Long-term responses of populations and communities of trees to selective logging in tropical rain forests in Guyana

Eric J.M.M. Arets

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Lange-termijn reacties van boompopulaties en -gemeenschappen op selectieve houtkap in tropisch regenwoud in Guyana

(met een samenvatting in het Nederlands)

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TROPENBOS INTERNATIONAL

The investigations reported in this thesis were carried out at study sites in the Mabura Hill area, central Guyana and were conducted within the framework of the Tropenbos-Guyana Programme, Georgetown, Guyana and the Plant Ecology Group, Utrecht University, the Netherlands.
This study was part of the project B7-6201/98-13/FOR, "*Conservation and Sustainable Use of Botanical Diversity in Guyana*" funded by the European Commission.

Voor mijn ouders

Voor Merel

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Chapter 1

General introduction

Tropical rain forests are among the most diverse ecosystems on this planet (Wilson 1995). Tree species diversity tends to increase with decreasing latitude (*e.g.* Gentry 1988a, Givnish 1999) with its peak in the wet tropics. For example in the western Amazon, a well-known biodiversity hot-spot, 289 tree species (out of 580 individuals > 10 cm diameter) have been found in a single hectare of forest (Gentry 1988b). Large differences in tree diversity exist, however, between continents and regions (Gentry 1988a, 1988b, Phillips *et al.* 1994, Givnish 1999, ter Steege *et al.* 2000, 2003b). Tropical forests are generally recognised as the indispensable habitat for vast amounts of plants and animals on Earth, and many more species are still expected to be discovered. Yet, during the past decades increasing local populations, slash and burn practises and the ever increasing hunger of developed countries for tropical timber and industrialised agricultural products like soy beans and palm-oil have lead to a rapid deforestation in the tropics.

From all commercial types of land use of tropical forests, the deleterious effects of logging often get the most negative attention in media. Nevertheless, even heavily logged forests maintain more biodiversity than most other types of land use like oil-palm or soy-bean plantations and cattle pastures (*e.g.* Putz *et al.* 2000). Although its structure may be altered considerably, after logging a residual forest stand usually still remains behind, whereas the latter types of utilisation imply complete conversion of the forest to other land-uses. In many developing tropical countries with rain forest, timber is an important source of income. Not only do governments need the revenues from logging for development of the country, also many people directly depend on employment in the forestry industry for their livelihoods. Hence, in most tropical countries it will be difficult to establish large conservation areas. Furthermore, outright protection of large areas is considered to be costly and therefore often not a feasible option (*e.g.* Putz *et al.* 2000, Pearce *et al.* 2003).

Currently, in Guyana – the focal country for this dissertation – only 1% of the total land area is part of a National Protected Area System (NPAS - ter Steege 2000), but the Government of Guyana is in the process of extending this. Ter Steege (2000) estimated, however, that 90% of Guyana’s land area harbour roughly 4500 unique species that are not found in the other 10%. This means that even if the total area of the NPAS will be increased to 10% of Guyana’s land area, still a part of its biodiversity will remain unprotected. Therefore, in addition to carefully and strategically planned areas in which representative and characteristic samples of a country’s biodiversity should be protected (*e.g.* ter Steege 2000), sustainably managed forests have to be an integral component of conservation strategies (Putz *et al.* 2000, ter Steege 2000). Albeit in recent years the conservation value of secondary forests and logged forests is obtaining more and more recognition (*e.g.* Putz & Viana 1996, Cannon *et al.* 1998, Chazdon 1998, Peña-Claros 2001), the long-term capacity to support biodiversity is still insufficiently known for tropical forests that are managed for timber.

In countries, like Guyana, that are committed to protecting biodiversity of their forests, but yet depend on its timber revenues, a balance has to be found in management types that on the one hand sustain timber yields over longer periods of time (providing lasting revenues and securing livelihoods) and on the other hand also conserve as much of the diversity as possible. Between these two aspects of sustainable forest management trade-offs are inevitably to be expected, *i.e.* higher yields will lead to stronger negative effects on biodiversity.

