts with seedlings or saplings, respectively. Seed production, dispersal and germination all occur within the same year. Each year SYMFOR loops over all functional groups and over all grid squares to calculate these processes as described below.

2.5.1 *Seed production and dispersal*

It is assumed that all trees equal to or larger than the minimum reproductive diameter (*MRD*) produce seeds every year. Trees with a DBH equal to or larger than the *MRD* will henceforth be referred to as parent trees.

Each year, for each functional group the seed density $\hat{SD}_q$ in grid square q is calculated by summing the seed densities the grid square receives from each parent tree of the same functional group as described in chapter 2. Given T_P parent trees the equation for the seed density in grid square q is:

$$\hat{S}D_q = \sum_{j=1}^{T_\mathrm{P}} \hat{S}D_{qj} =$$

$$\sum_{j=1}^{T_\mathrm{P}} SSP \cdot \left(\frac{D_j}{D_\mathrm{ref}}\right)^2 \cdot \frac{1}{\pi \cdot \left[\rho + \left(sd_0 + sd_1 \cdot D_j\right)\right]^2} \cdot \exp\left[-\left(\frac{r_{qj}}{\rho + \left(sd_0 + sd_1 \cdot D_j\right)}\right)^2\right] \qquad (1)$$

In this equation $\hat{S}D_{qj}$ is the seed density generated by the j^{th} parent tree in grid square q, D_j is the DBH of the j^{th} parent tree in centimetres and r_{qj} is the distance from the centre of grid square q to the centre of tree j in metres, using plot wrapping if necessary, to calculate the shortest distance. The first term in the equation determines the seed production. *SSP* is the standard seed production, *i.e.* the seed production of a tree at the reference DBH, D_ref. The second term describes how the seeds are distributed around the parent tree. The dispersion parameter ρ (in metres) determines the rate at which seed density decreases with distance from the parent tree. sd_0 and sd_1 are the intercept and slope of the linear relationship between crown radius (in metres) and the DBH. 99% of the seeds produced by a tree fall within a distance of $2.15 \cdot (\rho + sd_0$ and $sd_1 \cdot D_j)$ from the parent tree. Section 5.1 describes an adjustment to this equation.

Subsequently, the seed density is translated to the seed number, N_seed, by multiplying the seed density with the area of the grid square, A_q. The result of this procedure is the number of seeds in each grid square for each functional group for the current year. To obtain an accurate representation of the abundance and distribution of each utility group within the functional group the proportion of seeds contributed to the seed number in this grid square is stored in an array. This enables a more realistic response to, for example, logging since the utility groups that are being harvested will produce fewer seeds.

2.5.2 Seed germination

Following seed production and dispersal the probability of germination is calculated. Germination in the model depends on the densiometer value (an approximation of the canopy openness) in the grid square. As an approximation of the densiometer value L in grid square q the following inverse relation between the densiometer value and size of and distance to surrounding trees is used:

$$L = l_0 + \frac{l_1}{\sum_{j=1}^{T} \frac{BA_j}{r_{qj}}} \qquad (2)$$

where T is the number of trees (≥ 5cm DBH) within a specified maximum distance r_L (not in equation 2) from the centre of the grid square. BA_j is the basal area of tree j in square centimetres and r_{qj} is the distance in metres between the centres of grid square q and tree j. l_0 and l_1 are parameters obtained by regression. This relation can result in infinitely large values if there are no or few trees surrounding the centre of the grid square. Therefore, an upper limit to L, L_{m}, was introduced, which was set to be equal to the maximum value observed in the field. The value for L is equal for all functional groups in a grid square.

Following the approach in chapter 3 the angular transformed proportion of germination was calculated using a quadratic relation. To obtain the probability of germination, G, SYMFOR uses:

$$G = \left[\sin\left(g_0 + g_1 \cdot L + g_2 \cdot L^2\right)\right]^2 \tag{3}$$

where g_0, g_1 and g_2 are all parameters estimated in a regression analysis. The value is set to zero if the term in between the inner brackets returns a negative value. For species of which the germination probability decreases with light availability, *i.e.* if g_2 is negative, the probability is kept at the minimum value if L is larger than the value for L where this minimum is reached.

2.5.3 Cohort creation

The number of seedlings that are created in the grid square is calculated by multiplying the number of seeds with the probability of germination. Since this will generally result in a non-integer value, it is assumed that the number of seeds that germinates is at least the integer of this value. The remainder is compared against a random number to decide whether one additional seedling will be created. For example, if there are 5.5 seeds in the grid square and the probability of germination is 0.5, then 2.75 seedlings are expected. In 25 percent of the cases, this will result in two seedlings and in 75 percent, three seedlings will be created.

If seedlings are created in a specific year for a specific functional group in a specific grid square then a new juvenile cohort is created and its properties are assigned. The most important properties are the number of seedlings in the cohort (*i.e.* the number calculated as described above), the functional group, the distribution over utility groups, its DBH (which is set to 0 initially) and its height. The initial height after creation is represented by the parameter H_{init}. Seedlings do not grow or die in the year they are created.

2.6 Juvenile and tree allometry

Allometric relations are used in SYMFOR to calculate height and crown dimensions from the diameter of an individual or, in case of seedlings (< 2cm DBH), DBH from height.

The height of an individual, H, is calculated from its DBH, D, using the asymptotic relation:

$$H = h_2 \cdot \left[1 - \exp\left(-h_0 \cdot D^{h_1}\right)\right] \tag{4}$$

h_0 and h_1 determine the shape of the curve and h_2 is the asymptotic height. The reverse of this equation, with the same parameter values, is used to calculate the DBH from height for seedlings. The height is always given in metres, while the DBH is always given in centimetres.

The crown point of a tree is defined as the height at which the tree's crown is widest. Crowns are assumed to be ellipsoids meaning that the crown point will be located halfway up the crown. The crown point, C_{P}, is obtained using a linear relation with height:

$$C_{\mathrm{P}} = cp_0 \cdot H \tag{5}$$

cp_0 is a parameter obtained by regression. Both the crown point and the height are expressed in metres.

A tree's crown radius, C_{R} in metres, is given by:

$$C_{\mathrm{R}} = \left(\frac{cr_0}{D} + \frac{1}{cr_1} \right)^{cr_2} \tag{6}$$

D is again the diameter of the tree in centimetres and cr_0, cr_1 and cr_2 are parameters obtained by regression.

2.7 Competition index for juveniles and trees

The competition index is an important aspect of the growth and mortality models of trees and juvenile cohorts. This index reflects the degree of competition for light and other resources that an individual experiences from taller individuals. A high competition index indicates that an individual has limited access to resources. The competition index C_D consists of two parts. The first part, $C_{D(G)}$, describes the competition an individual receives from overtopping large trees (≥ 20cm DBH) within 15m of the focal object (*i.e.* individual or cohort). This part is similar to the canopy closure index G as described by Lieberman *et al.* (1995). Given T overtopping trees ≥ 20cm DBH and within 15m of the focal object the first part of the competition index is calculated with:

$$C_{D(G)} = \sum_{j=1}^{T} \left(\frac{H_j - H_f}{r_{fj}} \right) \tag{7}$$

In this equation, H_f and H_j are the heights in metres of the focal object and the j^{th} overtopping tree, respectively, and r_{fj} is the distance in metres between the treetop of the focal object and the top of the tree j. Since the exact position of individuals < 20cm DBH was not measured in the field, their position is assumed to be the centre of the grid square they are in.

The second part, $C_{D(O)}$, describes the competition received from individuals < 20cm DBH in the same grid square as the focal object that are larger than the focal object. This part is only calculated for individuals with a DBH of less than 20cm. Since the position of these individuals within a grid square is not known $C_{D(O)}$ is simply the sum of the height differences, or in formula:

$$C_{D(O)} = \frac{25}{A_q} \cdot \sum_{j=1}^{T} \left(H_j - H_f \right) \tag{8}$$

Here T is the number of overtopping individuals < 20cm DBH within the same grid square q as the focal object f. H_f and H_j are again the heights in metres of the focal object and the j^{th} overtopping individual and A_q is the area of grid square q in square metres. To remove the effect of grid square size $C_{D(O)}$ is standardized for grid squares of 25m^2. The two components of the competition index are combined using:

$$C_D = C_{D(G)} + C_{D(O)} \tag{9}$$

The competition index is made diameter independent for use in the growth model for saplings and trees. To this end a Weibull probability density function was fitted through C_D against diameter to obtain a relation for the average competition index $\hat{C}_D$ as a function of diameter. This relation is given by:

$$\hat{C}_D = cd_0 \cdot \frac{cd_1 \cdot D^{(cd_1 - 1)}}{cd_2^{\,cd_1}} \cdot \exp\left[-\left(\frac{D}{cd_2} \right)^2 \right] \tag{10}$$

The diameter independent competition index C for an individual is then obtained by subtracting the average from the absolute competition index:

$$C = C_D - \hat{C}_D \tag{11}$$

A value for C of zero indicates that the individual experiences average competition for its diameter. A positive value indicates above-average competition and a negative value below-average competition. The competition index is not decoupled from height for seedlings < 2cm DBH since the growth model for these individuals does not explicitly include height (Arets 2005).

2.8 Cohort processes

After the new cohorts in a grid square are created, SYMFOR loops over all cohorts created during previous years for each of the functional groups and calculates their growth and mortality. The growth and mortality models work with two seedling size classes: seedlings with a DBH of less than 2cm and saplings with a DBH of at least 2cm but less than 5cm. The main difference between these size classes is that the former grows in height while the latter grows in diameter. This is a consequence of the data collection. Small seedlings do not have a DBH yet, while for saplings the height cannot be measured sufficiently accurately to obtain correct height increments. The sapling cohorts ≥ 2cm DBH use the same growth and natural mortality models as individual trees.

Juvenile cohorts do not have a position within the grid square. If a position is required for calculations (for example for the competition index) then the centre of the grid square in which the cohort is located is taken as its position.

2.8.1 Cohort growth

All seedlings in a cohort grow at the same rate and consequently will always have the same height. Seedlings (DBH < 2cm DBH) grow in height using a stochastic growth model with autocorrelation following Arets (2005). First, the competition index for the cohort is calculated. The average height increment $\hat{I}_H$ is calculated as a function of competition index C_D using the equation:

$$\hat{I}_H = ih_0 \cdot \exp\left(-ih_1 \cdot C_D\right) \tag{12}$$

where id_0 and ih_1 are parameters obtained by regression. Then a random deviation z_{IH} from the average growth rate is drawn from a Gaussian distribution with $\hat{I}_H$ as the mean and σ_{IH} as the competition dependent standard deviation. σ_{IH} is given by:

$$\sigma_{\mathrm{IH}} = \sigma_0 \cdot \exp\left(-\sigma_1 \cdot C_D\right) \tag{13}$$

σ_0 and σ_1 are parameters obtained by regression. The actual height increment I_H of the cohort is then calculated with:

$$I_H = \hat{I}_H + z_{\mathrm{IH}} \cdot \sigma_{\mathrm{IH}} \tag{14}$$

To allow a differentiation between ‘slow’ and ‘fast’ growing cohorts, for example as a result of differences in soil fertility, autocorrelation in the deviation from the average growth rate is introduced. The first year a cohort grows the z_{IH} value is a random value drawn from the Gaussian distribution. In the following year, a new random value is drawn, but now the value is averaged with that of the previous year. The strength of the autocorrelation between years is determined by the weighting factor W_z. Since stem breakage is assumed not to be auto-correlated among years autocorrelation is not applied if the randomly drawn value for z_{IH} results in negative growth.

After the height increment is calculated the height of the individual is updated in SYMFOR and the DBH of the individuals in the cohort is derived using the reverse of the height-diameter relation given in section 2.6. If a cohort reaches a DBH of 2cm, it switches from height growth to DBH growth in the next year. Sapling cohorts use the same growth model as individual trees (see section 2.9.1).

2.8.2 Cohort mortality

SYMFOR uses two types of mortality. Individuals can be killed by falling trees and logging activities or they can die due to other causes, such as light deficit and infections. The former type of mortality will be referred to as ‘damage mortality’ and the latter type as ‘natural mortality’.

The proportion of area of the grid square, in which the focal cohort is located, that is damaged in the current year by fallen trees or logging activities is estimated by checking for N_{dp} points if they are in a damage area. These points are evenly spread over the grid square.

The proportion of the grid square that is damaged is then calculated by dividing the number of points in a damage area by N_{dp}. This proportion is multiplied with the number of seedlings in the cohort to obtain the number of seedlings that will die because of damage mortality. Since this multiplication can result in non-integer values, the non-integer part of the multiplication result is compared with a random number to decide whether an additional seedling will die. Finally, the number of seedlings in the cohort is updated by subtracting the number of killed seedlings from the current number. This method assumes that all seedlings that are in a damage area are killed. Damage areas for seedling mortality caused by falling trees have the exact shape of the tree in SYMFOR, *i.e.* the tree's silhouette, defined by the tree's DBH, height and crown dimensions (see section 2.6).

The models for natural mortality are identical for seedlings and saplings, but they use different parameters. The natural mortality of cohorts < 2cm DBH is simulated using a logistic survival model, which depends on the size-dependent competition index C_D. The annual probability of survival for seedlings, S, is calculated with:

$$S = \left(\frac{\exp\left(s_0 + s_1 \cdot C_D\right)}{1 + \exp\left(s_0 + s_1 \cdot C_D\right)} \right)^{\frac{1}{t_{\text{sdl}}}} \tag{15}$$

Herein s_0 and s_1 are parameters obtained by regression. t_{sdl} is the length of time interval in years during which the survival data were collected and converts the survival during that time interval to the annual survival probability. The new number of seedlings in the cohort is then calculated by multiplying the current number of seedlings with the survival probability S. The non-integer part of the multiplication is compared against a random number to decide if an additional seedling will survive. Cohorts with saplings use the same parameters as individual trees (section 2.9.2).

2.8.3 Tree creation

If a juvenile cohort reaches 5cm DBH, it is translated to individual trees in the same year the cohort reached the threshold. The number of trees that are created is equal to the number of seedlings left in the cohort. The characteristics of each of the trees, *i.e.* functional group, size and age, are equal to that of the cohort. The trees are created in the grid square of the cohort and the position within the grid square of each of the trees is chosen randomly. It is ensured that the random position does not overlap with an existing tree and is not in an area that is damaged by falling trees or logging activities during the life of the cohort. If no suitable position is found after 200 attempts, for example because a large part of the grid square has been damaged, then the tree will not be created. The utility group of a newly created tree is determined by comparing a random number with the cumulative proportion of individuals in each utility group for the cohort as determined during seed production and dispersal (see section 2.5.1).

2.9 Individual tree processes

Trees are all individuals equal to or larger than 5cm DBH. Trees are represented by separate objects in SYMFOR. Important tree characteristics are the functional and utility group, DBH and position within the plot (x and y coordinate). Each year the growth and mortality are calculated for each of the trees as described below. The processes are described in detail by Arets (2005).

2.9.1 Tree growth

The diameter increment of trees is modelled using an equation largely based on the Hossfeld IV equation. The diameter increment, I_D in centimetres, depends on the diameter D of the tree and its diameter independent competition index C and is calculated using the equation:

$$I_D = \frac{id_1 \cdot id_2 \cdot D^{(id_2 - 1)}}{\left(id_1 + \frac{D^{id_2}}{id_0} \right)^2} + id_3 \cdot C + id_4 \tag{16}$$

id_0 to id_4, are parameters obtained by regression. In SYMFOR the diameter is updated, *i.e.* the diameter and diameter increment are added only after the diameter increment of all trees is calculated.

2.9.2 Tree mortality

Like juvenile cohorts, trees can die due to damage inflicted by falling trees or logging activities (damage mortality) or due to causes such as light deficit (natural mortality). The damage mortality for trees is modelled slightly different from that for cohorts. For each tree, it is checked if it is in a damage area that was created this year. If so, it has a probability of P_{dmg} that it dies because of the damage inflicted. This probability is compared with a random number to decide if it will die. Trees that die of damage mortality never create any damage to the forest, *i.e.* they do not create new damage areas. For trees, the damage area created by a fallen tree has the shape of a kite, defined by the height, crown point and crown radius of the fallen tree.

The natural mortality of trees is modelled using the same logistic survival model as that described for the seedling cohorts. The annual survival probability, U, is given by:

$$U = \left(\frac{\exp(u_0 + u_1 \cdot C_D)}{1 + \exp(u_0 + u_1 \cdot C_D)} \right)^{\frac{1}{t_{\mathrm{sap}}}} \tag{17}$$

Here u_0 and u_1 are again parameters obtained by regression and t_{sap} is the length of census period in years. The calculated survival probability is compared against a random number to decide if it dies in that year.

If a tree dies in the natural mortality procedure, it has a chance of P_{fall} to fall over. This probability is compared against a random number to decide if it falls. If a tree falls down it will damage the surrounding vegetation, which is represented in SYMFOR by creating a new damage area defined by the dimensions of the tree. The shape of a damage area is a kite for trees and the tree's silhouette for cohorts, reflecting the observed damage in the field caused to the vegetation. The silhouette is slightly smaller than the kite. The direction in which the tree falls is chosen randomly.

2.10 Juvenile and pole initialization

Juveniles and poles are initialized at the start of a simulation since these individuals were inventoried in sub-samples only. This initialization takes place after the data for trees ≥ 20cm are read into memory and are translated to tree objects in SYMFOR.

First, the poles between 5 and 20cm DBH, are initialized. The number of poles that are created per hectare for each of the functional groups is given by the functional group specific parameter N_{pol}. For each of those poles the initial DBH is determined from the cumulative size distribution using:

$$D = \frac{-\ln\left[rnd \cdot \left(1 - \alpha_{\mathrm{pol}}\right) + \alpha_{\mathrm{pol}} \right]}{\mathit{\Delta}_{\mathrm{pol}}} + D_{\mathrm{low}} \tag{18}$$

where *rnd* is a random number, $\mathit{\Delta}_{\mathrm{pol}}$ is an estimated parameter that describes that cumulative size distribution for poles of that functional group and D_{low} is the lower DBH limit for trees, *i.e.* 5cm DBH. α_{pol} is the value of the fitted size distribution at the upper DBH limit for poles to be initialized D_{up}, *i.e.* 20cm DBH, and is given by:

$$\alpha_{\mathrm{pol}} = \exp\left[-\mathit{\Delta}_{\mathrm{pol}} \cdot \left(D_{\mathrm{up}} - D_{\mathrm{low}} \right) \right] \tag{19}$$

The utility group of the newly created pole is determined by drawing a random number, which is compared against the distribution over the utility groups as observed in the field for the functional group to which the tree belongs. In principle, the position of the tree within the plot is chosen randomly. However, if the chosen position overlaps with another tree a new random position is picked. To prevent the placement of shade-intolerant poles at dark locations an additional verification of the position is performed. For this verification, the competition index of the tree is calculated at its current position. If this competition index is higher than a threshold value, $C_{D(\mathrm{pol})}$, then a new random position is chosen. The average competition index will increase during the initialization process. Therefore, it was decided to start with the most shade-tolerant and end with the most shade-intolerant species, for which $C_{D(\mathrm{pol})}$ is lowest, to get the best distribution of functional groups with respect to the competition index. If no suitable position was found after 10 attempts, the tree was removed again.

Juvenile cohorts (< 5cm DBH) are initialized using a similar procedure. For each of the functional groups the number of seedlings that will be created per hectare is given by N_{juv}. During simulations, cohorts can contain more than one seedling. During the initialization procedure, however, this is not possible as the initialized heights are continuous and cohorts always consist of only one seedling. For each seedling that is created a height is chosen from the cumulative size distribution for that functional group with:

$$H = \frac{-\ln\left[rnd \cdot \left(1-\alpha_{\mathrm{juv}}\right) + \alpha_{\mathrm{juv}} \right]}{\mathit{\Delta}_{\mathrm{juv}}} + H_{\mathrm{init}} \tag{20}$$

In this equation, *rnd* is a random number, $\mathit{\Delta}_{\mathrm{juv}}$ is a parameter that describes that cumulative size distribution for seedlings and H_{init} is the minimum height of this functional group in SYMFOR, *i.e.* the height seedlings get assigned after germination. α_{juv} is the value of the equation that was fitted through the size distribution for seedlings of this functional group at the maximum height H_{up}, *i.e.* the height of a tree of 5cm DBH. H_{up} is calculated using the allometric height-diameter relation described in section 2.6. α_{juv} is defined as:

$$\alpha_{\mathrm{juv}} = \exp\left[-\mathit{\Delta}_{\mathrm{juv}} \cdot \left(H_{\mathrm{up}} - H_{\mathrm{init}} \right) \right] \tag{21}$$

If possible, the height of the seedling is used to calculate its DBH. Rather than assigning a utility group at initialization, a cohort is assigned an array with the proportions in each utility group as they were observed in the field. The final decision on the utility group membership of the individual is made when a cohort reaches 5cm DBH and is translated to a tree. Since cohorts do not have an exact position, they are placed in a randomly chosen grid square. The competition index for the seedling in the assigned grid square is calculated and compared with a threshold competition index, $C_{D(\mathrm{sdl})}$ for cohorts < 2cm DBH and $C_{D(\mathrm{sap})}$ for cohorts between 2 and 5cm DBH. If the competition index is above this threshold value, a new grid square is chosen. If no suitable grid square is found after 10 attempts, the cohort is deleted again. Like for the trees, the most shade-tolerant functional groups are initialized first and the least shade-tolerant groups last.

3 Data and parameter estimation

The data used to calibrate the functions in SYMFOR were collected at several locations in the tropical rain forest south of Mabura Hill, central Guyana, in the timber concession of Demerara Timbers Ltd. (DTL). The average daily temperature is 25.9°C and the area receives 2772mm rainfall annually (van Dam 2001). The data collection and the estimation of parameters from those data are described below. For some of the models additional data were collected from literature. Since the field data collection is described in detail in other chapters and in Arets (2005), descriptions are kept to a minimum here. The functional group specific parameters are given in separate tables. An overview of all parameters, their units and their values, if they are not functional group specific, is given in appendix A. The values given in the tables and appendix are in some cases adjusted as described in the Model tuning section (section 4).

3.1 Species groups

3.1.1 Functional groups

To enable an efficient data collection and to ensure data were collected for each functional group, species were classified *a priori* using morphological characteristics, rather than *a posteriori* based on actual species behaviour (*i.e.* growth, mortality and recruitment). The selected characteristics were available from literature and were considered effective proxies for species behaviour. These were wood density, seed mass, adult stature and seed dispersal type. Wood density is related to the maximum growth rate of a species (Arets *et al.* 2003). Seed mass is correlated with a number of regeneration processes, such as germination, seed dispersal and production, and initial seedlings size and survival (chapters 2 and 3, Armstrong and Westoby 1993, Augspurger and Franson 1987, Dalling and Hubbell 2002, Rose and Poorter 2003). Adult stature is a good predictor of the size at which a species starts reproducing (chapter 2) and may influence the amount of light a species receives at maturity. Finally, seed dispersal type influences the spatial distribution of seeds and the distance seeds travel (Willson 1993). The main sources from which data on these characteristics were extracted are Hammond and Brown (1995) and ter Steege (2000). Additional information was collected from Arets (unpublished data), CTFT (1989), Fanshawe (1961), Favrichon (1994), Gérard *et al.* (1996) and van Roosmalen (1985).

Adult stature was used to divide species into three groups: subcanopy, canopy and emergent species. Species were further classified by distinguishing between wind- and non-wind-dispersed species. This latter dispersal type was not further subdivided, both to reduce the number of functional groups and since proof of consistent differences between dispersal types is lacking. For wood density and seed mass no biologically meaningful groups could be distinguished. Therefore, these characteristics were used in a K-means cluster analysis in SPSS 8.0 for Windows. A clustering into three groups seemed to represent the original data best: a cluster of species with low wood densities and low seed masses, a cluster of species with low wood densities and high seed masses, and a cluster of species with high wood densities and high seed masses. Combining the four characteristics resulted in 18 functional groups. Three functional groups, all subcanopy groups with wind dispersal, contained no species, which left 15 groups (table 1). Henceforth the genus name of one important species in the group will be used to refer to the functional groups (table 1). The members of the functional groups and their characteristics are listed in appendix B.