Because tropical trees are slow growing and long-lived organisms (e.g Lieberman & Lieberman 1987, Korning & Balslev 1994, Chambers *et al.* 1998, Fichtler *et al.* 2003, Laurance *et al.* 2004), the consequences of changes in present day demographic trends (*e.g.* growth, survival and regeneration) caused by logging, can only be quantified after a long period of time. Therefore the impact of logging on forest composition and tree diversity in tropical forests may not be found until many years later, which in extreme cases may lead to time-delayed extinctions, referred to as “extinction debt” (Tilman *et al.* 1994, Loehle & Li 1996). Few long-term post-harvest monitoring data are available to study and predict the long-term effects of different management regimes on forest structure, species composition and diversity (but see ter Steege *et al.* 2002 and Sheil 2003 for examples of exceptional long-term studies). The study of ter Steege *et al.* (2002) was conducted in Guyana and covered a time span of 75 years. Although these studies are invaluable, they generally provide little insight in the effects of current logging practises because logging methods during at least a large part of the time period covered were distinctly different from current practises (*e.g.* logging by axe instead of chainsaw and without the use of skidders). Additionally, they provide little flexibility in testing different management regimes. This makes it difficult to develop and evaluate sustainable management criteria.

This study aims to develop, implement and calibrate novel forest simulation models capable of making instantaneous projections of the long-term effects of logging on tree populations. A population dynamics model for forests in central Guyana is developed within the SYMFOR modelling framework (see Phillips & van Gardingen 2001a, 2001b, Phillips *et al.* 2003, van Gardingen *et al.* 2003, Phillips *et al.* 2004, chapter 3). The model simulates the three key demographic processes, growth, mortality and regeneration. The calibration of such models can be done using relatively short-term data on population dynamics. While the use of such models does not necessarily amount to making ‘true’ predictions, it enables us to test hypotheses and ask ‘what-if’ questions about the potential consequences of present day population dynamics and the effects of forest management thereupon for the long-term fate of the forest.

In this thesis I will first determine short-term effects of logging on tree population dynamics, species composition and diversity (chapter 2). In chapter 3, I will describe the simulation model for tree population dynamics. Using this model, I will evaluate for various management regimes (with different felling cycles, minimum felling diameters and harvest intensities) whether sustained yields are possible and I will evaluate their long-term effects on forest structure and composition (chapter 4). I will address these issues mainly from an ecological point of view, but I am well aware of socio-economic constraints. The results of chapter 4 can be used by decision makers to formulate criteria for "evidence-based" forest management. Finally in chapter 5 I will describe a stochastic modelling approach for seedling growth. This seedling growth model was used in a new simulation model with detailed description of regeneration processes that is described in a partner project (van Ulft 2004a).

In this thesis, I will deal with the effects of logging on tree communities on the scale of hectares. The consequences of logging on a larger scale, like effects of roads, log-markets and fragmentation will not be addressed specifically, though these are considered important as well (see Laurance *et al.* 1998, 2003).

In the remainder of this chapter I will give an introduction to, and clarification of some theory and concepts regarding population dynamics (section 1) and species composition (section 2) and I will discuss the potential effects of logging (section 3). In addition, I will give an introduction to Guyana, the study area and the Tropenbos-Guyana Programme.

1 Disturbance and population dynamics

The population dynamics of tree species depend mainly on three demographic processes: recruitment, growth and mortality. The abundance of a tree population is directly governed by recruitment, which determines the number of new individuals, and mortality, which determines the number of individuals that disappear from the population in the same period of time. The difference between these two rates determines changes in abundance of the population. Between recruitment and mortality, trees may grow to maturity and once they reach a reproductive stage they are able to contribute to the recruitment.

In tropical forests, light is a major limiting resource for the three demographic rates (*e.g.* Whitmore 1996). In the forest understorey there exist strong vertical and horizontal gradients in light availability (Chazdon & Fetcher 1984, Clark *et al.* 1996, Arets 1998, Rose 2000, Poorter & Arets 2003) with irradiance levels of 1-2% of full sunlight under closed canopy and up to 25% in tree fall gaps (Chazdon & Fetcher 1984). These gaps are openings in the forest canopy that are created by falling trees and branches. Although gap formation will locally change many microclimatic and edaphic factors, increased light availability is the most obvious change (Chazdon & Fetcher 1984, van Dam *et al.* 1999, van Dam 2001). Hence disturbance is an important cause of spatial variation in light availability.

Species have been found to differ largely in combinations of morphological and physiological traits, such as seed size, dispersal syndrome, size at maturity, leaf area ratio, and photosynthetic capacity (*e.g.* Veneklaas & Poorter 1998, Reich 1998, Poorter 1999, Poorter 2001, Rose & Poorter 2003, Sterck *et al.* 2003, van Ulft 2004a, Poorter 2005). The inter-specific differences in traits and trade-offs among traits (Veneklaas & Poorter 1998, Brown *et al.* 1999) result in differences in light requirement for processes such as germination, growth and survival in the various life stages and affect the population dynamical rates of these processes. Generally, growth and survival of trees will increase with increasing light availability (or gap size) (*e.g.* Augspurger 1984, Zagt 1997, Kobe 1999, Rose 2000, de Souza & Valio 2001, Peña-Claros 2001, Poorter & Arets 2003, van Rheenen *et al.* 2004). Differences in life history traits are assumed, however, to give the various species advantages in a certain part of the spectrum of the spatial and temporal environmental variation that exists in the forest. The existence of species with different suites of life history characteristics allows partitioning of resources in the forest, and may thus contribute to coexistence of species (*e.g.* Denslow 1980, Davies *et al.* 1998, Brown & Jennings 1998, Poorter & Arets 2003).

2 Disturbance and diversity

As discussed in the previous section, disturbance creates spatial and temporal variation in environmental conditions (mainly light) providing different niches for species with different life history strategies. In addition to this, the intermediate disturbance hypothesis (IDH, figure 1) (Connell 1978, see also Sheil & Burslem 2003) provides a suitable theoretical framework for the study of the effects of disturbance (or logging) on diversity. According to this hypothesis diversity is highest at an intermediate level of disturbance and lowest at the extremes of the disturbance gradient through exclusion of species with certain life histories. If the forest is in succession soon after disturbance or if disturbances are frequent or large, especially species that have life-histories that are adapted to heavy disturbance (fast growth, low longevity) will find a suitable niche to establish and grow, while at the same time slow growing, shade tolerant species will not be able to reach maturity. Similar lines of reasoning would apply *vice versa*. At intermediate levels of disturbance there will be many different niches available, allowing many species to coexist.

Throughout this thesis I will use the term "diversity" in reference to the diversity of trees in small areas of one to several hectares.

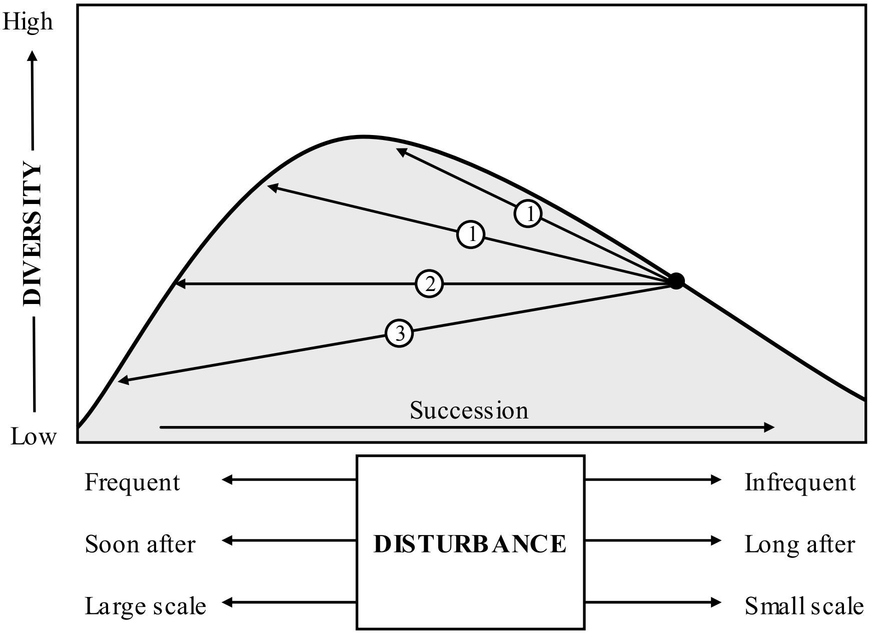

Figure 1 The Intermediate Disturbance Hypothesis (Connell 1978). Low diversity is hypothesised at both high (frequent, soon after and large scale) and low (infrequent, long after and small scale) disturbance levels, while highest diversity is achieved at intermediate levels of disturbance. The example shows the hypothetical position of a forest in Guyana (low levels of disturbance, relatively low diversity). Depending on the successional stage of the forest, increased disturbance (or logging) may result in ① increased diversity, ② equal diversity, or ③ decreased diversity.