3.1.2 Utility groups

The utility groups were defined using a list with species currently being harvested in Guyana and Appendix A in van der Hout (1999). The three most important timber species, *Chlorocardium rodiei*, *Peltogyne venosa* and *Catostemma fragrans*, were each put in a separate group. The fourth group contained five species, *Carapa guianensis*, *Goupia glabra*, *Hymenaea courbaril*, *Mora excelsa* and *Pouteria speciosa*, which are logged commercially at lower frequencies. Groups 5, 6 and 7 were defined as currently marketable species (minus

Table 1. The classification into functional groups, with the name that will be used to refer to each group, one or two important representatives of the group, the characteristics and the approximate number of species in the group (*n*). WD: wood density (low: < 0.8, high $\geq 0.8\text{g}\cdot\text{cm}^{-3}$), SM: seed mass (low: < 0.1, high ≥ 0.1g), AS: adult stature (S: subcanopy – maximum tree height (H_m) < 25m, C: canopy - 25m $\leq H_m < 35$m, E: emergent - $H_m \geq 35$m), DT: dispersal type (w: wind, nw: non-wind). Since the last two groups are both called *Aspidosperma*, the adult stature group was added to the name.

Name	Example species	WD	SM	AS	DT	*n*
Cecropia	*Cecropia spp., Miconia spp.*	low	low	S	nw	16
Simarouba	*Simarouba amara, Vismia macrophylla*	low	low	C	nw	4
Goupia	*Goupia glabra*	low	low	E	nw	6
-	-	low	low	S	w	0
Jacaranda	*Jacaranda copaia, Vochysia surinamensis*	low	low	C	w	2
Lueheopsis	*Lueheopsis rugosa*	low	low	E	w	1
Paypayrola	*Paypayrola spp., Unonopsis glaucopetala*	low	high	S	nw	17
Carapa	*Carapa guianensis, Catostemma fragrans*	low	high	C	nw	33
Virola	*Swartzia jenmanii, Virola spp.*	low	high	E	nw	20
-	-	low	high	S	w	0
Tachigali	*Tabebuia insignis, Tachigali rusbyi*	low	high	C	w	4
Sclerolobium	*Couratari guianensis, Sclerolobium guianense*	low	high	E	w	7
Oxandra	*Duguetia neglecta, Oxandra asbeckii*	high	high	S	nw	33
Chlorocardium	*Chlorocardium rodiei, Eschweilera sagotiana*	high	high	C	nw	59
Peltogyne	*Parinari campestris, Peltogyne venosa*	high	high	E	nw	18
-	-	high	high	S	w	0
Aspidosperma C	*Aspidosperma album, Tabebuia serratifolia*	high	high	C	w	4
Aspidosperma E	*Aspidosperma exselsum, Diplotropis purpurea*	high	high	E	w	3

those in the previous groups), potentially marketable species and commercially non-desirable species, respectively.

3.2 Juvenile cohort creation

3.2.1 Seed production and dispersal

Observations on the flowering and fruiting of trees in the Mabura Hill area revealed that the minimum reproductive DBH, *MRD*, was correlated with adult stature (chapter 2). Using the 10th percentile of the observed size distributions of the flowering and fruiting trees the *MRD* was set at 5, 15 and 23.4cm DBH for subcanopy, canopy and emergent functional groups, respectively.

Data for seed production and dispersal were collected in two plots of nine hectares each. One of these plots was located in the Mabura Hill Forest Reserve, which has never been logged commercially, and one in the East Pibiri compartment, which was logged approximately two years before the initial measurements (chapter 2). In these plots, all potential parent trees were identified and mapped and the seeds were counted in sample quadrates ($n = 1694$ in the undisturbed plot, 498 in the logged plot) twice after the initial measurement, covering a period of six months. Additional data were collected around isolated trees in the same area. It was attempted to collect seed production and dispersal data for one species per functional group and for two species for the most dominant functional groups. However, for several functional groups no or insufficient data were collected, especially for the small-seeded

Table 2. The seed production and dispersal parameters for each of the functional groups. † *SSP* and ρ were taken from another functional group; ‡ *SSP* and ρ were derived from literature. All abbreviations are summarized in appendix A.

	Seed dispersal and production					
Functional group	*SSP*	ρ	*MRD*	D_{ref}	sd_0	sd_1
Cecropia‡	246135	5.63	5.0	12.7	1.5517	0.0574
Simarouba†	246135	5.63	15.0	50.7	1.1320	0.0620
Goupia†	246135	5.63	23.4	55.5	1.8374	0.0640
Jacaranda‡	12065	14.70	15.0	27.0	1.1320	0.0620
Lueheopsis†	12065	14.70	23.4	36.0	1.8374	0.0640
Paypayrola†	24	2.72	5.0	10.6	1.5517	0.0574
Carapa	24	2.72	15.0	26.3	1.1320	0.0620
Virola†	24	2.72	23.4	42.5	1.8374	0.0640
Tachigali†	19660	12.27	15.0	33.4	1.1320	0.0620
Sclerolobium	19660	12.27	23.4	38.7	1.8374	0.0640
Oxandra	30	8.65	5.0	11.0	1.6286	0.0724
Chlorocardium	86	5.31	15.0	36.6	1.7602	0.0662
Peltogyne	4574	1.67	23.4	46.5	0.9976	0.0787
Aspidosperma C†	86	12.27	15.0	36.1	1.7602	0.0662
Aspidosperma E†	86	12.27	23.4	53.8	0.9976	0.0787

species with light wood, which are rare in Guyana (Arets *et al.* 2003, Hammond and Brown 1995). In the same sample quadrates, the ingrowth of seedlings was monitored for all species during one year in the logged and one-and-a-half years in the undisturbed plot.

Initially, the reference DBH, D_{ref}, was set to the overall average DBH of parent trees in the two nine-hectare plots: 25.6cm. The seed production and dispersal parameters, *SSP* and ρ, were estimated from the seed numbers in the quadrates in the two nine-hectare plots and around isolated trees using 'inverse modelling' (chapter 2, Clark *et al.* 1999, Dalling *et al.* 2002, Ribbens *et al.* 1994). In this process, the parameters were adjusted repeatedly until the best correlation was obtained between observed and expected seed numbers for each species separately. In principle, the parameters for a functional group were set to those of the representative species as estimated in chapter 2. If the parameters were available for two species belonging to the same functional group then the values were averaged. For functional groups for which the parameters could not be estimated due to a lack of data the parameters from other functional groups were used. *SSP* was taken from a group with similar wood density and seed mass and ρ was taken from a group with the same dispersal type. The parameters for the small-seeded species *Cecropia* were estimated from the data available in Alvarez-Buylla and Martínez Ramos (1990). The parameters for *Jacaranda* were estimated from the equation given in Dalling *et al.* (2002).

The linear relation between crown radius and DBH was estimated from unpublished data collected by Arets (see section 3.3). It was expected that allometry is mainly influenced by wood density and tree height and less by seed mass and dispersal type. Therefore, functional groups with similar wood density and adult stature were clustered to ensure that the

Table 3. The functional group specific parameters for the seed germination and establishment model. † germination parameters (g_0, g_1 and g_2) were taken from another functional group.

	Germination				Establishment	
Functional group	g_0	g_1	g_2	H_{init}	e_0	e_1
Cecropia	0	$5.39\cdot10^{-3}$	$-5.51\cdot10^{-5}$	0.05	0	$1.0\cdot10^{-3}$
Simarouba†	0	$6.10\cdot10^{-3}$	$-6.60\cdot10^{-5}$	0.06	0	$5.4\cdot10^{-4}$
Goupia	0	$6.78\cdot10^{-3}$	$-7.76\cdot10^{-5}$	0.03	0	$4.8\cdot10^{-4}$
Jacaranda	0	$2.22\cdot10^{-2}$	$-2.30\cdot10^{-4}$	0.05	0	$4.5\cdot10^{-4}$
Lueheopsis†	0	$2.22\cdot10^{-2}$	$-2.30\cdot10^{-4}$	0.04	0	$4.5\cdot10^{-4}$
Paypayrola†	1.5761	$-3.00\cdot10^{-2}$	$2.12\cdot10^{-4}$	0.12	0.12	0
Carapa	1.5761	$-3.00\cdot10^{-2}$	$2.12\cdot10^{-4}$	0.29	0.78	0
Virola†	1.5761	$-3.00\cdot10^{-2}$	$2.12\cdot10^{-4}$	0.27	0.21	0
Tachigali†	0	$1.12\cdot10^{-2}$	$-1.00\cdot10^{-4}$	0.11	0.04	0
Sclerolobium	0	$1.12\cdot10^{-2}$	$-1.00\cdot10^{-4}$	0.17	0.14	0
Oxandra	0.6295	$-1.89\cdot10^{-2}$	$1.45\cdot10^{-4}$	0.18	0.35	0
Chlorocardium	1.2305	$-2.87\cdot10^{-2}$	$2.09\cdot10^{-4}$	0.28	0.15	0
Peltogyne	0	$5.70\cdot10^{-3}$	$-6.15\cdot10^{-5}$	0.26	0.42	0
Aspidosperma C†	0.8845	$-2.18\cdot10^{-2}$	$1.50\cdot10^{-4}$	0.19	1.00	0
Aspidosperma E	0.8845	$-2.18\cdot10^{-2}$	$1.50\cdot10^{-4}$	0.11	0.01	0

parameters could be estimated accurately. The functional group specific parameters are summarized in table 2, including the adjustments described under Model tuning (section 4).

3.2.2 Seed germination

To relate light availability to the surrounding vegetation the vegetation cover was determined at one metre height in the sample quadrates in the nine-hectare plots described above. The vegetation cover was estimated using a densiometer (Model C (Concave), Robert E. Lemmon, Forest Densiometers, Bartlesville, OK, USA), which is a good predictor of canopy openness (chapter 4). In the plots, all trees larger than 15cm were mapped. For several subcanopy species, all trees larger than 5cm were mapped. The distances from each of the quadrates to all known trees were calculated. Several measures, radii and equations were tested to find the model that best predicted the densiometer value based on the surrounding vegetation. This was the inverse relation given in equation 1 using the sum of the basal area divided by the distance of all trees within a radius of 13.5m (n = 2191, F = 1009.58, R^2 = 0.316, $p < 0.001$).

Germination data were collected in the East Pibiri compartment of the DTL concession. In two understorey sites and eight logging gaps, differing in canopy openness, seeds were laid to germinate for several months. In principle, one common species per functional group was selected. For very abundant functional groups two species were selected. Not for all functional groups could sufficient seeds be found during the experiment. Germination was monitored every two weeks and at the end of the experiment the proportion of germination per species in each of the sites was calculated (chapter 3). For *Cecropia* one site was discarded from the analysis since seeds possibly had entered this site from surrounding vegetation. The parameters in equation 2 were estimated for each of the species using the proportion of germination and the densiometer value in each of the sites. These parameters were taken as the parameters for the functional group to which the species belonged. If germination was known for two species belonging to the same functional group, the parameters for the individual species were averaged. Functional groups for which insufficient seeds were found were assigned parameters from functional groups with the same wood density, seed mass and dispersal type (table 3).

No data were available on the initial height after germination, H_{init}. Therefore, data from Rose and Poorter (2003) were used to fit a relation between H_{init} and seed mass. Subsequently, a value for H_{init} was calculated per functional group from this relation using the average seed mass for each functional group (table 3).

3.3 Cohort and tree data collection

The remaining data, *i.e.* those used for model initialization, growth, mortality and tree allometry, were collected in the experimental Pibiri plots in the West Pibiri compartment of the timber concession. The 15 Pibiri plots were established in 1993 following a randomized block design of three blocks with five reduced impact logging (RIL) treatments each (van der Hout 2000, van der Hout 1999). Each plot covers 1.96 hectares (140 · 140m). In 1994 the plots were logged, applying each of following treatments to one plot per block: low intensity reduced impact logging (4 trees ha^{-1}), moderate intensity (8 trees ha^{-1}), high intensity (16 trees ha^{-1}), moderate intensity succeeded by a silvicultural post-harvest treatment and a control without intervention. The individuals in the plots were re-measured in 1995, 1997 and 2000. Trees of 20cm DBH and larger were measured in the entire plot, poles (between 5 and 20cm DBH) were measured in 25 subplots of 10 · 10m per plot, saplings (between 2 and 5cm DBH) in 25 subplots of 5 · 5m per plot and seedlings (between 30cm height and 2cm DBH) in 25 subplots of 2 · 2m per plot. For the large trees, the DBH and position of the trees were measured. For the smaller individuals, the position within the subplot was not determined. For poles the DBH was measured and for saplings and seedlings both the height and, if possible, the DBH were measured. The smallest individuals, between 30 and 150cm height, were measured for the first time in 1995.

Groups with different dispersal types were clustered under the assumption that dispersal type would not influence growth rate strongly. These clusters of functional groups will be referred to as GM (growth and mortality) clusters. In total, there are nine of these GM clusters. Despite this clustering insufficient data were collected for the small-seeded species with low wood density (the first five groups in table 1) to calibrate the growth and mortality models for each of the GM clusters separately. Therefore, these three clusters were all combined and have the same parameters for the height and diameter increment growth models and for the mortality of seedling cohorts (< 2cm DBH). For the mortality of sapling cohorts (≥ 2cm DBH) and trees (≥ 5cm DBH) only two GM clusters were combined, representing the subcanopy and canopy species with small seeds and low wood density.

Table 4. The allometry parameters for each of the functional groups. Note that groups with the same wood density and adult stature have the same parameters.

	Height-diameter relation			Crown radius		
Functional group	h_0	h_1	h_2	cr_0	cr_1	cr_2
Cecropia	0.053	1.08	33.3	2.11	$3.44 \cdot 10^7$	-0.45
Simarouba	0.053	1.03	38.5	3.61	$1.64 \cdot 10^5$	-0.51
Goupia	0.062	0.86	46.5	6.45	$2.76 \cdot 10^5$	-0.84
Jacaranda	0.053	1.03	38.5	3.61	$1.64 \cdot 10^5$	-0.51
Lueheopsis	0.062	0.86	46.5	6.45	$2.76 \cdot 10^5$	-0.84
Paypayrola	0.053	1.08	33.3	2.11	$3.44 \cdot 10^7$	-0.45
Carapa	0.053	1.03	38.5	3.61	$1.64 \cdot 10^5$	-0.51
Virola	0.062	0.86	46.5	6.45	$2.76 \cdot 10^5$	-0.84
Tachigali	0.053	1.03	38.5	3.61	$1.64 \cdot 10^5$	-0.51
Sclerolobium	0.062	0.86	46.5	6.45	$2.76 \cdot 10^5$	-0.84
Oxandra	0.064	1.02	32.1	1.86	$4.40 \cdot 10^0$	-1.00
Chlorocardium	0.058	0.91	42.3	2.36	$1.29 \cdot 10^5$	-0.52
Peltogyne	0.069	0.77	51.6	7.23	$2.54 \cdot 10^5$	-0.88
Aspidosperma C	0.058	0.91	42.3	2.36	$1.29 \cdot 10^5$	-0.52
Aspidosperma E	0.069	0.77	51.6	7.23	$2.54 \cdot 10^5$	-0.88

3.4 Allometry

In 2000 detailed allometry data were collected in the Pibiri plots for a sub-sample of individuals of all sizes. For 5642 individuals ranging from 1.3 to 58.3m tall the total tree height and the height to the lowest leaf was measured. The crown radii were measured in four directions for 3629 individuals. For the estimation of the allometry parameters functional groups with similar wood density and adult stature were clustered. Subsequently the parameters for the height-diameter relation, crown point and crown radius were estimated for each of these clustered functional groups. Since the crown point parameter hardly differed between the allometry clusters it was decided to make this parameter equal for all functional groups. The value for this parameter is 0.8. The functional group specific parameters are shown in table 4.

3.5 Competition index

The size-dependent competition indices used for the calibration of growth and mortality were calculated from the data as described in section 2.7. Rather than using the actual height of individuals, the height was calculated using the allometric relations described in section 2.6 since not for all individuals the height was measured in the field. A Weibull probability density function (equation 10) was fitted through the data to obtain a relation for the average competition index, $\hat{C}_D$, as a function of diameter. $\hat{C}_D$ is not functional group specific but an average of all groups combined. The parameters cd_0, cd_1 and cd_2 were obtained by regression and were 497.17, 0.69 and 10.08, respectively.

3.6 Cohort processes

The calibration of the growth and mortality models was done separately for individuals < 2cm DBH and those ≥ 2cm DBH. The calibration of the former size group is discussed in

Table 5. The parameters for the height growth and survival models for seedling cohorts (< 2cm DBH) for each of the functional groups. Note that the first five groups all have the same parameters and that dispersal type does not influence growth and survival.

	Average		Standard deviation			Survival	
Functional group	ih_0	ih_1	σ_0	σ_1	W_z	s_0	s_1
Cecropia	0.8828	0.0088	0.7293	0.0077	0.5	1.7200	-0.0161
Simarouba	0.8828	0.0088	0.7293	0.0077	0.5	1.7200	-0.0161
Goupia	0.8828	0.0088	0.7293	0.0077	0.5	1.7200	-0.0161
Jacaranda	0.8828	0.0088	0.7293	0.0077	0.5	1.7200	-0.0161
Lueheopsis	0.8828	0.0088	0.7293	0.0077	0.5	1.7200	-0.0161
Paypayrola	0.0591	0.0007	0.3199	0.0151	2.0	2.8390	-0.0113
Carapa	0.2471	0.0142	0.4050	0.0173	1.0	1.2882	-0.0091
Virola	1.0882	0.0334	0.8009	0.0227	0.5	1.6971	-0.0162
Tachigali	0.2471	0.0142	0.4050	0.0173	1.0	1.2882	-0.0091
Sclerolobium	1.0882	0.0334	0.8009	0.0227	0.5	1.6971	-0.0162
Oxandra	0.0991	0.0092	0.2782	0.0134	3.0	2.4036	-0.0076
Chlorocardium	0.0699	0.0026	0.2644	0.0119	2.0	1.8194	-0.0118
Peltogyne	0.1625	0.0105	0.4937	0.0181	1.0	2.4395	-0.0158
Aspidosperma C	0.0699	0.0026	0.2644	0.0119	2.0	1.8194	-0.0118
Aspidosperma E	0.1625	0.0105	0.4937	0.0181	1.0	2.4395	-0.0158

this section. The calibration of the models for the larger individuals is described in section 3.7.

3.6.1 Cohort growth

The annual height growth rate was calculated for all seedlings < 2cm DBH, *i.e.* those individuals for which the height growth was monitored. For each of the GM clusters equation 12 was fitted through the data to obtain the average growth rate as a function of competition index. Subsequently the absolute deviation from the average growth rate as given by equation 12 was calculated and equation 13 was fitted through these deviations to obtain the competition index dependent standard deviation. The degree of autocorrelation in the data was determined by calculating the correlation between the growth rate in the first and the second monitoring interval. Individuals with negative growth during one or both intervals were discarded from the autocorrelation analysis. The autocorrelation weighting factor, W_Z, was set at 0.5, 1, 2 or 3 in test runs in SYMFOR and the corresponding autocorrelation in SYMFOR was calculated for each GM cluster. The value of W_Z that resulted in the best correspondence between the observed and simulated autocorrelation was chosen as the final value for that GM cluster. The estimated parameters are given in table 5.

3.6.2 Cohort mortality

Only individuals that were enumerated during the first census in 1995 were used to calibrate the survival model for seedlings < 2cm DBH. The time interval parameter, t_{sdl}, was set to 5.02 years. The parameters in the logistic survival model (equation 15) were estimated using information on the survival of these individuals until the last census (in 2000) in relation to their competition index in 1995. Due to a very limited number of observations for the groups

Table 6. The functional group specific parameters for the diameter increment model for sapling cohorts (≥ 2cm DBH) and individual trees (≥ 5cm DBH). Note that dispersal type does not influence growth and that the small-seeded species with light wood all use the same parameters.

	Growth				
Functional group	id_0	id_1	id_2	id_3	id_4
Cecropia	11.230	460.060	2.680	-0.0049	0.1217
Simarouba	11.230	460.060	2.680	-0.0049	0.1217
Goupia	11.230	460.060	2.680	-0.0049	0.1217
Jacaranda	11.230	460.060	2.680	-0.0049	0.1217
Lueheopsis	11.230	460.060	2.680	-0.0049	0.1217
Paypayrola	9.658	1206948.000	4.606	-0.0019	0.0628
Carapa	67.375	45.826	1.631	-0.0090	0.0252
Virola	18.115	41279.960	3.581	-0.0063	0.1012
Tachigali	67.375	45.826	1.631	-0.0090	0.0252
Sclerolobium	18.115	41279.960	3.581	-0.0063	0.1012
Oxandra	-0.369	-58.170	2.290	-0.0036	0.1317
Chlorocardium	60.473	12.623	1.381	-0.0057	-0.0940
Peltogyne	1043197.000	0.419	1.036	-0.0032	-2.5167
Aspidosperma C	60.473	12.623	1.381	-0.0057	-0.0940
Aspidosperma E	1043197.000	0.419	1.036	-0.0032	-2.5167

with small seeds and light wood it was assumed that their survival was close to 1 (0.97) in the absence of competition. Seedlings that had obviously died due to falling trees or branches were omitted from the analysis, since this ‘damage mortality’ is modelled explicitly in SYMFOR. The parameter values are given in table 5.

3.7 Individual tree processes

3.7.1 Tree growth

For all individuals ≥ 2cm DBH the annual diameter increment and the diameter independent competition index were calculated. From these data, the parameters of the growth model (equation 16) were calibrated for each of the GM clusters using a non-linear regression analysis (table 6).

3.7.2 Tree mortality

The survival of individuals ≥ 2cm DBH was determined for the periods 1993 to 1997 and 1997 to 2000. The time interval, t_{sap}, between the censuses was approximately the same for both periods and was 3.5 years. Individuals that had died due to branch- or tree-fall or, in the RIL plots, as a result of the logging activities were discarded from the analysis, since these types of mortality are modelled explicitly in SYMFOR. Using each of the observations the logistic survival model was calibrated as a function of the competition index (equation 17) for each of the GM clusters (table 7).

The probability that a tree that has died falls over (P_{fall}) and the probability that a tree dies when it is damaged by a falling tree (P_{dmg}) could only be estimated roughly due to limited data on these rare events. They were estimated at 0.3 and 0.08, respectively.

Table 7. The estimated parameters used in the logistic survival model for sapling cohorts (≥ 2cm DBH) and individual trees (≥ 5cm DBH). Dispersal type is assumed not to influence survival.

Functional group	Survival			
	u_0	u_1	$D_{95\%}$	$D_{100\%}$
Cecropia	3.087	-0.061	28.0	29.0
Simarouba	3.087	-0.061	45.0	47.0
Goupia	2.639	0.000	67.0	87.0
Jacaranda	3.087	-0.061	37.0	37.0
Lueheopsis	2.639	0.000	67.0	87.0
Paypayrola	2.835	0.000	28.0	41.0
Carapa	3.241	-0.023	40.0	63.0
Virola	3.326	0.000	95.0	129.0
Tachigali	3.241	-0.023	70.0	70.0
Sclerolobium	3.326	0.000	74.0	75.0
Oxandra	3.390	0.000	23.0	43.0
Chlorocardium	3.701	-0.013	56.0	103.0
Peltogyne	4.019	-0.045	69.0	111.0
Aspidosperma C	3.701	-0.013	31.0	57.0
Aspidosperma E	4.019	-0.045	69.0	78.0

3.8 Juvenile and pole initialization

Initial data for poles, *i.e.* trees between 5 and 20cm DBH, were generated using equation 18, which is the inverse of the exponential probability distribution of DBH. This distribution gives for each DBH between 5 and 20cm the probability P_D that the DBH of a tree is equal to or larger than the specified DBH and is given by:

$$P_D = \exp\left[-\Delta_{\text{pol}} \cdot \left(D - D_{\text{low}}\right)\right] \tag{22}$$

where Δ_{pol} is a parameter that is estimated by regression, D is a DBH larger or equal to 5cm and smaller than 20cm and D_{low} is the lower DBH limit, *i.e.* 5cm in this study. The probability P_D has a value of one if $D = D_{\text{low}}$.

Equation 22 was calibrated using the frequency distribution over 15 DBH classes of 1cm for each functional group using the data from the 1995 census of the three control plots. Subsequently the inverse cumulative fraction (decreasing from 1 to 0) in each size class was calculated. These fractions were used to estimate Δ_{pol}. The total number of poles that is initialized per hectare, N_{pol}, was calculated for each functional group using the data of the control plots in 1995. Because the poles were inventoried in a sub-sample of the area, *i.e.* 0.25ha per plot, the numbers in the three control plots were summed and divided by the total area, *i.e.* 0.75ha. The parameters are given in table 8.