3 Logging

In Guyana, like in many tropical countries, timber is extracted from the forest through selective logging, *i.e.* only a small number of trees species of commercial value are harvested. Although the number of harvested trees is generally rather low, the damage to the remaining forest stand may be considerable (*e.g.* Johns *et al.* 1996, ter Steege *et al.* 1996, Bertault & Sist 1997, Sist *et al.* 1998, van der Hout 1999). Depending on the extent and intensity of the logging operation, logging may create more and larger gaps in the forests when compared to natural disturbance (van der Hout 1999), because only large and healthy trees are felled. During the removal of the logs from the forest with heavy machinery ("skidders") an additional number of the remaining trees is killed or damaged. Hence, through logging the intensity of disturbance will increase, and if logging is repeated over time, also the frequency of the occurrence of the disturbances will increase.

In many aspects the effects of logging on population dynamics and species composition may be similar to natural disturbance events of similar amplitude. Therefore, many of the concepts that are used to explain the effects of natural disturbance can also be used within the context of logging. Like natural disturbances, selective logging will locally change the environmental conditions. The associated increase in light conditions will generally lead to increased growth and survival of all species, but especially those species with life-history strategies that are adapted to high light conditions, *i.e.* pioneer species, are likely to take most advantage of it. The effect of logging on species diversity can also be expected to follow the predictions of the IDH (see also ter Steege 2003 and Molino & Sabatier 2001) as shown in figure 1. However, besides these long-term effects of logging that result from changes in population dynamics in logged forest, diversity in logged forest may decrease as a result of direct loss of species caused by removal and killing of trees.

The tropical rain forest of Guyana is an example of low-dynamical forests, generally characterised by small-scale disturbance events caused by tree falls (Hammond & Brown 1995, ter Steege & Hammond 2001). In a survey of natural tree fall gaps in Central Guyana, van Dam & Rose (1997) estimated annual rate of gap formation at 0.4% of the area, which is well below the rates found in other forests (1 to 2 % -*e.g.* Hartshorn 1990, van der Meer & Bongers 1996). Ter Steege & Hammond (2001) found that the forests in central Guyana - where this study was carried out - in comparison with other forests in Guyana are characterised by relatively low diversity, high abundance of trees with characteristics that are regarded superior in environments with little disturbance, high level of single tree dominance and a low percentage of pioneer species. These are all characteristics of forests that would be expected at the low disturbance end of the IDH curve (figure 1). Therefore it can be expected that, depending on its intensity, increased disturbance by logging will increase diversity as would be predicted by the IDH (see example in figure 1). Simultaneously it may be expected that more opportunities (more and larger gaps) are created for successful establishment for more pioneer species, which may alter the characteristics of the forest and reduce the opportunities of successful regeneration of commercial species, which are generally climax species.

Yet, there exist some important differences that distinct logging from natural disturbance that may influence species composition of logged forests. Logging will have a disproportionally large impact on a small group of timber species. The selective removal of large reproductive trees may have consequences for regeneration (see van Ulft 2004b.), which in the long run will affect the whole population (Tilman *et al.* 1994, Loehle & Li 1996). Additionally, log extraction by skidders destroys much of the vegetation in an area close to the stump of the felled trees and in skid-trails. Hence, this also destroys much of the "advance regeneration" which especially climax species depend on for successful regeneration when gaps are formed (*e.g.* Uhl *et al.* 1988, Zagt 1997, Zagt & Werger 1998).

To date, in Guyana information on the long-term sustainability of current logging practises is known only for a small number of important timber species (Zagt 1997, Zagt *et al.* 2000, ter Steege *et al.* 2002). From the results of a 75 year long monitoring study, ter Steege *et al.* (2002) concluded that although the effects on species diversity seemed to be negligible, the population of the tree species that was harvested most, Greenheart (C*hlorocardium rodiei*), greatly decreased. Only because Greenheart was such a dominant species before logging took place it still ranked third in abundance. Yet, the harvesting of Greenheart in that area is not likely to be sustainable on the long-term. Using results from a matrix-model, Zagt (1997) previously already concluded that sustainable extraction of Greenheart is only possible with felling cycles of 100 years or more, mainly due to the very slow growth rates of this species. For the faster growing Baromalli (*Catostemma commune*), on the other hand, felling cycles with a length of 30-50 years seemed to be possible (Zagt *et al.* 2000). Information on the long-term effects of logging on the level of whole tree communities, however, is still largely lacking.

4 Functional groups

High tree species diversity in tropical forests implies that many species are rare (figure 2). Little ecological information is available about most species and the abundance of many species is too low for statistically meaningful analyses of demographic processes like growth, mortality and recruitment or for the rigorous parameterisation of functions used in simulation models. To facilitate the analyses and to be able to identify general trends, tropical trees are often classified into a limited number of functional groups. In these, species

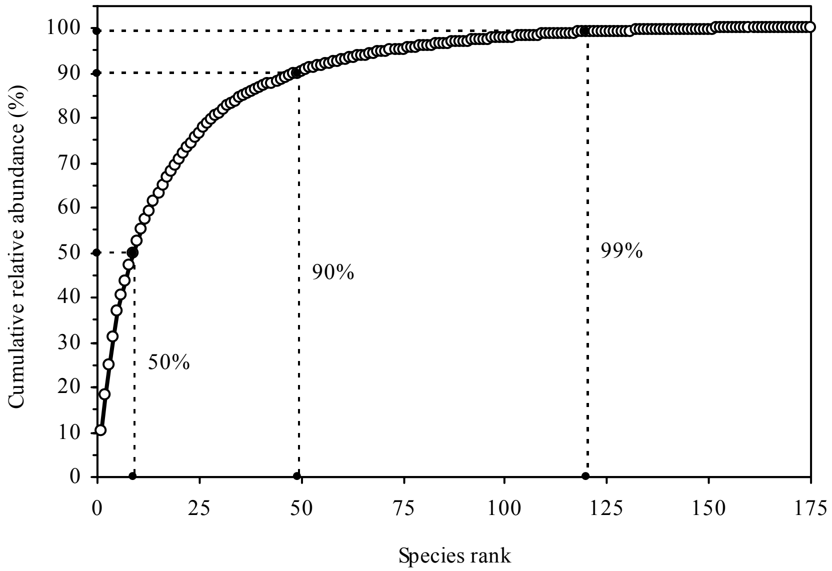

Figure 2 Cumulative relative abundance (%) of individuals > 5 cm DBH over species ranks ordered from most abundant species to least abundant species. For instance, the most abundant species (1 out of a total of 175, is 0.6% of all species) makes up more than 10% of all individuals, the 9 (5% of species) most abundant species represent 50% of all individuals, the 49 (28%) most abundant species represent 90% of the individuals and 120 species (69% of species) represent 99% of the individuals (or 1% of the individuals is made up by 55 (31%) species). The abundances were based on data for the 15 permanent sample plots combined (29.4 ha). The abundances of trees between 5 and 20 cm DBH were adjusted for their smaller sample areas.

with similar environmental requirements and similar ecological responses to changes in their environment are grouped (*e.g.* Lieberman *et al.* 1985, Manokaran & Kochummen 1987, Whitmore 1989, Köhler *et al.* 2000, Phillips *et al.* 2002). Obviously, the studies of different ecological phenomena need different classifications. Hence, in the case of this study, species should be classified into groups according to similarities and differences in their responses to disturbance in terms of regeneration, growth and mortality.

The basis of many such classifications is the stage of succession in which species become abundant in the forest (*e.g.* pioneer vs. climax dichotomy, Swaine & Whitmore 1988), which is related to the light demand of the species. Other classifications depend directly on environmental requirements (*e.g.* obligate gap vs. gap-independent species, Popma *et al.* 1992). Although groups get different names, the results of these different approaches are similar. Throughout this thesis I will use the terms pioneer and climax species for the classification as these appear most widely used in tropical ecology. Yet, many more terms are in use to describe the same sets of characteristics. Pioneers are fast growing and light demanding species that appear early in gaps during succession while climax species grow slower, are more shade-tolerant and become abundant late in the succession sequence. An intermediate group of long-lived pioneers is often recognised within the two extremes of the pioneers and climax species (*e.g.* Finegan 1996, Peña-Claros 2001). Species in this broad group are often able to establish and survive in more shaded conditions than pioneers, and respond with rather high growth rates to increased light availability (Peña-Claros 2001). It should be realised, however, that these classifications are only a tool to facilitate analyses of data and to calibrate the model. In reality the species will cover a whole continuum of characteristics, responses and requirements (*e.g.* Whitmore 1989, Davies 2001, Poorter & Arets 2003) that even may change during an individual's ontogeny (Clark & Clark 1992).