The initialization of juveniles, *i.e.* individuals between initial height after germination, H_{init}, and 5cm DBH, was calibrated using the same approach. The inverse cumulative probability distribution (equation 23) gives for each height H between H_{init} and the height of a tree of 5cm DBH, H_{up}, the probability P_H that the height of a tree is equal to or larger than the specified height.

Table 8. The parameters that are used to initialize the poles and juvenile cohorts at the start of each simulation.

	Initialization of poles			Initialization of cohorts			
Functional group	N_{pol}	Δ_{pol}	$C_{D(\text{pol})}$	N_{juv}	Δ_{juv}	$C_{D(\text{sdl})}$	$C_{D(\text{sap})}$
Cecropia	5	0.5788	21.87	73	0.3604	149.66	39.84
Simarouba	0	1.0000	21.87	0	1.0000	149.66	39.84
Goupia	12	0.3094	21.63	11	0.0816	149.66	36.54
Jacaranda	0	1.0000	21.87	0	1.0000	149.66	39.84
Lueheopsis	0	1.0000	21.87	0	1.0000	149.66	39.84
Paypayrola	55	0.2678	34.37	2621	0.4068	186.67	65.45
Carapa	189	0.2600	31.13	3716	0.7816	201.17	58.45
Virola	19	0.2342	32.83	218	0.7692	166.48	48.26
Tachigali	1	0.3849	31.13	117	0.6600	201.17	58.45
Sclerolobium	1	0.6446	32.83	0	1.0000	166.48	48.26
Oxandra	253	0.3439	32.47	5762	0.5583	189.24	60.43
Chlorocardium	249	0.1917	32.10	11202	1.0554	221.56	55.68
Peltogyne	28	0.2206	29.93	444	0.8112	194.21	47.87
Aspidosperma C	0	0.0000	32.10	34	2.1486	221.56	55.68
Aspidosperma E	9	0.2653	29.93	202	0.9542	194.21	47.87

$$P_H = \exp\left[-\Delta_{\text{juv}} \cdot \left(H - H_{\text{init}}\right)\right] \tag{23}$$

In this equation, Δ_{juv} is a parameter that is estimated by regression.

Equation 23 was calibrated using the frequency distribution over height classes of 0.3m (starting from the initial height) for each functional group for the subplots containing seedlings and saplings as observed in the 1995 census of the three control plots. Subsequently the inverse cumulative fraction (decreasing from 1 to 0) of seedlings and saplings was calculated for each size class to estimate the parameter Δ_{juv} (table 8). As for poles, the total number of individuals of each functional group that has to be initialized per hectare, N_{juv}, was calculated using the number of seedlings and saplings in the 1995 census data of the three control plots, divided by the total sample area.

4 Model tuning

Initial test runs clearly showed a number of problems with the seedling creation and mortality models. These problems could not be solved with the available data and point out lacunas in the knowledge of tropical forest ecosystems, either specifically for Guyana or for tropical forests in general. Therefore, some pragmatic solutions were implemented in SYMFOR to enable further development and analysis of the model. The problems and their solutions are described below.

4.1 Seed production

Initially each year far too many seeds were produced in SYMFOR, mainly for the taller species groups, leading to a rapid increase of the number of individuals in SYMFOR. The extent of this problem cannot be determined, since the seed densities were only monitored for a few species and even for those species the monitoring period was quite short. The problem seemed to be caused at least partly by working with functional groups, or more specifically, by differences in the population structure of the species for which the seed densities were known and that of the functional groups. Since seed production scales linearly with basal area (*i.e.* a tree that is twice as thick produces four times as many seeds), small deviations in the population structure can have large consequences for the seed production of the population.

To solve the overproduction of seeds the reference DBH, D_{ref}, for the standard seed production, *SSP*, was made functional group specific rather than using a D_{ref} of 25.6cm for all functional groups. Additionally, the seed production term of equation 1 was replaced with:

$$SSP \cdot \left(\frac{D_j}{D_{\text{ref}}} \right)^2 \Rightarrow \text{replaced by } \Rightarrow SSP \cdot \left(\frac{D_j - MRD}{D_{\text{ref}} - MRD} \right)^2 \tag{24}$$

The estimated *SSP* values were recalculated with D_{ref} set to the median of the DBH of the species for which the data were collected. This resulted in similar correlations between observed and expected seed numbers as the original equation. To calculate the seed production in SYMFOR the D_{ref} was set to the median of the DBH of the functional group, rather than the median of the DBH for which *SSP* was estimated (table 2). The result of this adjustment is a lower seed production for small- to medium-sized trees and a higher seed production for very large trees. Overall, the seed production of the subcanopy species increased somewhat, while it decreased for the canopy and especially the emergent species.

4.2 Seedling establishment

Despite the reduced seed production the simulated population still expanded rapidly. Therefore, the number of seedlings that was created annually in SYMFOR per functional group was compared with the annual ingrowth observed in the field. For this purpose, 100 simulations of one year each were run for the central hectare of the three control plots and the three plots with the 4 trees per hectare treatment in Pibiri and 25 simulations of one year for the undisturbed nine-hectare plot in the Mabura Hill Reserve. As input only the trees ≥ 20cm DBH in the plots were used since all smaller individuals would be created in SYMFOR at initialization. Growth and mortality were set to zero for these simulations to make the similarity between the real and simulated forest as large as possible and to exclude possible errors in these processes. In the field data, unidentified seedlings were distributed over the functional groups in proportion to their abundance. This comparison between field data and simulated ingrowth revealed that too many seedlings were created annually for nearly all functional groups.

An explanation for this overproduction of seedlings in SYMFOR may be that establishment of seedlings is not included. Currently seeds germinate and the resulting juveniles immediately behave as larger seedlings. To solve this problem an establishment probability,

E, was implemented so that the simulated and observed new numbers of seedlings were equal. For all functional groups with large seeds this establishment probability was simply defined as the observed divided by the simulated annual ingrowth (parameter e_0 in table 3). In contrast to large-seeded species, early seedling survival of small-seeded species differs between low- and high-light environments (Boot 1996, Rose and Poorter 2003). Therefore, establishment of small-seeded species was implemented as a function of the light index, L. Since field data to estimate this relation were lacking, it was assumed that establishment increased linearly with L and that no seedlings would establish if there was no light ($L = 0$). From the field data the average L for the seedlings of each of the small-seeded functional groups was calculated. This average L was used to calculate the expected number of seedlings given the number of seeds predicted by the SYMFOR simulations. Finally, the ratio between observed and expected seed numbers was calculated per small-seeded functional group and this ratio was divided by the average L for the group to obtain the slope of the relation between establishment and L (parameter e_1 in table 3). For both e_0 and e_1 the ratio between observed and expected seed numbers was set to 0.01 if no seedlings were observed or expected. The calculated establishment chance is simply multiplied by the number of germinated seeds to obtain the number of established seedlings. Only after this adjustment is the value rounded to entire seedlings.

4.3 Additional mortality

Mortality is a rare event and hence information on mortality rates was limited. Estimated relations could therefore be less accurate for less abundant functional groups and sizes. In SYMFOR, this seemed to lead to problems in two cases.

Small-seeded species with low wood density, the classical pioneer species, are typically found in high-light environments and few data are available on their behaviour in darker environments. Therefore, the survival function will be based mainly on the survival in high-light environments. Calculating the survival from this function will most likely result in an overestimation of the survival in dark sites for the small-seeded, light-wood species. For this reason it was decided to implement additional mortality for these functional groups in SYMFOR. The median, $C_{D50\%}$, and the 95th percentile, $C_{D95\%}$, of competition indices observed in the field were determined for the individuals < 2cm DBH of the five groups with small seeds and light wood combined. $C_{D50\%}$ and $C_{D95\%}$ had values of 67 and 196 respectively. It was assumed that no seedlings of the selected functional groups would survive at locations with a competition index larger than $C_{D95\%}$. In SYMFOR, the additional mortality was implemented so that the survival decreased linearly with competition index from the survival at $C_{D50\%}$ to a survival chance of 0 at $C_{D95\%}$.

A similar approach was chosen for the mortality of very large trees. In test runs, trees became too large and regularly obtained diameters far larger than those found in the field. The 95th percentile, $D_{95\%}$, and maximum observed DBH, $D_{100\%}$, were determined per functional group (table 7). In SYMFOR, the annual survival chance is reduced if a tree is larger than $D_{95\%}$. The value that is subtracted from the annual survival chance increases linearly with DBH from zero at $D_{95\%}$ to u_2 at $D_{100\%}$. In addition, if a simulated tree is larger than $D_{100\%}$ the subtracted value increases according to this linear relation. u_2 was set to 0.1 since this gave acceptable results.

5 Performance and sensitivity

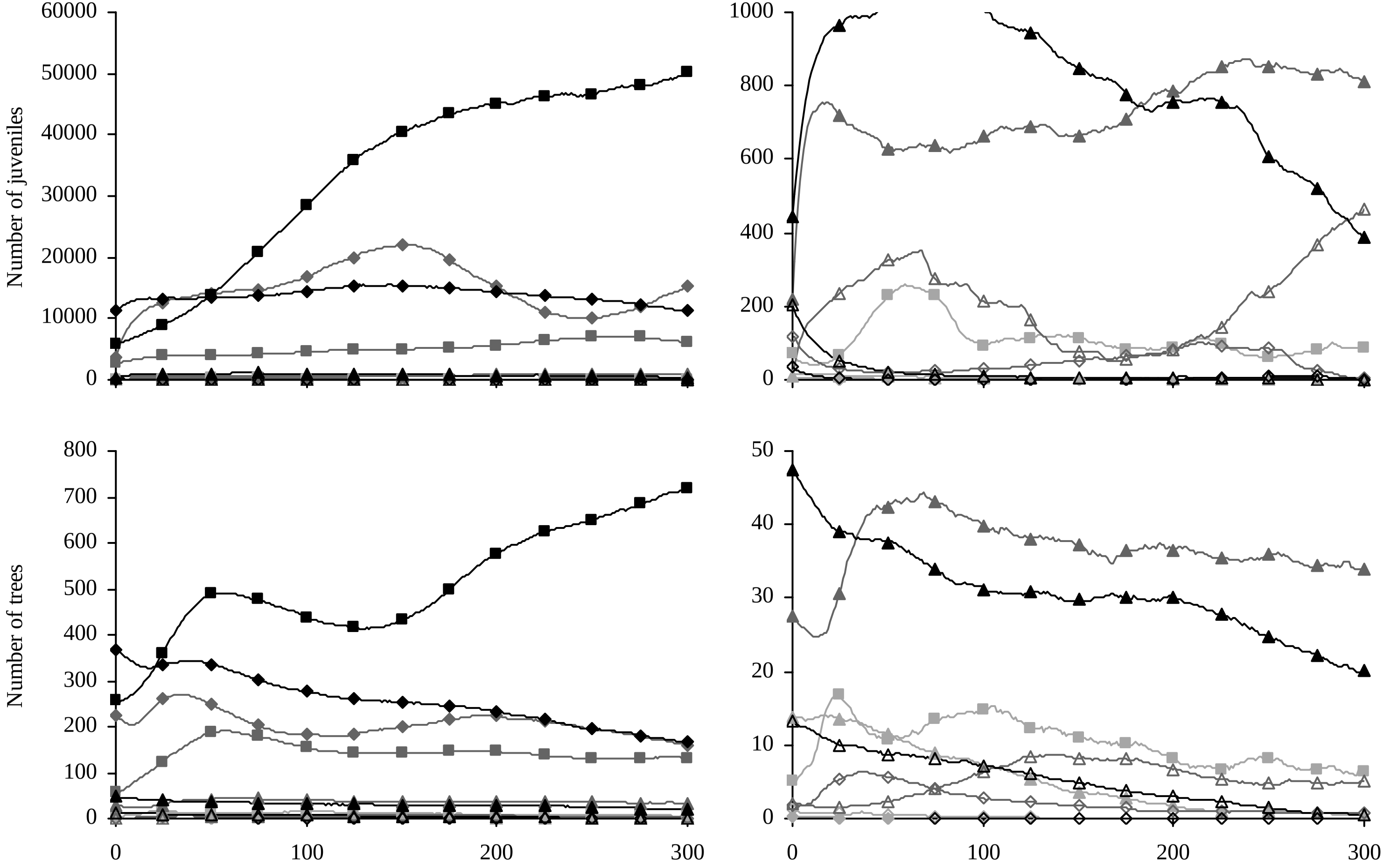
The performance of SYMFOR as described in the previous sections will be evaluated in four different ways. First, a series of control simulations, without logging or any other additional disturbance, will be discussed. Subsequently simulations with two different logging scenarios will be performed and the results will be compared with the control simulations. Then a sensitivity analysis is performed to determine those processes that have the largest influence on the simulation results. Finally, the net changes in the number of individuals and the performance of individual processes are compared against field data.

5.1 Control simulations

To evaluate the performance of SYMFOR without interventions and to create a reference for the sensitivity analysis a series of simulations was performed with the model as described in the previous sections. The pre-harvest census (1993) of the Pibiri dataset was used as input for the trees equal to or larger than 20cm DBH. Since the variation between plots in the number of trees, basal area and composition was considerable it was decided to use more than one plot. However, to enable a comparison of the individual processes between the field and simulations it was decided to leave out the heavily disturbed plots, since the simulations also represent an undisturbed situation. Therefore, the 1993 (pre-harvest) data from the central hectare of the three control plots and the three plots with the lowest harvest intensity were used as tree input for the control simulations. Each of the model plots was one hectare in size and was divided into 100 grid squares of 10 by 10m. Since several processes contain stochastic components five repetitions were run for each of the six plots. Each simulation was run for 300 years. For each year, a summarizing output was generated.

Assuming that the species composition in Guyana’s forest will not change dramatically within 300 years under normal circumstances (*i.e.* in the absence of disturbance in the form of logging or large-scale natural disturbances, and assuming that the present forest is not recovering from prior large-scale disturbances), it was expected that the simulated number of individuals and the basal area per species group would remain approximately constant in the control simulations. From figure 1 it is clear that this was not true. Several functional groups showed large changes during the simulated period. The numbers of juveniles and trees of some groups changed very rapidly in the first 50 years of the simulations (*e.g.* the number of trees for *Oxandra* and the number of seedlings for *Carapa*, *Virola* and *Peltogyne*) after which the changes became more gradual or the numbers of individuals stabilized. Overall, the number of trees and basal area increased with a factor 1.2 during the simulations, while the number of seedlings became 3.5 times as high. Although the absolute values varied considerably between some of the runs, the overall pattern was relatively constant.

Control simulation results



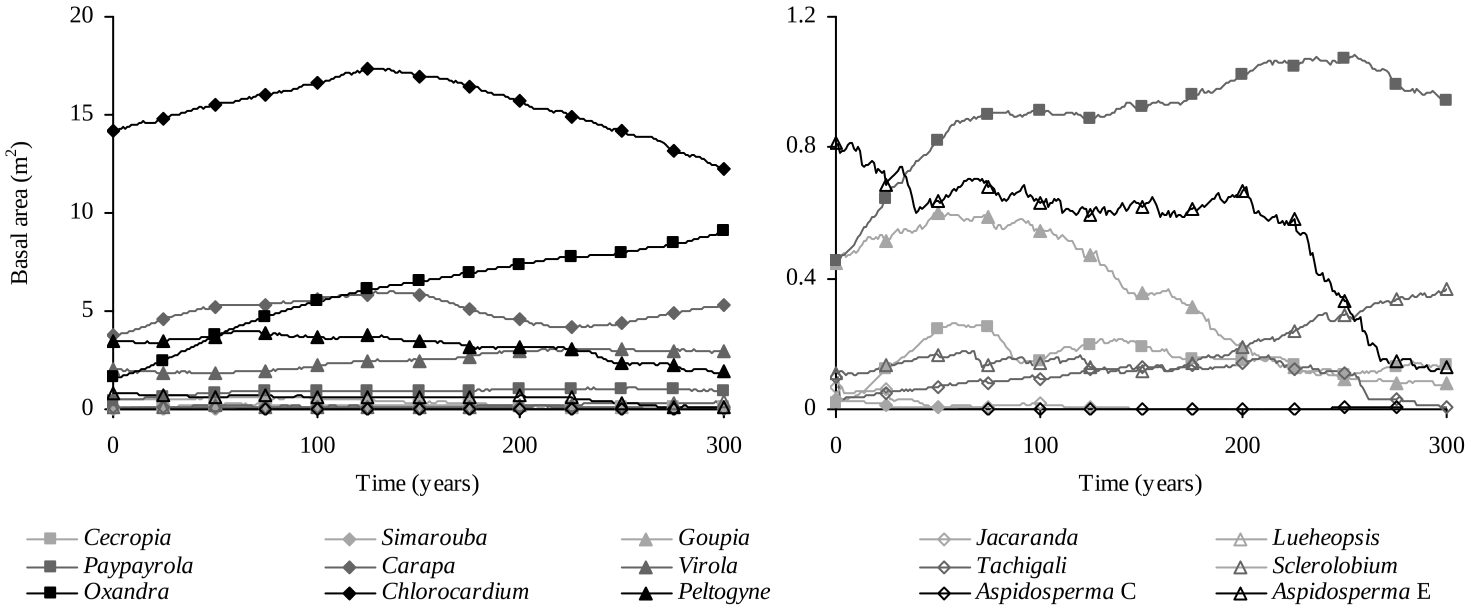
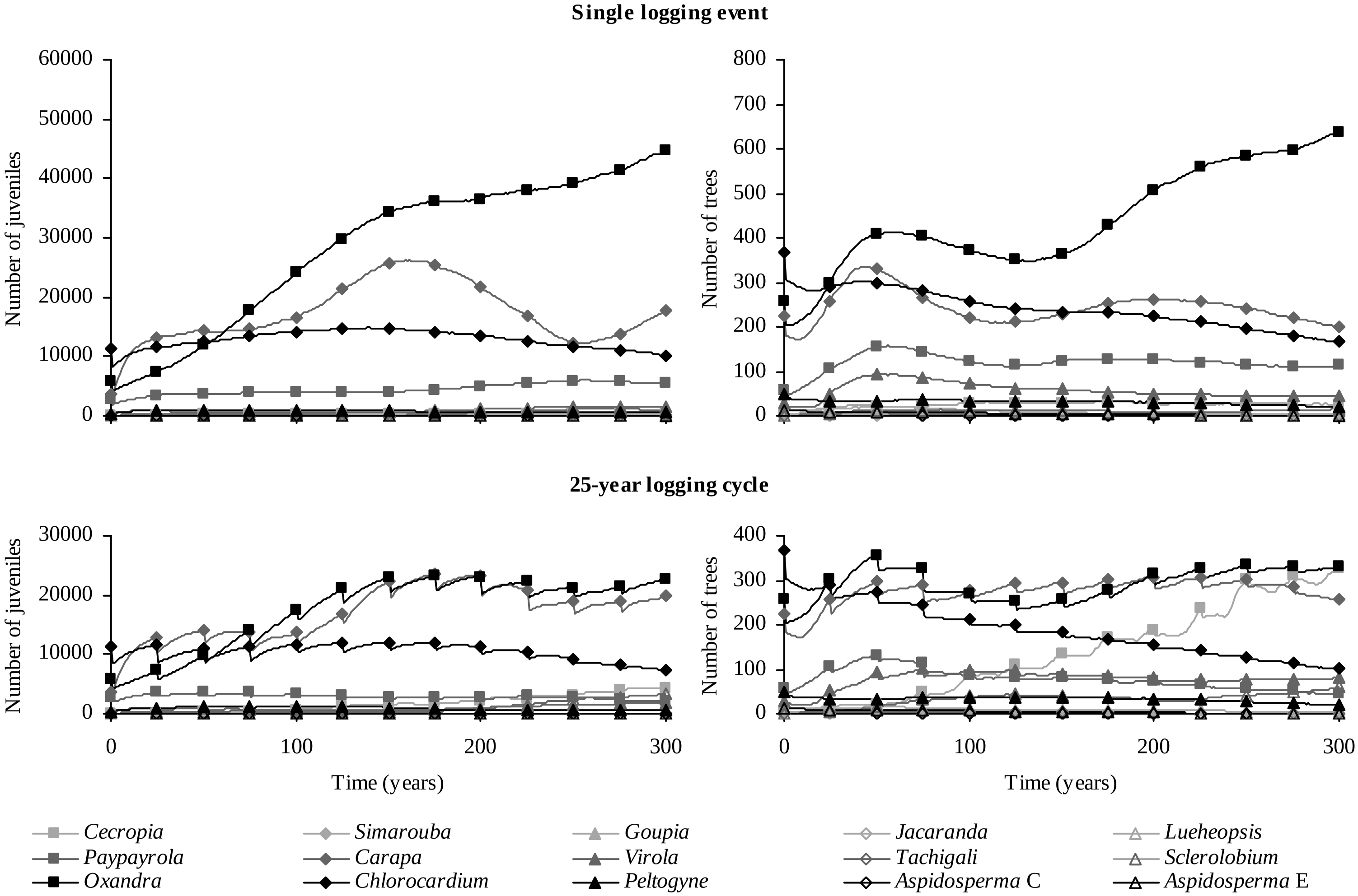


Figure 1. The results of the control simulations. Each line represents the average of 30 simulations for one functional group. The top figures show the number of juveniles (< 5cm DBH), the middle figures the number of trees (≥ 5cm DBH) and the bottom figures show the basal area of the trees in square metres. The right hand figures are magnifications of the lower portion of the left hand figures. The light grey lines represent groups with light wood and small seeds, the dark grey lines represent groups with light wood and large seeds and the black lines groups with high wood density and large seeds. The square markers represent subcanopy groups, the diamonds canopy groups and the triangles emergent groups. Non-wind-dispersed groups have filled markers, those of wind-dispersed groups are open. The markers are shown only to identify the lines.


Single logging event
60000
50000
40000
30000
20000
10000
0
Number of juveniles
800
700
600
500
400
300
200
100
0
Number of trees
25-year logging cycle
30000
20000
10000
0
Number of juveniles
400
300
200
100
0
Number of trees
0
100
200
300
Time (years)
0
100
200
300
Time (years)
Cecropia
Paypayrola
Oxandra
Simarouba
Carapa
Chlorocardium
Goupia
Virola
Peltogyne
Jacaranda
Tachigali
Aspidosperma C
Lueheopsis
Sclerolobium
Aspidosperma E

The most predominant change was that of the *Oxandra* group, of which the number of trees nearly tripled, the basal area increased a factor 5.7 and the number of juveniles became almost nine times as high as the initial number. For the *Paypayrola* and *Sclerolobium* groups the number of trees doubled. For *Paypayrola* the number of seedlings also doubled (*Sclerolobium* started without seedlings). While for *Carapa* and *Virola* the final number of trees was comparable to that at the start of the runs, their number of seedlings increased fourfold. *Tachigali*, *Chlorocardium* and *Peltogyne* ended up with half of the initial number of trees and *Goupia*, *Jacaranda* and *Aspidosperma* E (nearly) went extinct. The most dominant group at the start of the simulations was *Chlorocardium*. Within fifty years, *Chlorocardium* lost its position in terms of the number of individuals to *Oxandra*. However, as trees of this subcanopy group rarely attain diameters of more than 30cm, the *Chlorocardium* group remained the most dominant group in terms of basal area throughout the simulations, although it decreased consistently during the second half of the simulations.

It should be realized that the values fluctuate throughout the simulations and hence the length of the run will determine the conclusions if only the final values are considered. Additionally the results will probably continue to change in longer simulations as no equilibrium was reached after 300 years.

5.2 Logging scenarios

To test how simulated forest stands would respond to disturbance caused by logging two logging scenarios were simulated. In the first scenario logging occurred only once at the start of the simulation and in the second scenario trees were harvested every 25 years. During each logging event a maximum of eight trees were felled per hectare. Only trees larger than 50cm DBH of the three most important timber species (*Chlorocardium rodiei*, *Peltogyne venosa* and *Catostemma fragrans*) were selected for felling. This felling intensity is approximately similar to that currently employed in Guyana in patches that are logged, although occasionally other species and smaller trees are felled. The felled trees were removed from the forest, which caused damage to the forest in the form of skid trails and dragging damage. The plots that were used as input for the large trees and the parameters for the ecological functions were identical to those used for the control simulations. Per scenario five repetitions per plot were run, resulting in 30 runs per scenario. The run length was 300 years.