My classification was objectively based on differences in three morphological characteristics: wood density, seed mass and adult stature, which are predictors of species' responses to disturbance in terms of growth, recruitment and survival (see Swaine & Whitmore 1988, Favrichon 1994, Finegan 1996, ter Steege & Hammond 1996, ter Steege & Hammond 2001). These morphological variables have an advantage over population dynamical characteristics, as they even for locally rare species are relatively easy to obtain from floras and existing data-bases.

Wood density was believed to be a good proxy for maximum potential growth rate of species. Although this assumption is often made by foresters and ecologists, at the start of this study still little quantitative evidence was available. Therefore in chapter 2 this relation was examined in detail. In the mean time the validity of the assumption was also confirmed by other studies (Verburg & van Eijk-Bos 2003, Verburg *et al.* 2003, ter Steege *et al.* 2003a, Muller-Landau 2004). Furthermore wood density was found to be correlated with seedling persistence in deep shade (Augspurger 1984). Seed mass of a species is correlated with many determinants of the success of recruitment, like seed dispersal, germination, initial seedling size and early seedling survival (*e.g.* Foster & Janson 1985, Hammond & Brown 1995, Boot 1996, Rose 2000, Dalling & Hubbell 2002, Rose & Poorter 2003, van Ulft 2004b, but see Grubb 1996). Adult stature is a measure for environmental conditions at which trees reproduce, timing of reproduction and longevity (Lieberman *et al.* 1985). It is also found to be related to shade tolerance and growth (Swaine & Whitmore 1988, Davies & Ashton 1999), likely reflecting a trade-off in investment between growth and reproduction.

In chapter 2 wood density and seed mass were used to quantify three life history strategies (pioneers, long-lived pioneers and climax species), while in the chapters 3 to 5, these life history groups were further divided in three subgroups each, depending on adult stature (small, medium and tall stature, which relate to understorey, canopy and emergent positions in closed forests). This combination of life history and adult stature groups resulted in nine functional groups. A complete list of the classification for all species present in the dataset is provided in appendix A, at the end of this thesis.

An inevitable disadvantage of the use of functional groups is that species composition can only be determined in broad terms of the functional groups, while species diversity cannot be studied at all. Therefore with the simulation model, species composition can only be determined at the functional group level. However, scenario studies of different management alternatives using functional groups can still provide valuable information on composition by identifying for instance the type of species that may be at risk or the type of species that will most likely increase in abundance.

5 Guyana and study area

5.1 Guyana

The fieldwork for this study was performed in Guyana (figure 3). The country is situated at the north-eastern coast of South America (between 1-9°N and 56-62°W), bordered by Venezuela, Brazil and Suriname. Guyana is part of the Guiana Shield, a massif of hard and mainly Proterozoic rock (see ter Steege 2000). Guyana has a tropical climate with average daily temperatures of 25-27 °C. The average annual rainfall in the research area was 2772 mm in the period 1996-2000 (van Dam 2001, figure 4). Although rain falls throughout the year there are two distinct rainy seasons, a long season from May to August and a shorter season in December and January.

Guyana is covered with 17 million hectares of forest, which is about 80% of its land area. Currently the majority of the forest is still untouched, but roughly 8.9 million hectares are designated state forest lands of which in 1997 roughly 75% had been allocated for timber harvesting (van der Hout 1999). Forest concessions are given out with three different tenures ranging from 1 year up to 25 years. So far approximately 2.2 million ha have been logged, while annually an estimated 160,000 ha is added to this number (FAO 2001). In 1996 the

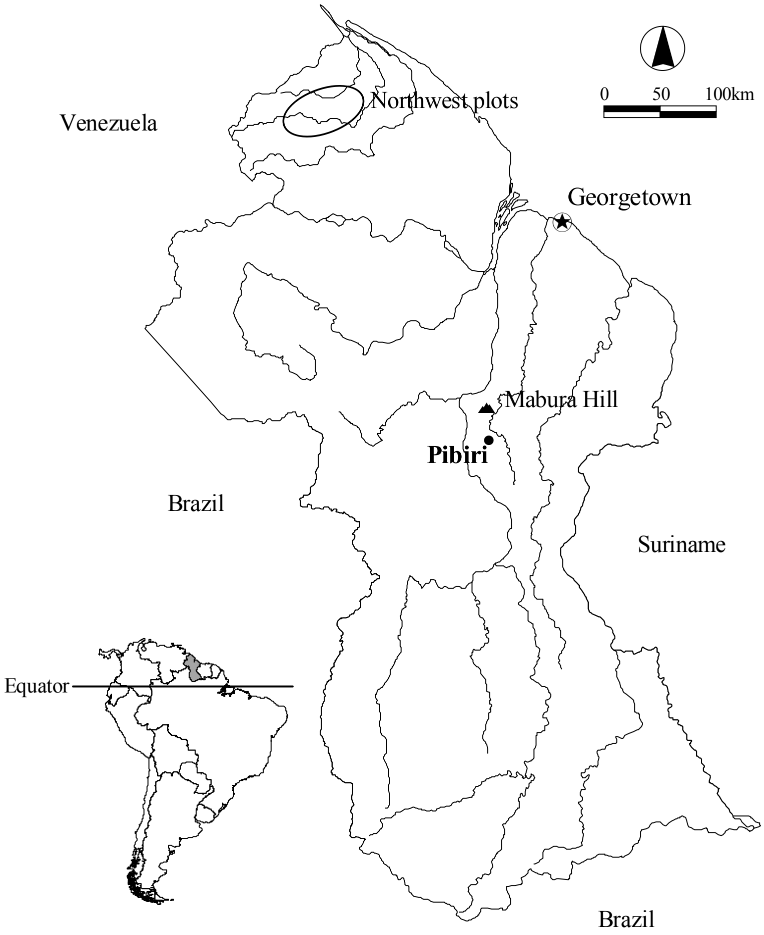

Figure 3 Map of Guyana with the locations of Georgetown, its capital, the township at Mabura Hill, the Pibiri research area and the Northwest plots. In the inset Guyana's position in South America is shown.

forestry industry contributed almost 5% to the Gross Domestic Product. Traditionally only a few number of species were harvested with Greenheart (*Chlorocardium rodiei*) forming the pillar of the forestry industry with over 40% of the annual log extraction in the period 1955-1990. With the recent establishment of a large foreign owned plywood mill, Greenheart's position as the most extracted species was taken over by Baromalli (*Catostemma* 2 spp.). Generally, logging is selective with recorded harvest intensities that can be as low as 5 m^3 ha^{-1}, but that also show large variations on the rather small scale of hectares (GFC 2000). Although the overall damage to the forest may be small, locally the damage to the forest may be substantial (ter Steege *et al.* 1996, Zagt 1997, van der Hout 1999).

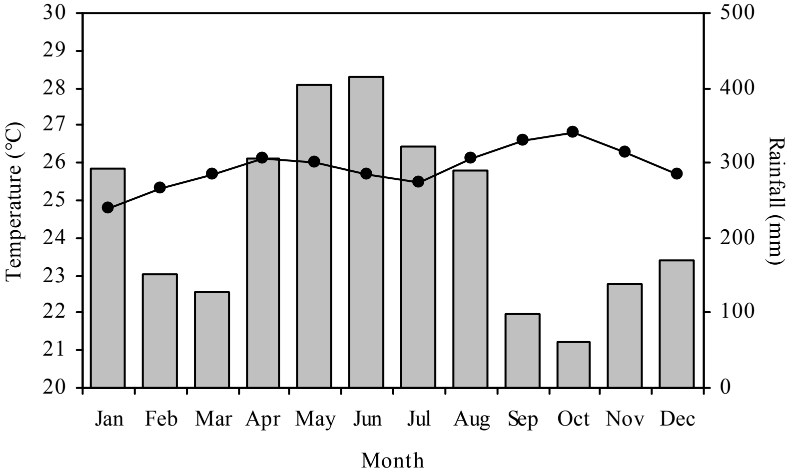

Figure 4 The average monthly temperature (line) and rainfall (bars) in the Pibiri research area. The values are averages from April 1996 to May 2000. Data are from van Dam (2001).

5.2 Study area

Most of the research in this study was based on data from 15 experimental sample plots (ESP) in the West-Pibiri compartment (henceforth referred to as Pibiri data) of Demerara Timbers Ltd.'s concession in central Guyana, approximately 50 km south of Mabura Hill (5°02' N, 58°37' W) (see figure 3). Additionally, in Chapter 2 data from the Barama Company Ltd.'s (BCL) timber concession in the Northwest district of Guyana (henceforth referred to as Northwest-data) were used. This area is described more detailed in Chapter 2.