To test the differences in the number of juveniles, poles and large trees and basal area (the state variables) between the logging scenarios and the control simulations repeated measures analyses were performed in SPSS for Windows 10. One test was performed per scenario per state variable for the sum of all functional groups and per functional group. No tests were

◄

Figure 2. The number of juveniles (< 5cm DBH, left hand figures) and the number of trees (≥ 5cm DBH, right hand figures) for the simulations with a single logging event in the first year (top figures) and for the simulations with a 25-year logging cycle (bottom figures). The legend is identical to that used in the previous figure.

performed for the least abundant functional groups. To keep the tests comprehensible, the state variables were compared only every 25 years (just before the harvest), resulting in the use of 13 values for each of the state variables per simulation. Time was taken as the within-subject factor and the treatment as between-subjects factor. The Wilks' Lambda test was used to test the significance of time and the interaction between time and treatment. Year 0 was excluded for the pairwise comparisons since the number of juveniles and poles that is initialized is always the same. If the interaction was significant then pairwise comparisons of the means were performed to investigate the points in the simulation at which the state variables in the logging scenarios differed from those in the control simulations. If the interaction was not significant but the main effect of treatment was, then the overall means were compared with the control simulations. To specifically analyse the direct effect of one logging event, pairwise comparisons were performed between the first year of the control simulation and that of the single logging scenario. Because of the large number of significance tests (1198 tests) performed for the analyses it was decided to apply a Bonferroni correction and for all significance tests performed for the analysis of the logging scenarios the *p*-value was multiplied by 1198.

In the scenario with logging in the first year only, on average seven trees were felled, of which 5.8 were *Chlorocardium rodiei*. The average DBH of the felled trees was 67.2cm. The effect of one logging event was limited (figure 2, top). Immediately after logging the number of juveniles and poles was approximately 20 to 30% lower than in the control simulations for the majority of the functional groups, probably caused by damage to individuals resulting from felling and skidding. The number of large trees was not significantly lower than in the control for any of the functional groups. The basal area decreased by 10 to 20%. However only for *Oxandra* and *Chlorocardium* this difference was significant. For the remainder of the simulations there were hardly any differences with the control simulations. The only functional group that had less individuals and basal area at nearly all of the 25-year points was the subcanopy group *Oxandra*. One of the other subcanopy groups, *Paypayrola*, also had fewer poles up to the first 125 years, but then recovered. The *Carapa* group benefited somewhat and had more individuals and a larger basal area.

The effect of a 25-year logging cycle was quite dramatic, both for the population (figure 2, bottom) and for the harvest. The number of trees that was harvested decreased from 7 to 1.5 during the simulations. The average number of harvested *Chlorocardium* trees decreased from 5.8 during the first harvest until the harvest in year 151 after which it remained constantly around 0.75 trees per harvest. Of *Peltogyne* one tree was harvested in year one after which on average only 0.1 trees were felled per logging event. The number of felled *Catostemma* trees increased slightly, probably since this was the only harvestable species left in the simulations. However, the number of trees of this species that were felled was limited, since only few trees reach sizes of more than 50cm DBH.

The total number of juveniles was always lower for the 25-year cycle scenario than for the control simulations, while the number of poles, large trees and basal area were only significantly lower during the first 150 years of the runs (note that the 25 year-points, which where used for the analyses, are always one year before a logging event). There was a clear separation between functional groups in the response to logging. The two subcanopy groups *Paypayrola* and *Oxandra* and the *Chlorocardium* group had fewer individuals and a smaller basal area than in the control simulations. Initially the difference was around 15 to 25%, however after 300 years it was up to 70%. The *Carapa* group, to which the timber species *Catostemma* belongs, showed an increase in the number of individuals and basal area compared to the control simulations, although the difference seemed to weaken towards the end of the simulations. The *Cecropia* group benefited most from the logging and became one of the most dominant groups. At the end of the simulations it had 50 times as many juveniles, 55 times as many poles and 33 times as many large trees as in the control simulations. Its basal area was 25 times as high. The remaining tested functional groups (*Goupia*, *Virola*, *Sclerolobium* and *Peltogyne*) did not differ significantly from the control simulations.

5.3 Sensitivity analysis

Through a sensitivity analysis the components to which the model results are most sensitive (*i.e.* which influence the results most) can be identified. This information can be used in combination with information on the uncertainty of the data collection and parameter estimation for the model components to evaluate to which extent the instable model results may be caused by errors in the data and estimated parameter values.

5.3.1 Analysis setup and statistics

A sensitivity analysis can be performed by varying individual parameters, functions or sub-models and observing the corresponding change in important state variables (Jørgensen 1986). Because the model in SYMFOR as described here uses over 1000 ecological parameters and because parameter values in some of the functions are correlated, it was decided to mainly vary function results. In total, the sensitivity of the model to twelve, partly overlapping, processes was investigated (table 9). If the varied process contained functional group specific components then the process was varied for all groups simultaneously. To evaluate both the sensitivity to both an over- and an underestimation the original value was changed in both negative and positive direction for each of the processes by subtracting and adding 25% of the original value:

$$V_{\mathrm{adj}} = V \pm 0.25 \cdot V \tag{25}$$

where V is the original value for the process and V_{adj} is the value that is used in the sensitivity analysis. The percentage with which the processes were varied was chosen arbitrarily after some test runs. The change of 25% seems rather dramatic, however it was reasoned that it would be better to find that the model is sensitive to all processes and then compare the severity of the adjustments, rather then finding that the model is not sensitive to any process.

For the sensitivity analysis the same plots as those used for the control simulations were taken as input for the large trees. Again, five repetitions were run of 300 years each for each plot. At the start of the run and every 25 years the number of juveniles, poles and trees ≥

20cm DBH and the basal area of all trees were stored as state variables, resulting in 13 values of each of the state variables per simulation. These state variables were stored for each functional group separately. The sensitivity of the model was tested for the sum of all functional groups and five selected functional groups. These were the four most dominant groups (*Carapa*, *Oxandra*, *Chlorocardium* and *Peltogyne*) and the group for which the strongest response to the treatment was expected (the *Cecropia* group).

It was decided to vary mortality rather than survival since the latter option would either result in the extinction of all functional groups within a few years, or in the survival of all individuals. Additionally, it seems very unlikely that this would be a realistic error in the data under normal circumstances.

The analysis of the sensitivity to competition includes both the competition indices and the densiometer value L. It should be noted that while a high competition index indicates a low-light environment, a high densiometer value means much light. Therefore, these values were varied in opposite directions. The –25% treatment means less competition, *i.e.* more light than in the control simulations and the +25% means more competition or less light.

To test the significance of the sensitivity of the model to the varied processes repeated measures analyses were performed, similar to those performed for the logging scenarios (section 5.2). One test was performed per process per state variable per selected functional group (and for the sum of all functional groups). Time was taken as the within-subject factor (the 13 values for the state variable) and the treatment (-25%, control, +25%) as between-subjects factor. The significances of time and the interaction between time and set were analysed with the Wilks' Lambda test. As for the logging scenarios, year 0 was excluded for the pairwise comparisons. If the interaction was significant then pairwise comparisons where

Table 9. The processes that were adjusted in the sensitivity analysis with a short description of the parameters or functions that were varied.

Process	Adjustment
Number of individuals initialization	Parameters N_{juv} and N_{pol}
Size distribution initialization	Parameters Δ_{juv} (eqs. 17, 18) and Δ_{pol} (eqs. 19, 20)
Seed dispersal	ρ + crown radius (eq. 1)
Recruitment	Final number of new seedlings per grid square per functional group, *i.e.* the result of $N_{\text{seed}} \cdot G \cdot E$ (sections 2.5.1 and 4.1, eq. 3 and section 4.2, respectively)
Cohort growth	I_H (eq. 13) and I_D (eq. 15) for saplings
Tree growth	I_D (eq. 15) for trees
Cohort + tree growth	I_H (eq. 13) and I_D (eq. 15)
Cohort mortality	1-S (eq. 14) for seedlings and 1-U (eq. 16) for saplings, including additional mortality as in section 4.3
Tree mortality	1-U (eq. 16) for trees, including additional mortality as in section 4.3
Cohort + tree mortality	1-S (eq. 14) and 1-U (eq. 16), including additional mortality as in section 4.3
Competition	L (eq. 2), C_D (eq. 9) and C (eq. 10)
Disturbance	P_{fall} and P_{dmg} (section 2.9.2)

performed to determine the time at which the first significant deviation occurred, the maximum deviation (either positive or negative) and the deviation at the end of the simulation. If the interaction was not significant but the main effect of treatment was, then the overall means for the two treatments were compared with the control simulation. A Bonferroni correction was applied to all 5144 significance tests in the sensitivity analysis by multiplying the *p*-values with 5144. Because of the complexity of the analysis only the general patterns will be discussed.

5.3.2 Sensitivity analysis results

The effect of the within-subject factor, time, was always significant. This means that for none of the tested processes and groups the state variables (numbers of individuals and basal area) were constant during the simulations for all treatments. For the majority of the studied processes both the interaction between time and treatment and the main effect of treatment were significant (tables 10a-d). Responses were quite rapid. Usually the first significant difference was found before year 100. The few cases in which the response was shown later during the simulations did not seem to be specific for a particular process or state variable.

The sensitivity of SYMFOR to variations in the number of initialized juveniles and poles was limited: the total number of juveniles, poles and large trees changed less than 12.5% and for the basal area none of the pairwise comparisons was significant. The responses for the individual functional groups were largest for the poles. Although the maximum deviations were quite large for some of the functional groups, the deviations were never significant at the end of the simulations. This suggests that the deviations were a direct result of the lower or higher number of individuals at the start of the run and that the effect gradually disappeared during the simulations. Remarkably, the *Cecropia* and *Carapa* groups had more individuals if the run started with fewer individuals, while the total and other functional groups showed the opposite pattern.

Similar responses, though in the opposite direction, were observed for variation in the size distribution of the initialized juveniles and poles (note that the –25% treatment results in larger individuals and the +25% in smaller individuals). The effect of variation in initial size on the numbers of individuals was largest for the poles, followed by the large trees, while the basal area hardly changed. Generally, starting with larger individuals resulted in a higher abundance. Again, *Cecropia* and *Carapa* showed the opposite trend, but only for the number of poles (and the basal area for *Carapa*). At the end of the simulations the effect of variation in the size distribution was not significant for any of the state variables.

The only process for which the –25% and +25% treatments had no effect on the simulation results for any of the state variables was seed dispersal. This may have been caused by the limited size of the simulated plots (one hectare) and the large grid squares (10 · 10m) in combination with limited dispersal distances. Even if seeds are dispersed slightly further they may still fall in the same grid square. Additionally, the advantage of dispersal may be limited in SYMFOR. SYMFOR currently does not include distance- and density-dependent mortality from which the seeds can escape through dispersal, and the number of gaps that can be recruited may be too low in a simulation without additional disturbance. Finally, the spatial distribution may have changed during the simulation, *i.e.* individuals may have become more or less aggregated, however this was not analysed.

The model was not very sensitive to variations in recruitment. The effects of treatment and interaction were significant for both the number of juveniles and the poles. However, pairwise comparisons were only significant for the juveniles. Decreasing the annual creation of seedlings led to 10 to 25% fewer juveniles while an increase resulted in a higher number of juveniles for all groups combined and for the three most abundant groups. At the end of the run, only the total number of juveniles (both treatments) and that of the *Oxandra* (both treatments) and *Chlorocardium* (-25% recruits) groups still differed from the control simulations. Apparently, the effect of variations in the number of recruits was not sufficiently large to affect the entire population within the simulated 300 years.

Variation in the growth rate (for juveniles, trees and these two combined) had a large effect on the results of SYMFOR. Generally, slower growth than in the control simulations increased the total numbers of individuals and basal area somewhat, while faster growth led to a slight decrease of the total state variables. At the end of the simulations, the majority of the total state variables still differed from the control simulations and in several cases the largest deviation was in fact reached at the end of the simulations. For the individual functional groups the sensitivity simulations still differed from the control simulations in year 300 in approximately half of the cases. If the juvenile growth rate was decreased then *Cecropia* and *Carapa* responded positively (had more individuals and a larger basal area) while the remaining three groups responded negatively or the differences were not

►

Table 10. The results of the sensitivity analysis for a. the juveniles (< 5cm DBH), b. the poles, c. the large trees and d. the basal area for each of the twelve processes that were varied (table 9). The upper half of the table shows the results for all functional groups combined, *i.e.* the total number of juveniles, poles, large trees and basal area. The first the rows give the Bonferroni corrected significance of the interaction between time and treatment (-25% and +25% of the value in the control simulations) and the main effect of treatment (the significance of the main effect of time is not shown as this was always highly significant). The next rows give the first of the 25 year points (year 0 excluded) at which the value of the state variable significantly differed from that in the control simulations for the low and the high treatment. Then the largest deviation (negative or positive) from the control simulations is shown. The lower half shows the results for five selected functional groups. For the individual functional groups the largest deviation is shown if the interaction was significant for that functional group or the overall deviation if the interaction was not significant but treatment was. Empty cells indicate non-significant results. *p*-values: * < 0.05, ** < 0.01, *** < 0.001. For the first years and deviations ‘○’ indicates that the interaction or treatment were significant but none of the pairwise comparisons was. Deviations are given relative to the control simulations, *i.e.* a deviation of – 0.10 indicates that there were 10% less individuals than in the controls and + 1.00 indicates twice the number of individuals. – signs indicate negative deviations, + signs indicate positive deviations. If the signs are grey (in contrast to black and bold) this means that the there was no significant difference anymore at the end of the run (year 300). 1 sign: deviations from ± 0.00 to ± 0.125 (inclusive), 2 signs: ± 0.125 to ± 0.25, 3 signs: ± 0.25 to ± 0.50, 4 signs: ± 0.50 to ± 1.00, 5 signs: + 1.00 to + 5.00, 6 signs: deviations of more than + 5.00 (negative deviations cannot be more (more negative) than – 1.00 as this would result in negative numbers).

Table 10a. Sensitivity analysis results for the juveniles (DBH < 5cm).

		Initialization				Growth			Mortality				
		Numbers	Size distribution	Dispersal	Recruitment	Juveniles & trees	Juveniles	Trees	Juveniles & trees	Juveniles	Trees	Competition	Disturbance
Time · treatment		***	***		***	***		***	***	***	***	***	***
Treatment		***	**		***	***		***	***	***	***	***	***
First year	-25%	125	75		25	50		50	25	25	50	75	225
	+25%	75	o		25	50		50	25	50	75	100	125
Largest deviation	-25%	-	+		--	---		---	+++	++	++	++	+
	+25%	+	○		++	++		+++	---	--	--	--	-
Cecropia	-25%	+++++				++++++	+++++	○			○	++++++	○
	+25%	○				○	○	○			++++	○	○
Carapa	-25%	+++	○		--	+++	+++	---	++++	○	+++	++++	○
	+25%	○	○		+++	+++	---	++++	---	○	--	---	○
Oxandra	-25%	-	++		--	---	--	---	+++	+	++	++	++
	+25%	○	--		++	++	○	++	---	-	--	-	--
Chlorocardium	-25%	○			--	--		--	++++	++	+++	++	
	+25%	○			++	○		++	---	○	---	--	
Peltogyne	-25%	○				○						+++++	
	+25%	○				○						---	

Table 10b. Sensitivity analysis results for the poles (5cm ≤ DBH < 20cm).

		Initialization				Growth			Mortality				
		Numbers	Size distribution	Dispersal	Recruitment	Juveniles & trees	Juveniles	Trees	Juveniles & trees	Juveniles	Trees	Competition	Disturbance
Time · treatment		***	***		**	***	***	***	***	***	***	***	***
Treatment		***	***		***	***	***	***	***	***		***	***
First year	-25%	25	25		○	25	25	25	25	75	75	25	75
	+25%	25	25		○	25	25	50	25	75	○	25	50
Largest deviation	-25%	-	++		○	--	**--**	**++**	+	+	-	**+++**	**+**
	+25%	+	-		○	**++**	**++**	**--**	**-**	-	○	**--**	**-**
Cecropia	-25%	++++	---			**++++++**	**+++++**	○	○		○	**++++++**	○
	+25%	○	++++			○	○	○	+++++		**++++**	---	○
Carapa	-25%	+++	--			**++++**	**+++**	+++	---	○	---	**+++++**	**---**
	+25%	---	++			**---**	**---**	+++	○	○	+++	**----**	**+++**
Oxandra	-25%	--	++			**---**	**---**	**++**	**--**	**-**	○	+++	**+**
	+25%	+	--			++	**+++**	**--**	-	○	-	**--**	**--**
Chlorocardium	-25%	-	+++			---	**---**	+++	**++++**	**++++**	--	+++	○
	+25%	++	--			++	**+++**	--	**---**	**---**	+	--	○
Peltogyne	-25%	--				**++++**	---	++++				+++	
	+25%	+++				○	++++	---				--	

Table 10c. Sensitivity analysis results for the large trees (≥ 20cm DBH).

		Initialization				Growth			Mortality				
		Numbers	Size distribution	Dispersal	Recruitment	Juveniles & trees	Juveniles	Trees	Juveniles & trees	Juveniles	Trees	Competition	Disturbance
Time · treatment		***	***			***	***	***	***		***	***	
Treatment		***	***			***	***	***	***	***	***	***	***
First year	-25%	50	25			50	150	50	50		50	50	
	+25%	75	50			50	150	50	50		50	75	
Largest deviation	-25%	-	+			**---**	**-**	**--**	**++**	○	**++**	**+++**	○
	+25%	+	-			**++**	**+**	**++**	**--**	○	**--**	**--**	**-**
Cecropia	-25%	○				++++++	○	○	○		○	**++++++**	○
	+25%	○				+++++	○	----	○		++++	○	○
Carapa	-25%	+++	++			**---**	**+++**	**---**	---		---	**++++**	**---**
	+25%	--	○			+++	**---**	++++	--		--	**---**	○
Oxandra	-25%	--	++++			**----**	**---**	**----**	+++		+++	+++	++
	+25%	○	---			**++++**	**+++**	**++++**	---		---	---	--
Chlorocardium	-25%	--	++			**--**	**---**	--	**+++**	**++**	++	++	
	+25%	○	○			++	**++**	++	**---**	○	--	--	
Peltogyne	-25%					○		○					
	+25%					○		○					

Table 10d. Sensitivity analysis results for the basal area of all trees (≥ 5cm DBH).

		Initialization				Growth			Mortality				
		Numbers	Size distribution	Dispersal	Recruitment	Juveniles & trees	Juveniles	Trees	Juveniles & trees	Juveniles	Trees	Competition	Disturbance
Time · treatment		**				***		***	***		***	***	
Treatment						***	***	***	***		***	***	***
First year	-25%	○				50		50	50		50	50	
	+25%	○				25		50	50		50	50	
Largest deviation	-25%	○				**--**	**-**	**--**	**+++**		**++**	**+++**	○
	+25%	○				**++**	○	**++**	**--**		**--**	**--**	○
Cecropia	-25%	○				**+++++**	**+++++**	○	○		○	**++++++**	○
	+25%	○				+++	○	○	---		**++++**	---	○
Carapa	-25%	++	--			--	**+++**	**---**	++		++	**++++**	**--**
	+25%	○	○			++	**---**	**++++**	--		--	**---**	○
Oxandra	-25%	-	++			**---**	**---**	--	++	**--**	**++**	+++	**++**
	+25%	○	--			**++**	**++**	+	--	○	**--**	--	**--**
Chlorocardium	-25%					**--**		--	**+++**		**+++**	○	
	+25%					++		++	**---**		**--**	○	
Peltogyne	-25%					○							
	+25%					○							

significant. Decreasing tree growth rate had a negative effect or no effect on the number of juveniles, trees (except for *Cecropia*) and basal area, while for the poles decreasing the tree growth rate resulted in more individuals. This latter result may be caused by an accumulation of poles since the transition of juveniles continues at the normal rate while the transition from poles to large trees is slowed down. The results do not show that the model is more sensitive to either juvenile or tree growth. The strength of the responses to both processes was similar and the simulations where both juvenile and tree growth were varied were a mixture of the simulations where the processes were varied separately.

Mortality had a substantial influence on the simulation results. Generally decreasing the mortality probability had a positive effect on the total numbers of individuals and basal area, while increasing mortality probability had a negative effect. In the majority of the cases these effects were significant until the end of the simulations. The *Cecropia* group again often showed the opposite pattern with more individuals or a larger basal area if mortality was increased. For the poles some of the other functional groups had less individuals if tree or juvenile and tree mortality were decreased. This may be caused by an increased competition index for juveniles and poles due to the increased number of large trees. Tree mortality was somewhat more important than juvenile mortality as the latter only had a limited influence on the number of large trees and basal area. If only tree mortality was varied then the number of large trees did not differ from the control simulations at the end of the runs while the basal area did. This suggests that mortality finally had a larger effect on the size distribution than on the tree abundance. The *Chlorocardium* group seemed especially sensitive to variations in the mortality probability.

The model was quite sensitive to variations in the competition indices. For all of the state variables the totals were 25 to 40% higher than in the control simulations if competition was decreased and 16 to 25% lower if competition was increased. These differences were observed until the end of the simulations. All functional groups showed similar responses as the overall pattern, although the magnitude differed. The *Cecropia* and *Carapa* groups showed the strongest responses, especially if competition was decreased. These were also the only two groups for which the differences were consistently significant at the end of the simulations. For the remaining groups only the number of juveniles differed from the control simulations in year 300.

Varying the amount of disturbance by 25% did not have a large influence on the simulation results. The simulations with a reduction in the amount of disturbance had more juveniles and poles, while increasing the disturbance resulted in somewhat fewer juveniles, poles and trees. *Carapa* responded in the opposite direction. Of the remaining functional groups only *Oxandra* responded significantly to the variations in disturbance, possibly because this is a group of subcanopy species and is therefore most likely to be damaged by falling trees throughout its life.

5.4 Comparison with field data

The model was not stable even without additional disturbance. In a perfectly stable model, the number of individuals that enters any arbitrary size class should equal the number of individuals that exits the size class. If the input and output for a size class are not balanced over an extended period this will result in an increase (input > output) or a decrease (input < output) in the number of individuals. From this point of view the net changes in the number of individuals were investigated for seedlings, saplings, poles and large trees and compared with those observed in the field, to obtain insight into the causes of the unstable model behaviour. Additionally the performance of the recruitment, growth and mortality models will be compared with field data to determine from which of these processes differences in the net changes in the number of individuals are most likely to originate.

5.4.1 Changes in the number of individuals

Because the number of individuals changes throughout the simulations, the transitions will also change as time proceeds. For this reason, only the changes in the number of individuals during the first ten years of the simulations were analysed. For each year and functional group, the number of seedlings, saplings, poles and large trees at the start of the year was subtracted from that at the end of the year to obtain the net change in the number of individuals for each of the size classes. The same calculations were made for the field data from the three control plots in the West Pibiri compartment. Since these data were not collected annually and in sub-plots only, the values were corrected for monitoring period and sample area to obtain the annual net changes per hectare. The differences between the SYMFOR results and field data were tested for significance using Mann-Whitney U tests in SPSS for Windows. Functional groups without individuals for a certain size class in either SYMFOR or the plots were excluded from the analysis for that size class. The *p*-values were Bonferroni corrected.

Figure 3 clearly shows that the net changes in SYMFOR were not always similar to those observed in the control plots. However, due to the large variation between plots in combination with the Bonferroni correction, the differences between simulated and observed shifts were significant in only a few cases. For most groups, the number of seedlings increased during the simulations, while in the field several groups decreased in number of seedlings. The simulated and observed net changes differed significantly only for the canopy *Aspidosperma* group, for which only one seedling was found in the plots. The average net change in the number of saplings was positive for all functional groups in the SYMFOR simulations, *i.e.* on average the number of saplings increased during the first ten years for all functional groups. For the *Virola, Oxandra* and *Chlorocardium* groups these values were significantly higher than those observed in the field. For these three groups and four others, the number of saplings in the Pibiri plots decreased on average. For the subcanopy groups *Paypayrola* and *Oxandra* the simulated number of poles increased while that of the remaining functional groups remained approximately constant or decreased. In the field, the *Paypayrola* and *Carapa* groups clearly decreased in number of poles while the *Oxandra* and *Chlorocardium* groups increased. Differences were significant only for *Paypayrola* and

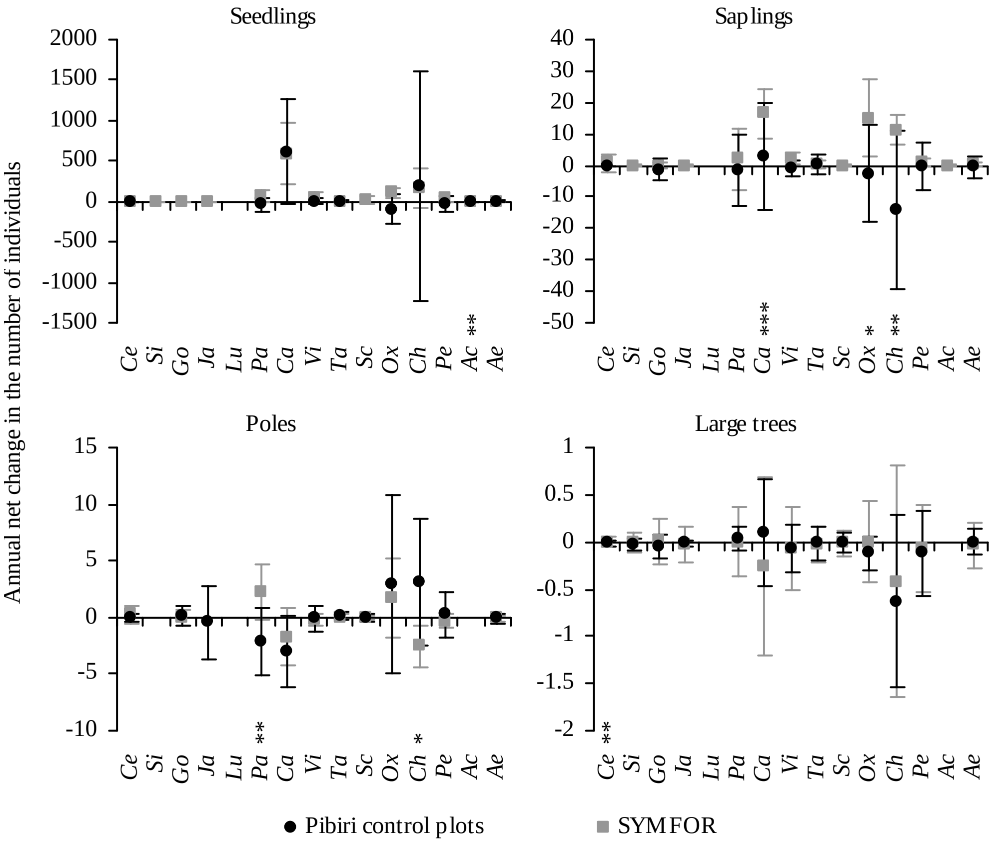


Figure 3. The average annual net change per hectare (± 1 · standard deviation) in the number of seedlings, saplings, poles and large trees for the three control plots in West Pibiri (black circles and bars) and for the first ten years of the control simulations in SYMFOR (grey squares and bars) for each of the functional groups. Functional group names are abbreviated to the first two letters, except for the last two groups where the second letter refers to canopy or emergent, respectively. The functional groups are shown in the same order as in the tables. Functional groups without individuals are not shown. Significant differences are indicated by the asterisks above the abbreviated names. *p*-values: * < 0.05, ** < 0.01, *** < 0.001.

Chlorocardium. *Cecropia* was the only group for which the net change in the number of large trees differed significantly between the simulations (which showed a slight increase) and the field data (which showed a slight decrease).

5.4.2 Performance of individual processes

Differences between simulations and field data in the number of individuals are the result of differences in the number of newly recruited seedlings, growth, natural mortality and competition index, which regulates growth and mortality. Since this chapter is concerned with the implementation of a new recruitment sub-model, it was decided to analyse these processes for the juveniles only. Additionally the damage mortality and gap creation will be evaluated. The performance of the processes for larger individuals is analysed elsewhere (Arets 2005). A few functional groups with a large change in the number of juveniles in the first years of the simulations and sufficient field data were selected for the analyses. These were *Paypayrola*, *Carapa*, *Oxandra*, *Chlorocardium* and *Peltogyne*, all with an initially increasing number of juveniles, and the emergent *Aspidosperma* group, which was the most common group with a consistent decrease. For each of the functional groups the annual recruitment and the proportion of seedlings and saplings that died due to natural mortality per hectare were determined for the control plots in West Pibiri and for the first ten years of the simulations. Differences in recruitment and the proportion of mortality were tested for significance using Mann-Whitney U tests in SPSS for Windows. The average growth and competition index were calculated from both data sets for size classes of one metre height for the seedlings, starting from the initial height, and for one centimetre diameter for the saplings. Because functional groups differ in initial height also the boundaries of the height classes differed slightly between the functional groups. Since it is possible for seedlings to break and become smaller than their initial height, a class was added to include these broken seedlings. This class and the class with the tallest individuals had a class width of less than one metre. Differences in the growth rate and competition index could not be tested for significance due to the way simulation results were stored and will be discussed on the basis of graphs. Also the damage mortality and gap creation could not be tested statistically due to limited field data availability.

Differences in the number of recruits should be limited at the start of the runs, since the establishment chance was calibrated so that the number of recruits in SYMFOR simulations equalled that observed in the field. Nevertheless, significant differences did exist between the recruitment observed in the field and that found in the SYMFOR simulations (table 11). For the *Paypayrola* and the *Oxandra* group, the recruitment was lower in the field than in the simulations. The observed differences in the annual recruitment, whether significant or not, are largely explained by differences in the number of recruits between the control plots used for table 11 and those used for the calibration of establishment. For example, for the *Paypayrola* and *Oxandra* groups the annual numbers of recruits per hectare in the three control plots were 49 and 92, respectively. However, they were 182 and 374 if also the other plots that were used for the calibration of the establishment were included (the undisturbed

Table 11. The average and standard deviation of the annual number of recruits per hectare observed in the Pibiri control plots and in the SYMFOR control simulations, and the Bonferroni corrected significance of the differences between the recruitment in the field and in SYMFOR. *p*-values: ** < 0.01, *** < 0.001.

Functional group	Pibiri	SYMFOR	*p*
Paypayrola	48.9 ± 64.3	182.8 ± 92.4	**
Carapa	998.7 ± 589.7	1369.4 ± 480.2	
Oxandra	91.9 ± 88.3	376.0 ± 59.3	***
Chlorocardium	1801.6 ± 1333.4	1213.3 ± 321.2	
Peltogyne	35.2 ± 63.7	88.1 ± 48.4	
Aspidosperma E	0.0	1.2 ± 1.4	

plot in the Mabura Hill Reserve and the Pibiri plots in which four trees per hectare were harvested). These differences in the recruitment explain at least partly the observed differences in the net changes of the number of seedlings between field and SYMFOR. The number of newly established seedlings of the six selected groups that will reach the saplings stage within ten years is negligible. Therefore, the differences in recruitment will not have contributed to the differences in the net changes in the number of saplings.

In figure 4 it can be seen that seedlings of the six selected functional groups tended to grow slightly slower in height in the control Pibiri plots than during the first ten years of the simulations. The seedling competition index tended to be higher in the field than in the SYMFOR simulations (figure 4). However, given the large amount of variation it seems unlikely that any of the differences was significant. Also the saplings tended to grow slower and experience more competition in the field than in the simulations for four of the six groups (figure 5). The relatively rare *Peltogyne* and *Aspidosperma* groups did not clearly show this trend, possibly because of the limited field data availability. Again, the variation was large and probably none of the differences was significant. The differences in the competition index for seedlings and saplings were most likely caused by the initialization of juveniles and poles at the start of the simulations. The function that was used to perform this initialization did not perfectly fit the observed size distributions and resulted in slightly smaller individuals, which will lead to a decrease in the amount of competition. However, the decrease in the competition index was generally not sufficiently large to explain the observed increased growth rate in SYMFOR compared to that in the field. The portion of the difference that could not be explained by the competition index is most likely caused again by differences between the control and harvested plots other than the competition index, such as differences in nutrient availability. An increased growth rate can have a large effect on the net changes in the number of individuals, since it decreases the time needed to reach maturity. This influences not only the age at which individuals start to reproduce, but also the number of individuals that will reach maturity.

As natural mortality in SYMFOR is regulated by the competition index it may be expected that a difference in the competition index between the field and model would also result in a

Table 12. The average proportion of seedlings (left) and saplings (right) that died annually per hectare due to natural causes (not resulting from damage) and the corresponding standard deviation for the West Pibiri control plots and the SYMFOR control simulations. *p*-values for significance of differences between field and SYMFOR mortality: ** < 0.01, *** < 0.001.

	Seedlings			Saplings		
Functional group	Pibiri	SYMFOR	*p*	Pibiri	SYMFOR	*p*
Paypayrola	0.037 ± 0.034	0.029 ± 0.004		0.019 ± 0.024	0.011 ± 0.004	
Carapa	0.100 ± 0.051	0.089 ± 0.011		0.026 ± 0.032	0.015 ± 0.007	
Oxandra	0.032 ± 0.022	0.032 ± 0.003		0.012 ± 0.010	0.006 ± 0.003	
Chlorocardium	0.136 ± 0.035	0.074 ± 0.004	**	0.022 ± 0.020	0.007 ± 0.006	***
Peltogyne	0.190 ± 0.192	0.060 ± 0.011		0.003 ± 0.009	0.014 ± 0.067	
Aspidosperma E	0.022 ± 0.045	0.059 ± 0.023		0.025 ± 0.076	0.013 ± 0.088	

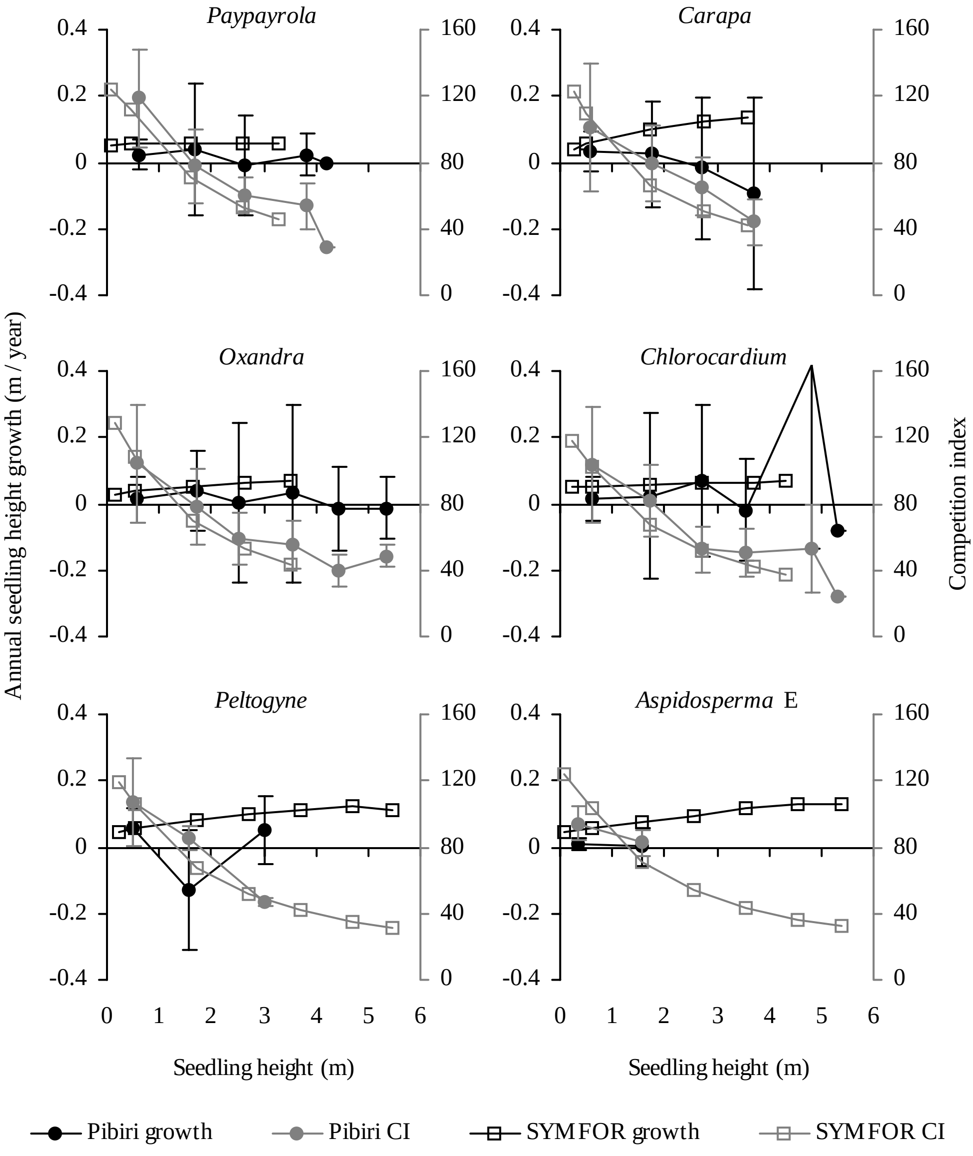


Figure 4. The average annual height growth (black symbols, left axis) and competition index (grey symbols, right axis) for the seedlings of six functional groups in the West Pibiri control plots (closed circles) and the SYMFOR control simulations (open squares). The averages are shown for height classes of, in principle, one metre (see text), at the average height in that class, rather than at the class middle. The error bars for the field data represent the standard deviation. The scaling of the axes is equal in all graphs.

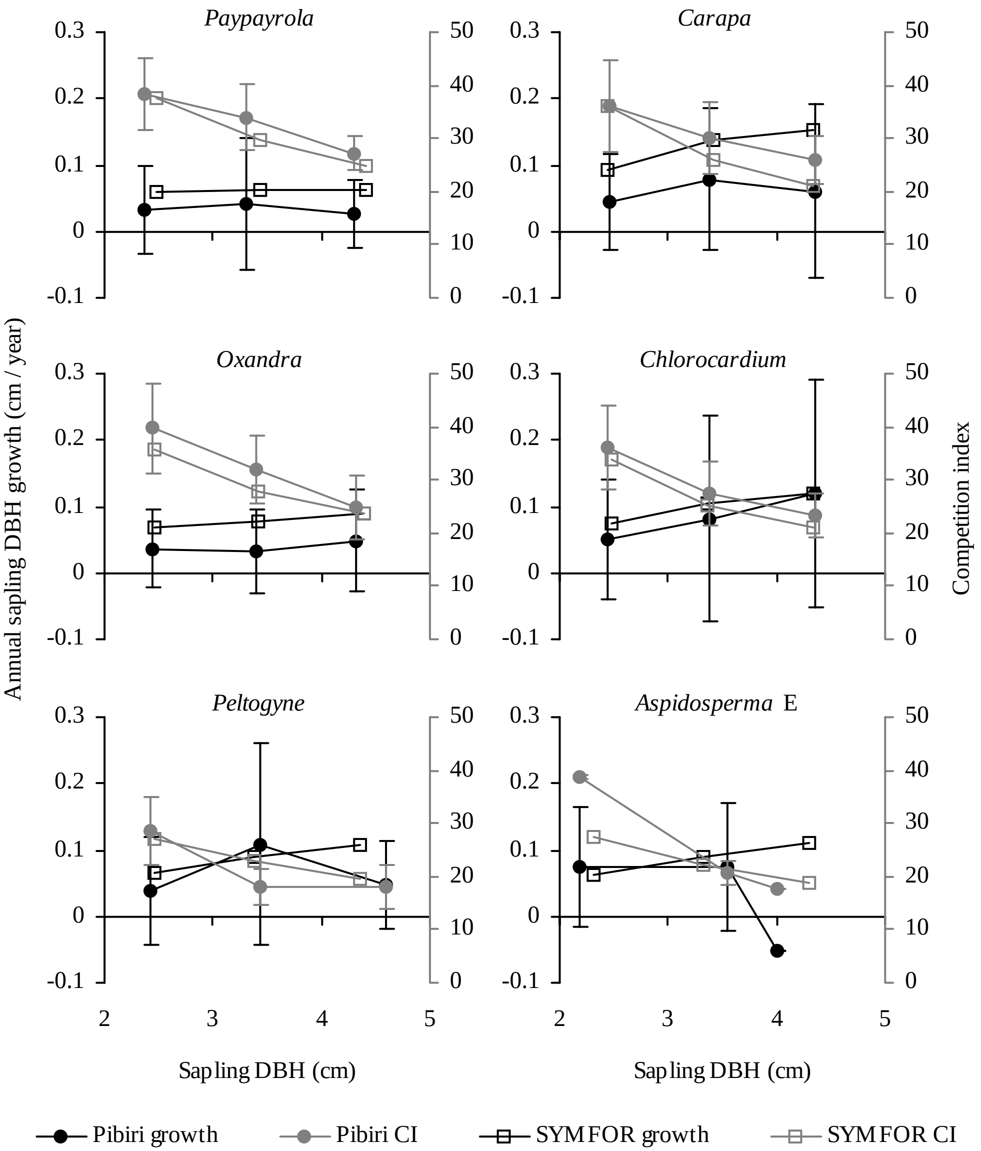


Figure 5. The average annual DBH growth (left axis) and the average competition index (right axis) of saplings per diameter class of one centimetre for six common functional groups in the West Pibiri control plots and in the control SYMFOR simulations. For the field data the standard deviation is plotted.

difference in the natural mortality. For the majority of the tested functional groups the natural mortality appeared to be higher in the field, where there was slightly more competition, than in the simulations (table 12). Exceptions were the seedlings of the *Oxandra* group, which are very shade tolerant, the seedlings of the *Aspidosperma* group and the saplings of the *Peltogyne* group, which are both relatively rare and did not clearly show a difference in the competition index between field and simulations. Due to the large variation, the differences in natural mortality were significant for the seedlings and saplings of the *Chlorocardium* group only. However, the tendency towards a lower mortality in the simulations will have contributed to the observed differences in the net changes in the numbers of seedlings and saplings between the field and SYMFOR.

In the Pibiri control plots annually only 21 juveniles died per hectare due to damage inflicted by falling trees or branches. In the simulations, 346 juveniles died annually due to damage mortality. Most likely, the damage mortality in the field was underestimated, since all seedlings of which the mortality cause was unknown were treated as natural mortality. This explains at least part of the difference between the field and SYMFOR, however, the extent of the underestimation and hence the accuracy of the simulated damage mortality cannot be estimated. On average 114 square metres were damaged by falling trees annually in the SYMFOR simulations, which corresponds to 1.14% of the area. The maximum area that was damaged due to falling trees in a year was 614m^2 (6.14%). The average percentage of the area that was damaged annually is within the range of gap creation rates reported in literature (Hartshorn 1990, van der Meer and Bongers 1996, 2001). It should be realized that the tree silhouette as used in SYMFOR to calculate the damaged area does not match any of the existing gap definitions and not all of the smaller trees that fall and damage juveniles will create canopy gaps. Nevertheless, neither the number of seedlings that died due to damage mortality nor the percentage of area damaged by falling trees appeared exceptionally low or high.

5.5 Evaluation of the model performance

It was expected that the functional group composition and abundance would not change severely during 300-year simulations representing an undisturbed forest patch. However, the results of the control simulations clearly show that the adapted model is not stable in situations without any disturbance other than natural treefall. Not only did the total number of juveniles and trees and basal area fluctuate during the simulations, but also the relative abundance of the functional groups changed. Gradually the model forest transformed from a forest with shade-tolerant canopy groups to a forest with shade-tolerant subcanopy groups. The *Chlorocardium* group, which dominated the forest at the start of the simulations, consistently declined in abundance and will probably go extinct in longer simulations. The two subcanopy groups *Paypayrola* and, especially, *Oxandra* thrived well and dominated the forest in terms of number of juveniles and trees after approximately fifty years.

SYMFOR did respond to logging as was expected. If trees were harvested only once at a moderate intensity the differences with the control simulations were limited. However, if a

25-year logging cycle was applied the abundance of functional groups changed dramatically. The forest gradually changed from a primary forest with mainly shade-tolerant groups to a secondary forest where the light-demanding *Cecropia* group was among the most dominant groups.

Why were the functional group composition and abundance not stable in the control simulations? Unfortunately, there is no straightforward answer to this question due to the complexity of the model. Numerous minor, often insignificant problems were found and often responses of different functional groups and size classes contrasted without a clear pattern. For this reason, only a few general trends will be discussed for the most common groups.

Comparison with field data showed that for the majority of the tested groups the simulated annual recruitment was higher than in the control plots. Despite the weaknesses in the seedling creation functions, their impact on the unstable model results is probably limited as the sensitivity analysis indicated that seed dispersal had no effect on the model results and the effect of variation in the annual recruitment was restricted to juveniles. However, for some of the functional groups the difference between simulated recruitment and that in the control plots was larger than the amount of variation that was used for the sensitivity analysis. This means that the actual effect of recruitment had, may be larger than suggested by the sensitivity analysis.

During the first ten years of the simulations, juveniles tended to grow faster and survive better in SYMFOR than in the field, partly caused by a lower competition index. This probably contributed significantly to instability of the model results, as the model was quite sensitive to deviations in growth and mortality and especially to the competition index, which regulates growth and mortality. The effect of these processes may have been larger than suggested by the sensitivity analysis as the comparison with field data revealed that the deviation of juvenile growth and mortality was often larger than that applied in the sensitivity analysis. The deviations observed for the competition index were similar to those used in the sensitivity analysis.

The amount of disturbance caused by falling trees in SYMFOR matched that observed in the field reasonably well. Additionally, the model was not very sensitive to variation in the amount of disturbance. Hence, the unstable results cannot be attributed to uncertainties in the probability that a tree falls and damages vegetation.

Thus, generally too many new seedlings were produced annually, juveniles grew too fast and too few juveniles died. These observations explain at least part of the rapidly increasing number of juveniles for several groups at the start of the simulations and the increasing number of trees for the subcanopy groups *Paypayrola* and *Oxandra*. If the number of trees increases then the model becomes self-propelling as more trees produce more seeds which in turn result in more trees etc. This process will continue until recruitment and mortality, which will increase due to the increased competition index, are in balance. For the *Oxandra* group this balance was not reached after 300 years. The slow but steady decline of

Chlorocardium trees cannot be explained on the basis of juvenile behaviour, as the number of juveniles increased and growth appeared faster than, or at least similar to, that in the field. Therefore, the reduction in the number of *Chlorocardium* trees may have been caused by inaccuracies in the tree growth and mortality, which were not analysed in this chapter.

The influence of the juvenile and pole initialization at the start of the simulations on the results cannot be estimated well. The problem in this case is not the similarity between model and field, but the uncertainty in the field data, as the variation between plots was large. The initialization parameters are based on small sub-samples of the area and as plants are not distributed homogeneously over the forest it is possible that the sampled area is not representative for the entire area. Potentially, deviations in the number of individuals and their sizes can have a large impact on the simulation results, although the sensitivity analysis indicates that these differences disappear before the end of the simulations. Nevertheless, if the sampled area happens to contain relatively more large juveniles than the entire population, this may lead to too many poles in the first few years of the simulations. This may have been the case for *Oxandra*, while the opposite may have been true for *Chlorocardium*. Variation between plots may have been a general cause of the instability of the model results as also the number of trees larger than 20cm DBH and the basal area differed substantially between plots.

An important observation was that the net changes in the numbers of individuals in the field were rarely zero and varied strongly between plots and monitoring periods. Several of the net changes observed in the field explain patterns observed in the simulations. For example, the large increase in the simulated number of seedlings for the *Carapa* group was also observed in the field, where on average the number of seedlings increased by 610 per year per hectare. This suggests that not only the SYMFOR simulations were unstable, but that the number of individuals also changed in the sampled plots during the monitoring period.

6 Conclusions

In this chapter the adaptation of the existing SYMFOR framework to include the explicit modelling of recruitment via seed production and dispersal, germination, establishment and juvenile growth and mortality was described and the performance of this adapted model was evaluated. The adapted model did not predict a stable functional group composition in an undisturbed situation. Simulations with logging showed that one logging event will not have a large effect on the forest, when compared with the control simulations. However, a 25-year logging cycle with a moderate logging intensity altered the functional group composition significantly. These simulations indicated that a 25-year logging cycle is not sustainable, since the number of harvested *Chlorocardium* trees dropped to less than one per hectare. If these predictions are correct, the current forest management should urgently be revised. This shows the need for accurate models, as the 25-year logging cycle was intended to simulate the currently applied logging intensity in Guyana.

Unfortunately, the version of SYMFOR developed in this chapter appeared too unreliable to use it as a tool to evaluate harvest regimes or study ecological theories. No major cause for the instability of the model results was found. There were, however, numerous minor problems, which apparently cumulated to large deviations from stability over the course of the simulations of 300 years. Many of these may have been caused by limited data availability and by variation between plots wherein the data were collected. This problem was most apparent for the recruitment functions (seed production and dispersal, germination). For the calibration of these functions data for only one or two species per functional group were available, spanning only short periods of time, and for several groups no or insufficient data were collected. For these groups data from other functional groups or data available in literature had to be used. For the growth and mortality functions more data were collected, however data for rare groups and rare circumstances were limited. Examples are the growth and mortality of the small-seeded groups, especially in undisturbed forest, and the mortality of very large trees. Additionally, the explained variation for any of the processes was generally low (chapters 2 and 3, Arets 2005), which, unfortunately, seems to be a characteristic of ecological field research, but can result in large problems in simulation models such as SYMFOR.

SYMFOR currently contains the most important processes. However, there are still numerous non-trivial processes, extensions of included processes and environmental influences missing. Some examples are pollination, a seed bank, long-distance dispersal (enabling extinct groups to re-establish), fruiting frequencies (currently all mature trees fruit every year), advanced regeneration (allowing already established juveniles to survive in newly created gaps), a more detailed competition index and lianas and (hemi-) epiphytes, which inhibit regeneration in gaps (Schnitzer *et al.* 2000) and limit tree growth (Clark and Clark 1990, Grauel and Putz 2004). Currently the only mechanism controlling population growth is the competition index. The inclusion of other stabilizing mechanisms, such as seed production related to resource availability and density-dependent mortality, will reduce the chance that one functional group will increase in number, such as the *Oxandra* group. However, the challenge for any process that is currently missing in SYMFOR is not so much to define the model logic, but to collect field data that provide an accurate description of the process. Additionally, a choice has to be made between a complex model that includes as many processes as possible, but requires decennia of fieldwork, and a conceptual model with fewer processes, but whose behaviour is easy to understand.

An important realization was that the field data of the control plots suggested that there might be large shifts in the species composition in the field as well. This questions the validity of the assumption that the species composition in Guyana will not change over a period of 300 years. Although it is unlikely that the forests in entire central Guyana will shift in species composition, the composition in forest patches may continuously cycle between various stages of succession, driven by infrequent large-scale disturbances. Although secondary succession has been studied quite well, information on the development or cycling of primary forest on the time scale of the simulations is lacking. This again points at the need for large-scale, long-term monitoring of permanent sample plots and long running, carefully planned experiments. This effort has to be made in order to collect sufficient information on population dynamics to develop reliable models to study forest dynamics, both from the perspective of nature conservation and of timber extraction.

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Appendix A. An overview of the parameter, variables and abbreviations used in the chapter and their corresponding values, if any. FG: functional-group specific parameters.

Name	Context or description	Value
A	The area of a grid square in m^2	100
BA	Basal area in cm^2	
C	Diameter independent competition index	
C_D	Competition index, diameter dependent	
$\hat{C}_D$	Average diameter dependent competition index	
$C_{D(G)}$	The contribution of trees ≥ 20cm DBH to the C_D	
$C_{D(O)}$	The contribution of juveniles and poles to the C_D	
$C_{D(\mathrm{pol})}$	Maximum allowed C_D for the initialization of poles	FG
$C_{D(\mathrm{sap})}$	Idem but for saplings	FG
$C_{D(\mathrm{sdl})}$	Idem but for seedlings	FG
cd_0	Parameter for the Weibull function for the average C_D	497.17
cd_1	Idem	0.69
cd_2	Idem	10.08
$C_{D50\%}$	Median C_D for groups with small seeds and light wood	67
$C_{D95\%}$	95th percentile of the C_D for groups with small seeds and light wood	196
C_P	Height where the crown is widest in metres	
cp_0	Parameter in crown point equation	0.8
C_R	Crown radius in metres	
$cr_{0\text{ - }2}$	Parameters for the crown radius - diameter relation	FG
D	Abbreviation for DBH used in equations	
$D_{100\%}$	Maximum observed DBH	FG
$D_{95\%}$	95th percentile of the DBH distribution	FG
DBH	Diameter at breast height (1.30m above the ground) in centimetres	
D_low	Lower DBH limit of the initialized poles	5
D_ref	Reference DBH for seed production	FG
DTL	Demerara Timbers Ltd.	
D_up	Upper DBH limit of the initialized poles	20
E	Probability of establishment	
$e_{0\text{ - }1}$	Seedling establishment parameters	FG
G	Probability of germination	
$g_{0\text{ - }2}$	Germination parameters	FG
GM	Clusters of functional groups with the same growth and mortality parameters	
H	Tree height in metres	
$h_{0\text{ - }2}$	Parameters for the height - diameter relation	FG
H_init	Initial seedling height after germination in metres	FG
H_m	Maximum tree height in metres	
H_up	Upper height limit of initialized juveniles in metres	FG
I_D	Diameter increment in $cm \cdot year^{-1}$	
$id_{0\text{ - }4}$	Diameter increment parameters	FG
I_H	Realized height increment in $m \cdot year^{-1}$	
$\hat{I}_H$	Average height growth in $m \cdot year^{-1}$	
$ih_{0\text{ - }1}$	Seedling height increment parameters	FG
juveniles	Seedlings and saplings, individuals < 5cm DBH	
L	Light index for germination	
l_0	Parameter for germination light index	5.7598
l_1	Idem	6778.72
large trees	Individuals larger than 20cm DBH	
L_m	Maximum allowed L, light index for germination	87.3
MRD	Minimum reproductive DBH in centimetres	FG
N_dp	Number of sample points to assess grid square damage	100

Name	Context or description	Value
N_{juv}	Number of juveniles to be initialized	FG
N_{pol}	Number of poles to be initialized	FG
N_{seed}	Number of seeds in a grid square	
P_{D}	Probability that a randomly chosen DBH is larger than or equal to D	
P_{dmg}	Probability that a tree dies if another tree falls on top of it	0.08
P_{fall}	Probability that a tree falls over after it died	0.3
P_{H}	Probability that a randomly selected height is larger than or equal to H	
poles	Individuals with $5 \leq$ DBH < 20cm	
PSP	Permanent sample plot	
r	Distance between two points in metres	
RIL	Reduced impact logging	
r_{L}	Trees within this distance in metres from a grid square are included for L	13.5
rnd	Random number	
S	Survival probability for seedlings	
$s_{0\text{ - }1}$	Seedling cohort survival parameters	FG
saplings	Individuals with $2 \leq$ DBH < 5cm	
$\hat{S}D_q$	Seed density in grid square q (m^{-2})	
sd_0	Intercept of crown radius - diameter relation for seed dispersal	FG
sd_1	Slope of crown radius - diameter relation for seed dispersal	FG
seedlings	Individuals < 2cm DBH	
SSP	Standard seed production at D_{ref}	FG
T	Number of trees in summations	
t_{sap}	Length of time interval during which survival data were collected for saplings	3.5
T_{P}	Number of parent trees in summations	
trees	Poles and large trees, individuals ≥ 5cm DBH	
t_{sdl}	Length of time interval during which seedling survival data were collected	5.02
U	Survival probability for individuals ≥ 2cm DBH	
$u_{0\text{ - }1}$	Parameters for the survival of saplings and trees	FG
u_2	Parameter for the survival of saplings and trees	0.1
W_{z}	Weighting factor for the seedling growth autocorrelation	FG
z_{IH}	Random deviation from average seedling growth rate	
α_{juv}	Value of fitted height distribution at H_{up} for the pole initialization	
α_{pol}	Value of fitted DBH distribution at D_{up} for the juvenile initialization	
Δ_{juv}	Parameter for cumulative height distribution of juveniles	FG
Δ_{pol}	Parameter for cumulative DBH distribution of poles	FG
ρ	Seed dispersion parameter in metres	FG
$\sigma_{0\text{ - }1}$	Parameters for standard deviation of seedling growth	FG
σ_{IH}	Competition dependent standard deviation for deviations from average seedling growth rate	

Appendix B. The members of each of the functional groups and their characteristics. WD: wood density in g·cm^{-3}, SM: seed mass in grams in logarithmic classes (1: 10^{-5} - 10^{-4}g, 2: 10^{-4} - 10^{-3}g, ….. 8 ≥ 100g), H_m: maximum tree height in metres, DT: dispersal type (b: bird, h: water, m: monkey, r: rodents, u: unassisted, v: bat, w: wind). Nomenclature largely follows Ek (1997) and van der Hout (1999). Data were derived from several sources (see text).

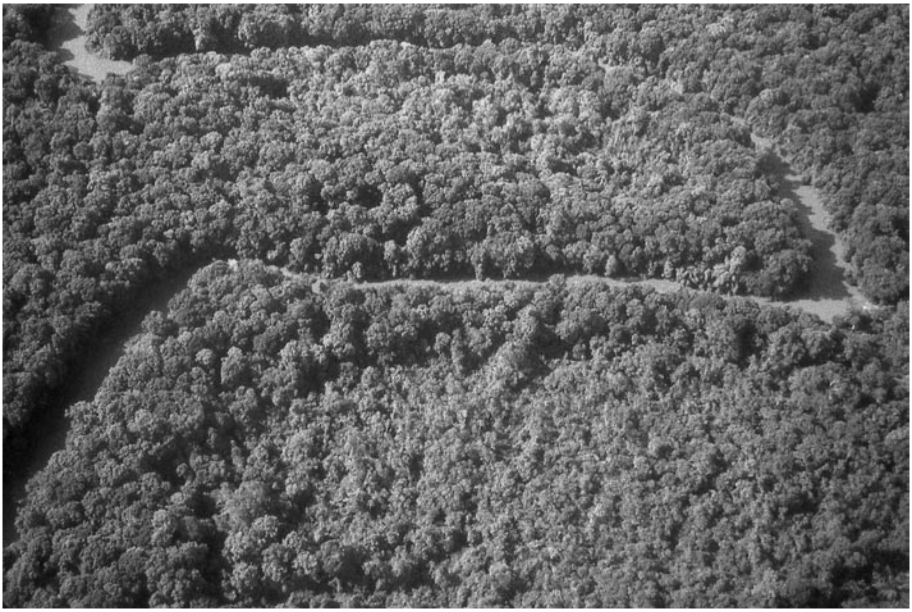
Family	Species	Vernacular name	WD	SM	H_m	DT
***Cecropia* group**: low wood density, small seeds, subcanopy, non-wind dispersal						
Annonaceae	*Rollinia exsucca*	Koyechi	0.44	4	17	bm
Apocynaceae	*Ambelania acida*	Makoriro	0.55	4	6	m
Cecropiaceae	*Cecropia obtusa*	Congo pump, common	0.40	2	21	bmv
	Cecropia sciadophylla	Congo pump, long leaf	0.40	2	21	bmv
Flacourtiaceae	*Casearia sp.* / *Ryania speciosa* var. *tormentosa*	Kibihidan	0.72	4	10	b
Melastomataceae	*Bellucia grossularioides*	Sakwasepere	0.70	2	25	m
	Miconia hypoleuca	Wakaradan	0.70	1	15	b
	Miconia lepidota	Waraia, lepidota	0.70	1	15	b
	Miconia punctata	Waraia, punctata	0.70	1	15	b
	Miconia spp.	Waraia	0.70	1	15	b
Rubiaceae	*Palicioura crocea*	Kamadan, red/orange flower	0.66	4	15	b
	Palicioura guianensis var. *occidentalis*	Kamadan, yellow flower	0.66	4	15	b
	Psychotria capitata / *P. puberulenta*	Kamadan, white flower	0.66	4	15	b
Rutaceae	*Zanthoxylum apiculata*	Sada	0.51	3	15	b
***Simarouba* group**: low wood density, small seeds, canopy, non-wind dispersal						
Guttiferae	*Vismia macrophylla*	Bloodwood, broad leaf	0.58	3	26	b
Euphorbiaceae	*Hyeronima alchorneoides* var. *alchorneoi*	Suradan	0.78	4	30	bm
Simaroubaceae	*Simarouba amara*	Simarupa	0.40	4	30	m
Tiliaceae	*Apeiba petoumo*	Duru	0.56	3	30	bm
***Goupia* group**: low wood density, small seeds, emergent, non-wind dispersal						
Annonaceae	*Xylopia benthamii*	Weshiraure	0.68	4	38	bm
	Xylopia nitida	Kuyama, white	0.68	4	38	bm
	Xylopia pulcherrima	Kuyama, red	0.68	4	38	bm
Celastraceae	*Goupia glabra*	Kabukalli	0.78	2	40	bm
Flacourtiaceae	*Laetia procera*	Warakairo	0.68	3	37	bm
Mimosaceae	*Parkia pendula*	Hipanai	0.48	4	40	mr
***Jacaranda* group**: low wood density, small seeds, canopy, wind dispersal						
Bignoniaceae	*Jacaranda copaia*	Futui	0.43	3	30	w
Vochysiaceae	*Vochysia surinamensis* var. *surinamensis*	Iteballi	0.56	4	34	hw
***Lueheopsis* group**: low wood density, small seeds, emergent, wind dispersal						
Tiliaceae	*Lueheopsis rugosa*	Koyechiballi	0.64	3	37	hw
***Paypayrola* group**: low wood density, large seeds, subcanopy, non-wind dispersal						
Annonaceae	*Anaxagorea dolichocarpa*	Kurihikoyoko	0.67	6	9	u
	Guatteria sp.	Arara, smooth skin	0.65	5	20	m
	Unonopsis glaucopetala	Arara, broad leaf	0.72	5	20	bm
Aquifoliaceae	*Ilex martiniana*	Kakotaro	0.63	5	10	b
Boraginaceae	*Cordia nodosa*	Hurueroko / Ants tree	0.45	5	10	bm
Burseraceae	*Protium guianense* var. *guianense*	Haiawa	0.72	5	10	bm
Euphorbiaceae	*Alchornea sp.*	Kanakudiballi	0.48	5	20	bmv
	Aparisthmium cordatum	Mababalli	0.68	5	15	r
	Hevea pauciflora	Hatti	0.56	6	24	r
Lauraceae	*Aniba kappleri*	Gale, ginger	0.64	6	20	bm
	Endlicheria punctulata	Yekoro	0.60	6	15	bm

Family	Species	Vernacular name	WD	SM	H_m	DT
Lissocarpaceae	*Lissocarpa guianensis*	Barabara, charcoal	0.56	5	25	bm
Meliaceae	*Trichilia sp.*	Yuriballi	0.68	5	18	bm
Proteaceae	*Panopsis sessilifolia*	Mahoballi	0.60	6	20	hu
Simaroubaceae	*Simaba multiflora*	Hachiballi	0.41	5	10	b
Violaceae	*Paypayrola guianensis*	Adeboro	0.70	5	19	u
***Carapa* group**: low wood density, large seeds, canopy, non-wind dispersal						
Anacardiaceae	*Anacardium giganteum*	Ubudi	0.52	6	34	m
	Tapirira obtusa	Duka	0.44	5	30	bm
Annonaceae	*Bocageopsis multiflora*	Arara, fine leaf	0.72	5	29	b
Bombacaceae	*Catostemma fragrans*	Baromalli, sand	0.59	7	30	mr
Boraginaceae	*Cordia exaltata* var. *exaltata*	Table tree	0.48	5	27	bm
Burseraceae	*Protium decandrum*	Kurokai	0.52	6	27	bm
	Protium tenuifolium	Haiawaballi	0.64	5	30	bm
Caesalpiniaceae	*Cassia cowanii* var. *guianensis*	Warua	0.72	5	30	bm
Chrysobalanaceae	*Couepia guianensis*	Kauta, fine leaf	0.70	7	30	mrv
Ebenaceae	*Diospyros dichroa*	Barabara, fine leaf	0.56	5	30	bm
Lauraceae	*Aniba citrifolia*	Gale, almond	0.64	6	27	bm
	Aniba excelsa	Gale, greenheart	0.64	6	28	bm
	Aniba hypoglauca	Silverballi, yellow	0.64	6	30	bm
	Ocotea canaliculata	Silverballi, sawari skin	0.48	6	34	bm
	Ocotea floribunda cf.	Silverballi, pea's leaf kereti	0.38	6	34	bm
	Ocotea glomerata	Silverballi, kurahara	0.75	5	34	bm
	Ocotea oblonga	Silverballi, poor kereti	0.42	5	34	bm
	Ocotea puberula	Silverballi, kereti	0.54	5	34	bm
	Ocotea sp.	Silverballi, pear leaf	0.48	6	34	bm
Meliaceae	*Carapa guianensis*	Crabwood	0.66	7	35	hmr
Mimosaceae	*Inga alba*	Maporokon	0.64	5	34	bm
	Inga lateriflora	Shirada	0.67	5	30	bm
	Inga spp.	Warakosa	0.76	5	26	bm
Moraceae	*Bagassa guianensis*	Cow wood	0.79	5	29	bm
	Helicostylis tomentosa	Ituri-ishi-lokodo	0.76	5	30	m
	Pourouma guianensis subsp. *guianensis*	Buruma	0.44	5	27	bmv
Myristicaceae	*Iryanthera sagotiana*	Kirikaua	0.56	6	27	bm
Olacaceae	*Chaunochiton kappleri*	Hiwaradan	0.60	5	30	bm
	Dulacia guianensis	Hishirudan	0.60	6	30	bm
Papilionaceae	*Alexa imperatricis*	Haiariballi	0.64	6	34	ru
	Ormosia coccinea	Barakaro	0.72	6	34	b
	Ormosia coutinhoi	Korokororo	0.62	7	34	u
***Virola* group**: low wood density, large seeds, emergent, non-wind dispersal						
Apocynaceae	*Parahancornia fasciculata*	Dukali	0.60	5	40	m
Bombacaceae	*Catostemma commune*	Baromalli, swamp	0.59	7	38	mr
Burseraceae	*Trattinickia demerarae*	Ulu, rough skin	0.50	5	37	b
	Trattinickia rhoifolia	Ulu, smooth skin	0.50	5	37	b
Guttiferae	*Symphonia globulifera*	Manni	0.72	6	40	hm
Lauraceae	*Ocotea guianensis* var. *guianensis*	Silverballi, shirua	0.56	6	36	bm
	Ocotea tomentella	Baradan	0.56	6	37	bm
Mimosaceae	*Aberema jupunba* var. *trapezifolia*	Huruasa	0.64	5	38	bhmu
	Enterolobium barbebianum cf.	Devil grandfather's ear	0.42	6	40	m
	Enterolobium cyclocarpum	Devil's ear	0.42	6	40	m
	Parkia nitida	Manariballi, black	0.48	5	40	mr
	Parkia ulei	Uya	0.48	5	40	mr
Myristicaceae	*Virola michelii*	Dalli, hill	0.56	6	43	bm
	Virola sebifera	Dalli, like	0.56	6	43	bm
	Virola surinamensis	Dalli, swamp	0.56	6	43	bm
Papilionaceae	*Swartzia jenmanii*	Parakusan	0.72	6	38	mrv
Sapotaceae	*Pouteria caimito*	Asepokoballi, fine leaf	0.70	6	40	m
	Pouteria speciosa	Suya	0.56	8	37	m

Family	Species	Vernacular name	WD	SM	H_m	DT
Sterculiaceae	*Sterculia pruriens*	Maho, smooth leaf	0.48	6	35	mr
	Sterculia rugosa	Maho, rough leaf	0.48	6	35	bmr
***Tachigali* group**: low wood density, large seeds, canopy, wind dispersal						
Apocynaceae	*Himatanthus articulatus*	Mabwa	0.68	5	30	hw
Bignoniaceae	*Tabebuia insignis* var. *monophylla*	Cedar, white	0.68	5	27	hw
Caesalpiniaceae	*Tachigali rusbyi*	Yawaredan	0.77	5	30	w
Papilionaceae	*Hymenolobium petraeum*	Koraroballi	0.76	5	34	hw
***Sclerolobium* group**: low wood density, large seeds, emergent, wind dispersal						
Caesalpiniaceae	*Sclerolobium guianense* var. *guianense*	Kaditiri	0.76	6	40	w
Lecythidaceae	*Couratari guianensis*	Wadara	0.62	5	60	hw
Loganiaceae	*Antonia ovata*	Inyak	0.56	5	37	w
Mimosaceae	*Pseudopiptadenia suavolens*	Manariballi, like	0.79	5	50	w
Papilionaceae	*Hymenolobium flavum*	Darina	0.75	5	50	w
Vochysiaceae	*Ruizterania albiflora*	Muneridan	0.73	5	50	w
***Oxandra* group**: high wood density, large seeds, subcanopy, non-wind dispersal						
Annonaceae	*Duguetia neglecta*	Yari yari	0.98	5	9	b
	Duguetia yeshidan	Yeshidan	0.98	5	10	b
	Oxandra asbeckii	Karishiri	0.88	6	15	m
Chrysobalanaceae	*Hirtella caduca*	Fire tree	0.92	5	20	b
Dichapetalaceae	*Tapura guianensis*	Waiaballi	1.00	5	20	b
Eleocarpaceae	*Sloanea eichleri* cf.	Aruadan, broad rough leaf	1.00	6	20	bm
	Sloanea guianensis	Aruadan	1.00	6	18	bm
Guttiferae	*Rheedia benthamiana*	Asashi	0.85	4	15	m
	Tovomita spp.	Awasokule	0.92	6	14	bm
Hippocrateaceae	*Cheiloclinium cognatum*	Monkey syrup	0.82	5	12	m
Melastomataceae	*Mouriri sp.*	Mamuriballi	1.04	5	15	bm
Monimiaceae	*Siparuna decipiens*	Shitwood	0.80	4	10	v
	Siparuna sp.	Muniridan	0.80	4	15	v
Myrtaceae	*Calycolpus goetheanus*	Kakirio	0.88	7	20	bm
	Eugenia coffeifolia	Unknown C	0.92	5	15	bm
	Eugenia conjuncta	Konoko shrub	0.92	5	15	bm
	Eugenia patrisii	Hicha	1.00	5	15	bm
	Eugenia sp.	Turtle cherry	1.00	5	15	bm
	Marlierea montana	Kwako	1.07	5	15	b
	Marlierea schomburgkiana	Akarako	1.07	5	15	b
	Myrcia sp.	Ibibanaro	0.88	7	20	b
Olacaceae	*Heisteria cauliflora*	Makarasali	0.85	5	7	b
	Maburea trinervis	Maburea	0.95	7	20	m
Quiinaceae	*Quiina guianensis*	Okokonshi, fine leaf	1.10	5	15	m
	Quiina indigofera	Okokonshi, broad leaf	1.10	5	24	m
Rubiaceae	*Duroia eriophila* var. *eriophila*	Komaramara	0.92	5	10	bm
	Ixora aluminicola	Coffeeballi	0.90	5	10	bm
Sapindaceae	*Cupania hirsuta*	Kulishiri, black	0.90	5	15	bm
	Cupania scrobiculata	Kulishiri, white	0.90	5	10	bm
	Cupania sp.	Kulishiri	0.90	5	15	bm
	Matayba oligandra	Kulishiri, common	0.90	5	15	bm
***Chlorocardium* group**: high wood density, large seeds, canopy, non-wind dispersal						
Apocynaceae	*Geissospermum sericeum*	Manyokinaballi	0.96	5	26	bm
Caesalpiniaceae	*Chamaecrista adiantifolia* var. *pteridophylla*	Imirimiaballi	0.80	5	29	r
	Chamaecrista apoucouita	Apokaito	1.10	5	30	r
	Dicymbe altsonii	Wallaba, clump	0.88	7	32	ru
	Eperua grandiflora	Wallaba, ituri	0.99	7	27	ru
	Eperua rubiginosa	Watapa	0.99	7	27	ru
	Mora gonggrijpii	Morabukea	1.01	8	34	u
	Vouacapoua macropetala	Sarebebeballi	0.93	6	26	ru

Family	Species	Vernacular name	WD	SM	H_{m}	DT
Caryocaraceae	*Caryocar nuciferum*	Sawari	0.88	7	29	r
Celastraceae	*Maytenus myrsinoides*	Kaiarima	0.88	5	30	bm
Chrysobalanaceae	*Couepia exflexa* / *Hirtella racemosa* var. *hexandra*	Bokotokon	0.92	5	28	b
	Licania alba	Kautaballi	1.15	7	27	mrv
	Licania canescens	Marishiballi	1.04	7	30	mrv
	Licania cuprea	Konoko	1.00	7	30	mrv
	Licania heteromorpha var. *heteromorpha*	Buruburuli	1.03	6	30	mrv
	Licania heteromorpha var. *perplexans*	Kairiballi	1.03	6	30	mrv
	Licania hypoleuca	Unikiakia	1.12	7	29	mrv
	Licania laxiflora / *L. persaudii*	Kauta	1.20	7	30	mrv
	Licania sp.	Mahaicaballi	1.03	7	30	mrv
Euphorbiaceae	*Chaetocarpus schomburgkianus*	Ruri	0.83	5	26	bm
Guttiferae	*Platonia insignis*	Pakuri	0.85	7	34	m
Humiriaceae	*Humiria balsemifera* var. *floribunda*	Taurinero	0.88	5	32	bm
Icacinaceae	*Emmotum fagifolium*	Manobodin	0.84	5	30	b
Lauraceae	*Chlorocardium rodiei*	Greenheart	1.04	7	34	ru
Lecythidaceae	*Eschweilera alata*	Kakaralli, guave skin	1.12	6	30	mr
	Eschweilera coriacea / *E. decolorans*	Kakaralli, smooth leaf	1.00	6	32	mr
	Eschweilera sagotiana	Kakaralli, black	1.02	6	32	mr
	Eschweilera wachenheimii	Kakaralli, fine leaf thick skin	1.00	6	30	mr
	Lecythis confertiflora	Wirimiri	0.92	6	30	mr
	Lecythis corrugata	Wina	0.92	6	30	mr
	Lecythis holcogyne	Haudan	0.92	6	32	mr
	Lecythis zabucajo	Monkey pot	1.02	6	32	mrv
Linaceae	*Hebapetalum humiriifolium*	Shiballidan	1.00	4	26	m
Malpighiaceae	*Byrsonima aerugo*	Arikadako	0.88	6	35	b
	Byrsonima stipulacea	Kanoaballi	0.88	5	30	b
Mimosaceae	*Balizia pedicellaris*	Manariballi, red skin	0.80	5	27	ru
	Pentaclethra macroloba	Trysil	0.80	6	28	hu
Moraceae	*Brosimum guianense*	Tibokushi	1.17	5	26	bm
	Brosimum rubescens	Dukaliballi	0.92	5	30	bm
	Trymatococcus paraensis	Pasture tree	0.88	6	30	m
Nyctaginaceae	*Neea sp.*	Mamudan	0.87	5	30	bm
Olacaceae	*Minquartia guianensis*	Wanania	0.83	5	33	m
Papilionaceae	*Clathrotropis brachypetala* var. *brachypetala*	Aromata	1.10	7	29	ru
	Clathrotropis macrocarpa	Aromata, like	1.10	7	29	ru
	Dipteryx odorata	Tonka bean	1.11	6	32	rv
	Swartzia benthamiana var. *benthamiana*	Itikiboroballi	0.81	6	30	mrv
	Swartzia oblanceolata	Serebedan	0.89	6	30	mrv
	Swartzia spp.	Itikiboroballi, others	0.89	6	29	mrv
Sapindaceae	*Talisia squarrosa*	Moroballi	1.08	6	30	m
Sapotaceae	*Chrysophyllum pomiferum*	Paripiballi	0.95	6	34	m
	Chrysophyllum sanguinolentum	Barataballi	0.88	6	29	bm
	Micropholis venulosa	Kudibiushi	0.92	5	26	bm
	Pouteria cladantha	Aiomorakushi	1.20	5	27	bm
	Pouteria coriacea	Moraballi	1.04	6	26	m
	Pouteria egregia	Kokoritiballi, fine leaf	0.88	5	34	bm
	Pouteria filipes	Kamahora, fine leaf	1.12	6	34	m
	Pouteria guianensis	Asepoko	0.96	6	34	m
	Pouteria venosa subsp. *amazonica*	Kamahora, broad leaf	1.12	5	30	m
***Peltogyne* group**: high wood density, large seeds, emergent, non-wind dispersal						
Caesalpiniaceae	*Eperua falcata*	Wallaba, soft	0.86	6	36	ru
	Hymenaea courbaril	Locust	0.88	6	42	mr
	Mora excelsa	Mora	1.00	8	37	hu
	Peltogyne sp.	Purpleheart, saka	0.93	5	50	mrw

Family	Species	Vernacular name	WD	SM	H_m	DT
	Peltogyne venosa	Purpleheart	0.93	5	50	mrw
Chrysobalanaceae	*Licania majuscula*	Kautaballi, fine leaf	1.03	7	36	mrv
	Licania micrantha	Marishiballi, red	1.04	7	36	mrv
	Licania sp.	Konoko	1.03	7	36	mrv
	Parinari campestris	Burada	0.92	7	38	mrv
	Parinari excelsa	Aiomorodan	0.92	6	38	mrv
Combretaceae	*Terminalia amazonia*	Fukadi	0.80	5	43	m
	Terminalia dichotoma	Fukadi, swamp	0.80	5	43	hm
Euphorbiaceae	*Glycydendron amazonicum*	Devildoor tree	0.84	5	36	m
Humiriaceae	*Sacoglottis guianensis* var. *guianensis*	Dukuria	0.84	6	36	bmr
Lauraceae	*Licaria cannella*	Silverballi, brown	1.05	5	40	bm
Papilionaceae	*Swartzia leiocalycina*	Wamara	1.16	7	35	mrv
Sapotaceae	*Manilkara bidentata* subsp. *bidentata*	Bulletwood	1.07	6	38	m
	Pouteria reticulata subsp. *surinamensis*	Kokoritiballi, common	0.88	5	41	bm
***Aspidosperma* C group**: high wood density, large seeds, canopy, wind dispersal						
Apocynaceae	*Aspidosperma album*	Shibadan, smooth leaf	0.94	6	32	w
Bignoniaceae	*Tabebuia serratifolia*	Hakia	1.12	5	29	w
***Aspidosperma* E group**: high wood density, large seeds, emergent, wind dispersal						
Apocynaceae	*Aspidosperma cruentum*	Shibadan, boat leaf	0.92	5	40	w
	Aspidosperma exselsum	Yaruru	0.92	5	39	w
Papilionaceae	*Diplotropis purpurea*	Tatabu	1.03	5	48	w



Chapter 6

General discussion and summary

Regeneration and disturbance are thought to play key roles in the maintenance of the high tree species diversity in tropical rain forests. Nevertheless, the earliest stages in the regeneration of tropical rain forest trees, from seed production to established seedlings, have received little attention in population dynamical studies and in simulation models that are currently used to evaluate forest management. The pressure on tropical rain forests by disturbing anthropogenic activities has increased dramatically during the last decades, which may lead to shifts in the species composition. A better understanding of the interaction between tree regeneration and disturbance is needed to obtain insight in the regulation and maintenance of the high tree species diversity and to evaluate the consequences of the increased level of disturbance on the species diversity in tropical rain forests.

The aim of the research described in this thesis was to gather information on the earliest stages of the regeneration of tropical rain forest trees, and to use this knowledge in a simulation model to study the long-term effects of natural and anthropogenic disturbance on the composition of the forest. To this end, the seed production, seed dispersal, seed fate and spatial distribution of seedlings were investigated in natural and logged tropical rain forest in central Guyana. The collected information was combined with information from a partner project (Arets 2005[1]) and used to develop a new regeneration model within the SYMFOR modelling framework. The main results are summarized in this chapter.

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[1] Arets E.J.M.M. 2005. Responses of tree population dynamics and tree species composition to selective logging in a rain forest in Guyana. PhD thesis Utrecht University, Utrecht, the Netherlands. Tropenbos-Guyana Series. Tropenbos-Guyana Programme, Georgetown, Guyana. In preparation.

1 Regeneration of tropical rain forest trees

1.1 Seed production and dispersal

Species do not start to produce seeds at the same size. It was found that the size at which reproduction starts increased with the species-specific maximum height a tree can attain at maturity (chapter 2). On average, the minimum reproductive sizes were 4.1, 14.3 and 23.4cm DBH (*i.e.* diameter at breast height, 1.30m above the ground) for subcanopy (< 25m), canopy (25m ≥ maximum height < 35m) and emergent species (≥ 35m), respectively. While smaller species start producing seeds at smaller sizes, it was estimated that subcanopy and canopy species produced less seeds than emergent species at a given reference DBH (25.6cm). Subcanopy and canopy species had a seed production of 28 to 203 seeds at the reference DBH during the monitoring period of six months, while emergent species produced 627 to 14301 seeds. If the species-specific average size of reproducing trees is taken into account the differences become even larger and range from 37 for the subcanopy species to 46174 for one of the emergent species. Possibly the higher seeds production of emergent species can be attributed to fact that their adult trees generally have their crowns positioned in the high-light environment above the canopy, enabling them to capture more energy that can be spent on reproduction.

The emergent species that had the highest seed production in terms of numbers, *Sclerolobium guianense*, also had the smallest (lightest) seeds. Seeds of this species have a fresh mass of 0.3g, while *Chlorocardium rodiei* has seeds of 71.3g. It is known that a trade-off exists between seed mass and seed number. The results obtained in the present study also support this trade-off and generally the species-specific seed production of a tree at the reference DBH decreased with increasing seed mass. One clear exception to this rule was *Swartzia leiocalycina*, which had a mast fruiting year during the monitoring period and produced far more seeds than could be expected from its seed mass. The seed production of one species for which data from three consecutive years were available, *Chlorocardium rodiei*, produced two to three times as many seeds in one year than in the other two years, indicating that also species that do not exhibit clear mast fruiting can show considerably year to year variation in seed production.

Seeds were dispersed over short distances only. Estimated median dispersal distances (the radius within which 50% of the seeds is deposited) ranged from 3.7 to 13.5m and 99% of the seeds fell within 9.6 to 34.8m for trees with the reference DBH (note that dispersal distances increase somewhat with increasing tree size as crown radius is included in the equation). Seed mass did not only influence seed production, but also the distance over which seeds were dispersed. On average, the dispersal distance decreased with increasing seed mass. The effect of dispersal type could not be studied very well as only one wind-dispersed species was included. However, this wind-dispersed species, *Sclerolobium guianense*, did disperse its seeds furthest.

The estimated seed production of individual trees was higher in a logged than in an undisturbed forest patch. Possibly competition for resources decreases during the first years after logging, since trees are felled or damaged during the logging operation, enabling the remaining vegetation to produce more energy for the reproduction. Whether logging will result in higher seed availability in forest patches remains questionable, as the number of trees that produces seeds will decrease. This effect will be strongest for timber species of which a large proportion of the reproductive population can be removed.

1.2 Post-dispersal seed fate

Following dispersal a seed has to germinate before it is killed or loses its viability. Germination success was influenced by canopy openness (measure for the light availability) and correlated with species-specific seed mass (chapter 3). In the dark forest understorey, germination success (emergence success for the two species with the smallest seeds) increased with seed mass. For the species with the smallest seeds no germination was observed in the forest understorey, while for one of the larger seeded species all seeds germinated in one of the sites. However, as canopy openness increased the germination success of the small-seeded species increased slightly, and that of the species with larger seeds decreased sharply. For some of the large-seeded species no seeds germinated in the larger gaps. Consequently, the positive effect of seed mass on germination success disappeared as canopy openness increased. In the largest gaps, also the species with the smallest seeds germinated less well than in gaps with intermediate canopy openness.

The reduction in germination success as canopy openness increased for large-seeded species was caused by an increased chance of desiccation. Desiccation killed very few seeds in the forest understorey, but the proportion of seeds killed by desiccation increased rapidly as canopy openness increased. Small-seeded species suffered far less from desiccation than species with larger seeds.

Many seeds that were placed in the experimental sites were removed by biotic or abiotic vectors. The fate of these seeds could not be determined. It is possible that the removed seeds were eaten or cached by insects or mammals, that they were washed away during a rain shower or were blown away. The proportion of seeds that was removed decreased with seed mass but increased with canopy openness. Predation by insects and removal of seeds were the most important causes of failure to germinate for the small-seeded species. The proportion of seeds killed with certainty by insects decreased with seed mass. The main insect predators of small-seeded species were ants, while beetles and termites preferred larger seeds (personal observation). The proportion of seeds that was eaten by mammals was relatively low and increased with seed mass. Insect and mammal predation were not influenced by canopy openness. At the end of the experiment few seeds remained dormant and the majority of the seeds had either germinated or died, except for the seeds of *Parinari campestris*. 96% of the seeds of this species seemed to remain dormant throughout the experiment. Possibly this species simply requires a long time to germinate, or it may require a specific treatment to break through the extremely thick and hard shell.

1.3 Spatial distribution of seedlings

In chapter 4 the spatial distribution of seedlings was analysed in an undisturbed plot and in a plot that was logged approximately two years before the data collection. For nearly all of the species seedlings were clumped at a scale of 10 to 25m, rather than distributed randomly over the area. Seedlings of pioneer species (small seeds, low wood density) showed a stronger spatial autocorrelation (clumping) and were clumped over a slightly larger distance than long-lived pioneer (large seeds, low wood density) and climax species (large seeds, high wood density). Overall, the latter two functional groups showed a very similar degree of clumping.

Seedlings of the pioneer species were not clumped in the vicinity of parent trees, but rather at intermediate distances from parent trees. Half of the long-lived pioneers and the majority of the climax species had more seeds close to parents, than would be expected on the basis of a random distribution. Generally seedlings of these species were concentrated within ten metres from the closest conspecific adult tree. If seedlings are clumped around parent trees then the spatial autocorrelation of seedlings may be even stronger if the adult trees themselves are also clumped. For two thirds of the species adult trees were clumped. However, the adult trees were clumped at a far larger scale than seedlings and it seems unlikely that the observed spatial distribution patterns of seedlings were caused by the clumped distribution of the adult trees.

Pioneer species were clearly more abundant at sites with intermediate and high densiometer values (a measure for the light availability) than was expected under a random distribution. The majority of the long-lived and climax species were distributed randomly with respect to light availability, with a few exceptions that preferred either low- or high-light sites.

The distribution of seedlings over sites with different disturbance histories (undisturbed, natural gaps, skid trails, logging gaps and skid trails in logging gaps) was evaluated in the logged plot. For the majority of the species seedlings were not distributed randomly over the different disturbance types. All pioneer species were found more in logging gaps and especially on skid trails in logging gaps than was expected from a random distribution. The long-live pioneers and climax species did not show a clear pattern: some species were found more than expected in undisturbed patches, others more in logged patches and others did not show a preference. The effects of light and disturbance on the spatial distribution of seedlings cannot be separated well, since the logging gaps and skid trails in logging gaps also had the highest densiometer values.

The pioneers were distinguished from the other two functional groups by their small seeds, while the long-lived pioneer and climax species differed in wood density. The fact that generally pioneer species differed in their spatial distribution from the other two groups, while the long-lived pioneers and climax species showed very similar overall spatial distribution patterns, suggests that seed mass had a larger effect on the distribution pattern of seedlings than wood density.

1.4 Recruitment limitation

In chapters 2, 3 and 4 the first stages of tropical tree regeneration are described. Seed mass was found to be a very important factor influencing the regeneration of tropical tree species. Seed mass was correlated with seed production, seed dispersal (chapter 2), post-dispersal seed fate (chapter 3) and spatial distribution of seedlings (chapter 4). The results obtained in these chapters suggest that many species will be limited in their recruitment.

The recruitment of a species can be limited in two distinct ways: 1) it can be ‘seed limited’, *i.e.* fail to arrive at all sites suitable for germination, growth and survival, and 2) it can be ‘site limited’, *i.e.* limited in the availability of suitable sites for germination and growth.

Most species in central Guyana have large seeds. Species with large seeds will generally be seed limited. They produce few, large seeds that are dispersed over short distances only and the majority of the seeds will fall within a few metres from the crown. The seeds of large-seeded species germinate very well in the dark understorey, but do not tolerate the high insolation in open logging gaps very well. As canopy openness increases their germination success decreases due to desiccation. The short seed dispersal distances largely determine the spatial distribution patterns of their seedlings. The seedlings are clumped around adult trees and their distribution is not consistently related to light availability or disturbance history.

Species with small-seeds are rare in Guyana and their seed production and dispersal could not be studied, but generally it is assumed that seeds of these species are widely dispersed, either in space or in time (persistent seed bank). These species are more likely to be site limited. Their seeds germinate better in gaps with intermediate canopy openness than in the understorey or very large gaps. Their seedlings are clumped some distance away from adult trees in sites with intermediate light availability and in logging gaps, reflecting their germination requirements.

2 Modelling regeneration

Tree growth and yield simulation models that have been developed for tropical rain forests rarely include detailed descriptions of the regeneration. Generally the regeneration processes are aggregated into one or a few functions that are used to calculate the probability that a larger individual (of for example 5cm DBH) will recruit based on the surrounding vegetation. This method neglects the circumstances and events that occur during the decennia or centuries it may take to grow from a seed to a small tree. In addition the number of recruits generally is independent of the number of conspecific adults, assuming that seeds are ubiquitous. The results collected in chapters 2 and 4 indicate that this assumption will generally not hold for individual species. This implies that the functions included in existing models cannot accurately predict regeneration and it is expected that the omission of explicit functions for the regeneration of tree species will lead to an underestimation of the effect of natural and anthropogenic disturbance. The data on the regeneration processes that were collected in this thesis and data collected by Arets (2005) were used to develop a new model with detailed descriptions of the regeneration processes within the SYMFOR modelling framework (chapter 5). The SYMFOR framework includes descriptions of recruitment, growth and mortality and contains functions for a wide variety of silvicultural treatments that can be used to evaluate the effect of different logging scenarios on the forest.

To facilitate interpretation of the model results and to avoid a data shortage for many rare species, SYMFOR uses functional groups. For the present study species were classified into 15 functional groups based on their wood density, seed mass, adult stature and dispersal type. This classification is an extension of the classifications used in chapters 2 and 4. In principle, each functional group has its own set of parameters in SYMFOR.

The model is spatially explicit and individual-based for trees larger than 5cm DBH. For each of these trees the growth rate and mortality probability is calculated based on a competition index that is calculated from the surrounding vegetation. To calculate the regeneration (from seed production to trees of 5cm DBH) the simulated forest is divided into grid squares of ten by ten metres. The new model includes a seed production and dispersal function to calculate the seed density per functional group in each of the grid squares from the adult trees in the plot of the same functional group, as derived in chapter 2. A germination probability is calculated from the surrounding vegetation using the relation between germination success and densiometer value from chapter 3. If a seed germinates a new seedling cohort is made for that grid square. A seedling cohort is a group of seedlings in the same grid square of one functional group that were created in the same year. Each year the growth and mortality of the seedling cohorts are calculated using a competition index that depends on the surrounding vegetation. If a seedling cohort reaches 5cm DBH it becomes a tree. Throughout a tree’s life it can be damaged by falling trees and subsequently die.

As in most modelling studies, it was assumed that the forest is in dynamic equilibrium, meaning that on average the forest composition is assumed to remain constant. Test simulations of undisturbed forest with a length of 300 years showed that the functional group composition did not remain stable in the new model. In the first fifty years of the simulations the functional group abundances changed rapidly. Gradually the model forest transformed from a forest with large-seeded canopy groups to a forest with large-seeded subcanopy groups.

To test the response of the model forest to logging two scenarios were run, one with a single logging event at the start of the simulation and one with a 25-year logging cycle. In both scenarios at most eight trees were harvested per hectare. As was expected, one logging event did not lead to large changes in the forest composition compared with the control simulations. However, a 25-year logging cycle transformed the forest into a secondary forest dominated by pioneer species with small seeds and light wood and with low yields per logging event. Despite the seemingly correct response to logging it was decided that the model could not be used in this form to analyse the long-term effects of disturbance on the functional group composition. This decision was based on the large shifts in the forest composition in simulations of undisturbed forest.

To determine possible causes of the instability of the model under undisturbed circumstances a sensitivity analysis was performed and the individual regeneration processes during the first ten years of the simulations were compared with field data. These analyses did not reveal a major cause of the model instability, but many minor possible causes were found. During the first ten years of the simulations the annual recruitment was somewhat higher than that observed in the field and juveniles experienced somewhat less competition, grew faster and survived better (adult tree processes were not compared with field data). Probably the accuracy of the functions in the model could be improved if more data were available, for more species per functional group and spanning longer periods. In the current version of SYMFOR, the only mechanism through which the population growth is regulated is the competition index. Other stabilizing mechanisms, such as density-dependent mortality, are currently missing and will almost certainly increase the stability of the model once they are included. Finally, the assumption that the forest is in dynamic equilibrium may need to be verified. Shifts in the numbers of individuals in the field suggested that the populations in the sampled area were not stable, which may also partly explain the instable model results.

A major ‘problem’ of the current model is its complexity. The model developed in this thesis contains over 1000 parameters and all processes are related. This makes it extremely difficult to analyse the model and understand the model results. At the moment, it seems the best option to use existing models to evaluate forest management, keeping in mind that the effects of disturbances may be underestimated. From an ecological point of view it is worth the effort to improve models that include regeneration, since they may provide important information on the regulation and maintenance of the high species diversity in tropical rain forests.

3 Logging and tropical tree regeneration

The results obtained in this thesis indicate that logging can have large consequences for the regeneration of tropical trees species. Below the most important results relating to anthropogenic disturbance are summarized and their implications for forest management are discussed.

The seed production of three (non-pioneer) species was compared between trees in a forest patch that has never been logged and a patch that had been logged approximately two years before the data were collected. It was found that for these species the estimated seed production of individual trees was higher in the logged area than in the undisturbed area (chapter 2). This suggests that logging will increase the seed availability in an area. However, as a large proportion of the reproductive trees in an area can be felled or damaged during logging activities, the increased individual fecundity will not necessarily result in an increased seed availability.

The tropical tree species that were studied dispersed their seeds over short distances only (chapter 2). Usually, the majority of the seeds will be deposited within of few metres from the crown of the parent tree. Therefore, if a tree is felled, it is unlikely that new seeds of the timber species will arrive in the vicinity of the felled tree, unless there are other conspecific reproductive trees nearby. To ensure that seeds will be available throughout the logged area, a number of healthy, large trees should be left in the forest. Since seeds are dispersed over short distances only, it is important that these remaining seed trees are distributed evenly over the forest to optimize the distribution of seeds over the area. Seed production and dispersal functions (chapter 2) can be used to assist in defining the size and number of seed trees that should remain in the forest and what the distances between these trees should be.

Germination success strongly depends on the canopy openness (chapter 3). The creation of large, open gaps will lead to a dramatic reduction in the germination success of large-seeded species. Especially one of the most important timber species, *Chlorocardium rodiei* (greenheart), was extremely sensitive to an increased canopy openness and nearly all seeds of this species desiccated in logging gaps. It is therefore important to avoid the creation of large, open gaps, by minimizing both the gap size and the damage to the vegetation below felled trees caused during the felling and extraction of the trees. In addition, most seedlings of large-seeded species were found within ten metres from the adult trees (chapter 4). If all vegetation around trees selected for felling is damaged this will delay the regeneration, especially for the timber species, since all seedlings and saplings of the timber species growing below the felled that may eventually replace the felled tree will be killed and regeneration at that location has to start from scratch. If logging gaps become too large and frequent, it may be expected that the pioneer species will become much more abundant as they germinate better in high-light environments. In addition, their seedling distribution is less restricted by adult tree distribution than for the non-pioneer species and their seedlings were predominantly found in high-light sites and forest patches disturbed by logging.

Growth and yield models are being used to evaluate the forest management. For example, the Guyana Forestry commission uses a previously developed SYMFOR model, which is calibrated for Guyana. Unfortunately, existing models generally do not include detailed regeneration functions, which may result in an underestimation of the effect of disturbance. The model that was developed in this thesis, which explicitly models regeneration, suggests that, while one logging event will not have a large effect on the forest, a 25-year logging cycle will have dramatic consequences (chapter 5). Undesirable pioneer species with low wood density take over the dominant position of the hard wood species within 300 years and timber yields decrease rapidly. The model has to be improved before it can be used to test the effect of different silvicultural treatments. Currently, growth and yield models without detailed tree regeneration functions are the best tools available and should be used to evaluate sustainability of the applied forest management, both from an ecological and economical point of view.

Samenvatting

Tropische regenwouden staan om hun grote rijkdom aan boomsoorten bekend. Regeneratie en verstoring zijn twee belangrijke componenten in theorieën die het behoud van deze soortdiversiteit proberen te verklaren. Toch is nog relatief weinig bekend over de vroegste stadia van de regeneratie van tropische boomsoorten en de invloed die verstoring daarop heeft en meestal worden ze niet meegenomen in het opstellen van richtlijnen voor duurzaam bosbeheer. De afgelopen decennia is de hoeveelheid verstoring in tropische regenwouden enorm toegenomen door onder andere houtkap. Dit kan tot grote veranderingen in de samenstelling van het bos leiden en mogelijkerwijs zelfs tot het uitsterven van bepaalde soorten.

Het effect van verstoring op de regeneratie van tropische boomsoorten en op de soortensamenstelling is moeilijk te bestuderen omdat bomen honderden jaren oud kunnen worden. Een oplossing voor dit probleem is het gebruik van computer modellen waarmee het effect van verstoring op de lange termijn kan worden gesimuleerd. Dit type modellen is ook belangrijk voor het beoordelen van de duurzaamheid van bosbeheer. De meeste bestaande modellen bevatten echter geen beschrijving van de eerste stadia van de regeneratie, wat tot een onderschatting van het effect van verstoring op het bos zou kunnen leiden.

Het onderzoek beschreven in dit proefschrift heeft als doel om 1) meer inzicht in de vroegste stadia in de regeneratie (zaadproductie, zaadverspreiding, kieming en verdeling van zaailingen over het bos) van een aantal tropische boomsoorten te krijgen en het effect van verstoring daarop, en 2) om een simulatie model te ontwikkelen en dit te gebruiken om het effect van natuurlijke en aan houtkap gerelateerde verstoring op de samenstelling van het bos te bestuderen. Het onderzoek werd in het kader van het Tropenbos-Guyana Programme en het prioriteit programma ‘Biodiversiteit in verstoorde ecosystemen’ van NWO-ALW (de Nederlandse Organisatie voor Wetenschappelijk Onderzoek, Aard- en Levenswetenschappen) en WOTRO (Wetenschappelijk Onderzoek van de Tropen en Ontwikkelingslanden) uitgevoerd. De gegevens voor het onderzoek werden in het tropisch regenwoud in de omgeving van Mabura Hill in Guyana verzameld, in zowel de concessie van Demerara Timbers Ltd. en het Mabura Hill Forest Reserve. De belangrijkste resultaten worden in de volgende paragrafen kort beschreven.

1 Regeneratie van tropische bomen

1.1 Zaadproductie en –verspreiding

De grootte waarop een boom begint met het maken van zaden verschilt van soort tot soort. Het bleek dat de grootte waarop de reproductie begint toenam met de maximale hoogte die een soort kan bereiken (hoofdstuk 2). Ook het aantal zaden dat werd geproduceerd hing samen met de maximale hoogte. Naar schatting produceerden kleine soorten (maximale hoogte < 25m) en kronendaksoorten (maximale hoogte tussen 25 en 35m) 28 tot 203 zaden in zes maanden tijd bij de referentie diameter van 25.6cm (ongeveer de gemiddelde diameter van alle gemeten volwassen bomen), terwijl grote soorten (maximale hoogte meer dan 35m) 627 tot 14301 zaden maakten. Een mogelijke verklaring hiervoor is, dat de kronen van de volwassen bomen van de grote soorten boven het kronendak uitsteken en daardoor meer licht kunnen opvangen en meer energie beschikbaar hebben voor reproductie. De grote soort die de meeste zaden maakte, *Sclerolobium guianense*, had ook de lichtste zaden. Het is een bekend fenomeen, dat soorten met lichte zaden meer zaden kunnen produceren dan soorten met zware zaden. Dit werd ook in dit onderzoek gevonden. Het aantal zaden dat een boom met de referentie diameter maakte nam af met de zaadmassa.

De zaden werden slechts over kort afstanden verspreid. Naar schatting viel 50% van de zaden binnen 3.7 tot 13.5m van de boom viel en 99% van de zaden lag niet meer dan 9.6 tot 34.8m van de boom. Gemiddeld gezien nam de verspreidingsafstand van een soort af met de zaadmassa. Het effect van de manier van verspreiden kan niet goed worden onderzocht, omdat er maar één windverspreide soort werd onderzocht, maar deze soort verspreidde zijn zaden wel het verst.

Voor drie soorten kon de zaadproductie in een onverstoord stuk bos worden vergeleken met die in een stuk bos dat ongeveer twee jaar voor de metingen was gekapt. Bomen van deze soorten maakten minder zaden in het onverstoorde dan in het gekapte stuk bos, mogelijkerwijs doordat de concurrentie om licht en nutriënten onder grote bomen de eerste jaren na de kap lager is dan in een onverstoord bos. Alhoewel de zaadproductie per boom toeneemt, wil dat nog niet zeggen dat de totale zaadproductie in het gebied na kap ook toeneemt, aangezien er tijdens het kappen veel volwassen bomen kunnen worden verwijderd of beschadigd.

1.2 Kieming en overleving van zaden

De volgende stap in de regeneratie is de kieming. Zaden van elf soorten werden op twee plekken in de ondergroei van het bos en in acht openingen van verschillende grootten gelegd (hoofdstuk 3). Vervolgens werden de kieming en overleving van de zaden gedurende een aantal maanden onderzocht. De kiemingskans was aan de openheid van het kronendak (die samenhangt met de hoeveelheid licht) en de zaadmassa van een soort gerelateerd. In de donkere ondergroei nam de kiemingskans gemiddeld gezien toe met de zaadmassa. Soorten met kleine zaden kiemden niet of nauwelijks, terwijl van soorten met grote zaden bijna alle zaden kiemden. Met toenemende openheid van het kronendak nam de kieming van soorten met kleine zaden wat toe, terwijl soorten met grote zaden veel minder goed kiemden.

Hierdoor verdween het effect van zaadmassa op de kieming. De belangrijkste reden voor de afgenomen kieming van de soorten met grote zaden was dat de zaden van deze soorten in de felle zon uitdroogden voordat ze konden kiemen.

Een groot aantal zaden, met name van de soorten met kleine zaden, werd niet meer teruggevonden en het lot van deze zaden is onbekend. Ze kunnen door insecten of zoogdieren zijn meegenomen of opgegeten, of zijn weggeblazen of weggespoeld. Dit verdwijnen van zaden en vraat door insecten waren de belangrijkste oorzaken die de kieming van soorten met kleine zaden in de weg stonden. Vraat door insecten nam af met zaadmassa. Soorten met kleine zaden werden vooral opgegeten door mieren, terwijl soorten met grote zaden vooral door (larven van) kevers en termieten werden beschadigd. Slechts weinig zaden werden door zoogdieren opgegeten en de vraat door zoogdieren nam toe met zaadmassa. Tegen het einde van het experiment waren bijna alle zaden gekiemd, verdwenen of dood, met uitzondering van de zaden van *Parinari campestris*. Van deze soort bleven bijna alle zaden onaangetast en niet gekiemd liggen. Misschien hebben de zaden van deze soort een speciale behandeling nodig om kieming te stimuleren.

1.3 De ruimtelijke verdeling van zaailingen

De ruimtelijke verdeling van zaailingen werd onderzocht in een onverstoord stuk bos in het reservaat en in een gebied dat ongeveer twee jaar voor de metingen was gekapt (hoofdstuk 4). De verdeling van zaailingen was bijna nooit willekeurig. Voor bijna alle soorten kwamen zaailingen op een afstand van 10 tot 25m gegroepeerd voor. Zaailingen van pioniersoorten (soorten met kleine zaden en een lage houtdichtheid) waren iets sterker geclusterd dan zaailingen van langlevende pioniers (grote zaden, licht hout) en climaxsoorten (grote zaden, zwaar hout).

De verdeling van zaailingen werd aan de positie van volwassen bomen, aan licht en aan verstoring gerelateerd. Het bleek dat de zaailingen van pioniersoorten niet rondom, maar op een middelgrote afstand van ouderbomen waren geclusterd. Voor ongeveer de helft van de langlevende pionier- en climaxsoorten werden wel meer zaailingen binnen de eerste tien meter van volwassen bomen van dezelfde soort gevonden dan op basis van een willekeurige verdeling werd verwacht. De ouderbomen van de meeste onderzochte soorten kwamen ook gegroepeerd voor, maar op een grotere schaal dan de zaailingen. Daarom lijkt het onwaarschijnlijk dat de clustering van zaailingen door clustering van ouderbomen werd veroorzaakt en lijkt het eerder een gevolg van de geringe verspreiding van de zaden te zijn.

Zaailingen van pioniers kwamen veel meer op plaatsen met een hoge densiometerwaarde (een maat voor de hoeveelheid licht) voor dan op basis van een willekeurige verdeling werd verwacht. De ruimtelijke verdeling van zaailingen van de meeste langlevende pionier- en climaxsoorten leek niet door de hoeveelheid licht te zijn bepaald. Het effect van verstoring op de ruimtelijke verdeling van zaailingen werd alleen in het gekapte stuk bos onderzocht. Het bleek dat de zaailingen van pioniersoorten vooral in de grote openingen als gevolg van de houtkap voorkwamen en op de paden in die openingen waarover de boomstammen werden weggesleept. De langlevende pionier- en climaxsoorten lieten geen duidelijk patroon zien. Sommige van deze soorten leken vooral in verstoorde gebieden voor te komen, terwijl andere soorten deze juist leken te vermijden.

De ruimtelijke verdeling van de pionierzaailingen onderscheidde zich duidelijk van die van de langlevende pioniers en climaxsoorten, terwijl eigenlijk geen duidelijk verschil tussen die laatste twee groepen kon worden gevonden. Dit suggereert dat zaadmassa een grotere rol in het tot stand komen van de ruimtelijke verdeling van de zaailingen speelt dan de houtdichtheid.

1.4 Beperkingen op de regeneratie

Het onderzoek beschreven in hoofdstukken 2, 3 en 4 laat zien, dat zaadmassa een belangrijke rol speelt in de vroegste stadia van de regeneratie van tropische boomsoorten. Zaadmassa had een effect op de zaadproductie en zaadverspreiding (hoofdstuk 2), op de kieming en overleving van zaden (hoofdstuk 3) en op de ruimtelijke verdeling van zaailingen (hoofdstuk 4). Bovendien laat het onderzoek duidelijk zien, dat regeneratie niet onbeperkt is. De regeneratie van soorten kan ‘zaad-gelimiteerd’ of ‘plek-gelimiteerd’ zijn. In het eerste geval beperkt het aantal zaden het aantal zaailingen, in het tweede geval wordt het aantal zaailingen beperkt door het aantal plekken dat voor kieming en overleving geschikt is.

De bossen in het midden van Guyana worden door boomsoorten met grote zaden gekenmerkt. Deze soorten zullen waarschijnlijk meestal zaad-gelimiteerd zijn. Ze produceren een klein aantal grote zaden, die over beperkte afstanden worden verspreid. De zaden zullen dus niet overal beschikbaar zijn, maar vooral rondom ouderbomen worden gevonden. De grote zaden van deze soorten kiemen erg goed in de donkere ondergroei in onverstoorde bossen, maar drogen uit in grote openingen in het bos, waardoor veel minder zaden kiemen. Het lijkt erop, dat de geclusterde verdeling van hun zaailingen rondom ouderbomen voornamelijk door de korte verspreidingsafstand van de zaden wordt bepaald en dat de hoeveelheid licht en verstoring geen duidelijke rol in de verdeling van de zaailingen spelen.

Soorten met kleine zaden zijn zeldzaam in Guyana. Hierdoor kon de zaadproductie en verspreiding van deze soorten niet worden bestudeerd. Het is echter aannemelijk dat deze soorten veel zaden produceren en dat deze zaden ver kunnen worden verspreid of in de zaadbank kunnen overleven en daardoor overal aanwezig zijn. Soorten met kleine zaden zijn waarschijnlijk eerder plek-gelimiteerd. Ze kiemen beter in middelgrote openingen in het bos dan in de ondergroei. Bovendien komen hun zaailingen gegroepeerd voor op plekken met veel licht en in openingen die tijdens het kappen zijn ontstaan.

2 Het modelleren van regeneratie

Bestaande simulatiemodellen voor de groei en houtopbrengst voor tropische regenwouden bevatten meestal geen nauwkeurige beschrijving van de regeneratie. Vaak worden de jaren, decennia of zelfs eeuwen uit het leven van een boom samengevoegd tot één kansproces, dat afhangt van de hoeveelheid vegetatie in de directe omgeving. Het nadeel van deze manier van het modelleren van regeneratie is, dat deze niet door gebeurtenissen in het verleden wordt beïnvloed en onafhankelijk van het aantal ouderbomen van dezelfde soort is. Impliciet wordt in dit type modellen dus aangenomen dat zaden overal aanwezig zijn, terwijl eerder in dit proefschrift juist werd aangetoond dat dit niet het geval is. Mogelijkerwijs leidt dit tot een overschatting van de regeneratie in bossen waarin gekapt is en daardoor tot een onderschatting van het effect van kap op de samenstelling van het bos. De gegevens, die voor dit proefschrift werden verzameld, werden met gegevens van Arets (2005[1]) over onder andere de groei en mortaliteit van bomen gecombineerd, om zo een gedetailleerd regeneratiemodel voor SYMFOR te ontwikkelen (hoofdstuk 5). SYMFOR is een modelstructuur, die een aantal modellen voor de regeneratie, groei en mortaliteit van tropische bomen bevat, alsmede modellen waarmee de houtkap kan worden gesimuleerd.

Om de resultaten van het model te kunnen interpreteren werden de soorten ingedeeld in functionele groepen, d.w.z. soorten met dezelfde ecologische eigenschappen. Bovendien heeft dit als voordeel, dat zeldzame soorten, waarvoor te weinig data werden verzameld, toch in de ontwikkeling van het model kunnen worden meegenomen als onderdeel van één van de functionele groepen. De soorten werden op basis van hun houtdichtheid, zaadmassa, maximale hoogte en manier van zaadverspreiding in 15 functionele groepen ingedeeld. Elk van deze functionele groepen heeft in principe zijn eigen parameterwaarden in SYMFOR.

Het ontwikkelde model is ruimtelijk expliciet en werkt met individuele bomen voor individuen groter dan vijf centimeter diameter. Elk jaar wordt voor elk van deze bomen de groei en mortaliteit berekend aan de hand van een concurrentie-index, die afhangt van de omringende vegetatie. Voor het modelleren van de regeneratie wordt het te simuleren perceel in cellen van tien bij tien meter verdeeld. Voor elk van deze cellen wordt de zaaddichtheid per functionele groep met behulp van een zaadproductie- en verspreidingfunctie berekend, die gebruik maakt van de afstanden tot en grootten van ouderbomen van dezelfde functionele groep in het perceel. Vervolgens wordt de kiemkans van de zaden berekend op basis van een densiometerwaarde, die afhangt van de omringende vegetatie. Als één of meerdere zaden kiemen wordt een nieuwe zaailingcohort aangemaakt. Een zaailingcohort is dus een groep zaailingen van één functionele groep, die in dezelfde cel staan en in hetzelfde jaar gekiemd zijn. Elk jaar wordt de groei en overlevingskans voor elk van de zaailingcohorten op basis van de concurrentie-index uitgerekend. Als een zaailingcohort een diameter van 5cm heeft bereikt worden de zaailingen van de cohort individuele bomen en krijgen ze een eigen positie binnen de cel. Zowel zaailingen als bomen kunnen door omvallende bomen worden beschadigd en daardoor doodgaan.

Het bos werd verondersteld in een dynamisch evenwicht te verkeren, d.w.z. dat de samenstelling van het bos onder normale omstandigheden niet verandert. Onder deze aanname werd verwacht, dat ook het aandeel van de functionele groepen niet zou veranderen in modelsimulaties zonder houtkap. Dit was echter niet het geval. Vooral in de eerste vijftig jaar van de simulaties veranderde de samenstelling van het bos sterk en uiteindelijk werd het bos door kleine soorten met zware zaden gedomineerd, in plaats van de kronendaksoorten

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[1] Arets E.J.M.M. 2005. Responses of tree population dynamics and tree species composition to selective logging in a rain forest in Guyana. Proefschrift Universiteit Utrecht, Utrecht, Nederland. Tropenbos-Guyana Series. Tropenbos-Guyana Programme, Georgetown, Guyana. In voorbereiding.

met zware zaden. Het model reageerde wel op houtkap zoals werd verwacht. Eenmalig kappen leverde vergelijkbare resultaten op als de simulaties zonder kap, maar als elke 25 jaar werd gekapt veranderde de samenstelling van het bos sterk. Na 300 jaar werd het bos door typische pioniersoorten met kleine zaden en licht hout gedomineerd. Bovendien nam het aantal bomen dat per keer gekapt kon worden sterk af. Op grond van de sterk veranderende samenstelling van het bos in simulaties zonder kap werd echter besloten dat het model nog niet kan worden gebruikt voor gedetailleerde scenariostudies.

Mogelijke oorzaken van deze instabiele simulaties werden met behulp van een gevoeligheidsanalyse en middels vergelijking van de individuele processen gedurende de eerste tien jaar van de simulaties met veldwaarnemingen onderzocht. Er werd echter geen hoofdoorzaak van het probleem gevonden. Wel werden een aantal kleinere problemen gevonden, die mogelijk hebben bijgedragen aan de onverwachte resultaten. Tijdens de eerste tien jaar van de simulaties kwamen er per jaar gemiddeld wat meer zaailingen bij dan in het veld en kleine planten hadden een wat lagere concurrentie-index, groeiden sneller en overleefden beter. De nauwkeurigheid van deze processen kan waarschijnlijk vergroot worden als data voor meer soorten, over langere tijd en in grotere gebieden kunnen worden verzameld. Een andere mogelijke verbetering is het toevoegen van meer stabiliserende processen, zoals dichtheids- en afstandsafhankelijke sterfte. Momenteel is de concurrentie-index de enige beperking op de populatiegroei. Ook is het natuurlijk mogelijk, dat de aanname, dat het bos in een dynamisch evenwicht is, niet juist is. De gegevens uit het onderzoeksgebied laten ook zien, dat het aantal individuen per functionele groep in de loop van een paar jaar in kleine gebieden verandert.

Een belangrijk nadeel van het ontwikkelde model is dat het met zijn ruim duizend parameters en onderling afhankelijke processen te complex is om het model goed te kunnen analyseren en de resultaten te begrijpen. Totdat er een beter alternatief voor handen is lijkt het de beste optie om bestaande modellen, zoals eerdere modellen binnen SYMFOR, te gebruiken om bosbeheer te evalueren. Men mag echter niet uit het oog verliezen, dat deze modellen mogelijkerwijs het effect van verstoring onderschatten. Het is wel relevant om te proberen het model dat ontwikkeld werd in dit proefschrift te verbeteren of andere modellen met gedetailleerde regeneratiemodules te ontwikkelen om meer inzicht in de regulatie en het behoud van de grote diversiteit aan boomsoorten in het tropisch regenwoud te krijgen.

3 Houtkap en regeneratie

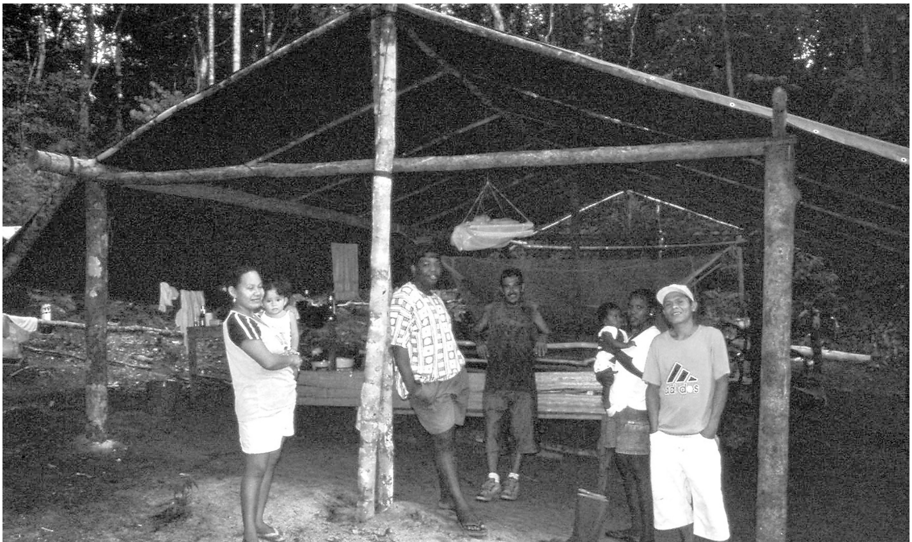
In dit proefschrift werd de regeneratie van tropische boomsoorten besproken en de rol die verstoring daarin speelt. Het bleek dat verstoring grote gevolgen kan hebben voor de zaadproductie en -verspreiding, de kieming en de ruimtelijke verdeling van zaailingen. Hieronder worden de belangrijkste resultaten in deze context samengevat en worden enkele aanbevelingen voor bosbeheer gegeven.

De zaadproductie van drie soorten werd vergeleken tussen een onverstoord en een gekapt stuk bos. De geschatte zaadproductie van individuele bomen was in het gekapte stuk bos hoger dan in het onverstoorde gebied (hoofdstuk 2). Dit suggereert, dat de beschikbaarheid van zaden toeneemt als gevolg van houtkap. Er moet echter wel rekening mee worden gehouden, dat een groot deel van de volwassen bomen kan worden gekapt of tijdens het kappen kan worden beschadigd. Om te onderzoeken of de hogere zaadproductie per boom het verdwijnen van bomen compenseert kan alleen worden bepaald door zowel voor als na de kap enkele jaren de beschikbaarheid aan zaden te bepalen.

De soorten die werden onderzocht verspreidden hun zaden maar over korte afstanden en de meeste zaden vielen onder de kroon of enkele meters daarbuiten. Doordat zaden maar over korte afstanden worden verspreid zullen slechts weinig zaden in de buurt van de stobben van gekapte bomen terechtkomen, tenzij er bomen van dezelfde soort in de buurt staan. Om ervoor te zorgen dat er na kap geen tekort aan zaden ontstaat is het noodzakelijk dat een aantal gezonde grote bomen van de commerciële soorten achterblijft. Vanwege de beperkte verspreiding van zaden is het van belang dat deze zaadbomen gelijkmatig over het gebied verdeeld zijn. De functie voor zaadproductie en -verspreiding (hoofdstuk 2) kan mogelijk worden gebruikt voor het definiëren van richtlijnen voor de minimale grootte, het aantal en de afstand tussen zaadbomen.

De kans op kieming werd sterk beïnvloed door de openheid van het kronendak (hoofdstuk 3). In grote openingen, die tijdens de houtkap waren ontstaan, kiemden veel minder zaden van soorten met grote zaden dan in de ondergroei. Vooral *Chlorocardium rodiei*, één van de meest gekapte soorten in Guyana, kon erg slecht tegen de hitte in de grote openingen, waarin bijna alle zaden van deze soort uitdroogden. Het is daarom van belang om te proberen openingen zo klein mogelijk te houden en om de vegetatie rondom de stobbe zo min mogelijk te beschadigen. Dit laatste zorgt er ook voor dat de regeneratie niet onnodig vertraagd wordt. De meeste zaailingen van de soorten met grote zaden werden namelijk binnen tien meter van de dichtstbijzijnde volwassen boom van dezelfde soort gevonden (hoofdstuk 4). Als de vegetatie rondom de stobbe ernstig beschadigd wordt kan dat betekenen, dat alle zaailingen en kleine bomen van die soort in dat stukje bos, die de plek van de gekapte boom kunnen innemen, worden vernietigd. Hierdoor moet de regeneratie weer van voren af aan beginnen wat mogelijk tientallen jaren vertraging kan opleveren. Als er te veel en te vaak wordt gekapt, kan dat leiden tot een sterke toename in het aantal pioniersoorten. Deze soorten kiemden beter in grote openingen dan in de ondergroei en de verdeling van hun zaailingen werd vooral bepaald door de locatie van openingen in het kronendak.

Simulatiemodellen worden al gebruikt om bosbeheer te evalueren. Helaas bevatten de meeste bestaande modellen geen gedetailleerde beschrijving van de regeneratie, waardoor mogelijkerwijs het effect van houtkap op de samenstelling van het bos onderschat wordt. Simulaties met het model dat in dit proefschrift ontwikkeld werd suggereren, dat eenmalig kappen geen grote veranderingen in het bos zal teweegbrengen. Echter, als elke 25 jaar wordt gekapt zal dat binnen 300 jaar tot een bos met veel meer pionier soorten met licht hout leiden dan het huidige bos in Guyana (hoofdstuk 5). Bovendien laten de simulaties zien, dat het aantal bomen dat per keer gekapt kan worden, sterk afneemt. Het model moet echter worden verbeterd voordat het kan worden gebruikt om definitieve uitspraken te doen over het effect van houtkap op de samenstelling van het bos. Op dit moment zijn echter modellen zonder uitgebreide regeneratiecomponenten de beste hulpmiddelen en deze moeten zoveel mogelijk worden gebruikt om de ecologische en economische duurzaamheid van verschillende mogelijkheden voor bosbeheer te bestuderen.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