Pibiri plots

The Pibiri experimental sample plots (ESP) were set up in 1993 as part of a study on the ecological, economic and silvicultural consequences of reduced impact logging (RIL) in Guyana (see van der Hout 1999, 2000 for more detailed information). Each ESP measures 140 x 140 m (1.96 ha), but treatments were also applied in a surrounding buffer zone of 50 m. The experiment covered five different intensities of RIL: control without intervention, low intensity RIL (4 trees ha^{-1}), moderate intensity RIL (8 trees ha^{-1}), high intensity RIL (16 trees ha^{-1}) and moderate intensity RIL followed by a post-harvest liberation thinning (van der Hout 1999, 2000). Reduced impact logging was carried out in 1994. The trees in the plots were re-censused at one (1995), three (1997) and six years (2000) after logging. At all censuses the DBH (diameter at breast height) of all trees were measured at the same point of measurement as in previous years and mortality and recruitment (in-growth into size class) were recorded. For seedlings and saplings lower than 1.5 m, total heights were measured instead of DBH. During 2000-2001 allometric properties like heights and crown dimensions of trees were measured for a sub-sample across all size classes. In each subsequent chapter more specific information is given on measurements, size classes and treatments that were used in those chapters.

The soils in the Pibiri area belong to the brown sand series with a moderate to high percentage of clay (Ferralsols) (Van der Hout, 1999). More information on the physical geography of the study area can be found in van Dam (2001).

The plots are situated in mixed Greenheart forest (Ek 1997, van der Hout 1999), dominated by *Tapura guianensis* (Waiaballi, 10.4%), *Oxandra asbeckii* (Karishiri, 7.8%), *Catostemma fragrans* (Sand Baromalli, 6.5%), *Chlorocardium rodiei* (Greenheart, 6.3%), *Lecythis confertiflora* (Wirimiri Kakaralli, 5.8%), *Mora gongrijpii* (Morabukea, 3.6%), *Eschweilera sagotiana* (Black Kakaralli, 3.3%) and *Licania heteromorpha* var. *perplexans* (Kairiballi, 3.2%). Together these 8 species account for just over 45% of the individuals larger than 5 cm DBH (see also figure 2).

6 Institutional setting

The present study was carried out within the Tropenbos-Guyana Programme and was part of a larger project funded by the European Commission. Here I will give a short overview of the Tropenbos-Guyana Programme and the EC project. More detailed information on Tropenbos can be found at their website: www.tropenbos.org.

6.1 Tropenbos International

Tropenbos International (TBI) is a non-governmental organisation based in the Netherlands that is funded by the Dutch Government. To meet demands of policy makers and forest users, TBI facilitates the development and implementation of participatory and multi-disciplinary research and capacity building programmes in tropical countries. The programmes focus particularly on sustainable use of forests. Presently Tropenbos International is operating and developing research sites in Colombia, Ghana, Indonesia, Suriname and Vietnam in cooperation with research institutes, government agencies and other stakeholders (Tropenbos International 2004). In previous phases TBI also had research sites in Guyana, Cameroon and Côte d'Ivoire.

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, 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 utilisation and management of the forest have been trained. After twelve years of research, and support to Guyanese research, policy and forest management organisations, the Tropenbos-Guyana Programme came to an end in December 2001. A Research Unit created within the Guyana Forestry Commission, continues to collect and analyse data, critical for the wise management of forests in Guyana.

6.2 European Commission Project

The present study was a sub-project within a project that was funded by the European Commission: B7-6201/98-13/FOR "*Conservation and Sustainable Use of Botanical Diversity in Guyana*". The objective of the overall project was to increase the knowledge of patterns and causes of plant diversity in Guyana and the effects of management thereupon. The results should assist the Government of Guyana to set up a National Protected Area System, based on sound scientific criteria and determine long-term capacity of protected areas and logged forests to maintain certain levels of plant diversity. Other sub-projects dealt with patterns of biodiversity to assist the development of a Protected Areas strategy (ter Steege 2000) and effects of logging on liana diversity and abundance (Zagt *et al*. 2003).

7 Objectives and outline of this thesis

7.1 Aims of the thesis

Since only a small area of Guyana can be effectively protected as part of a National Protected Area System and because timber harvesting is an important source of income, logged forests will play an important role in the conservation of biodiversity in Guyana. To develop sustainable management strategies it is of paramount importance to get to know the long-term consequences of present day logging on future timber yields as well as on composition of the remaining forest stand.

The aims of this study are:

To elucidate the long-term effects of selective logging on tree population dynamics, forest composition and tree diversity.

- To develop and parameterise a simulation model that enables the study of long-term effects of alternative logging scenarios on functional group composition.
- To evaluate the sustainability of alternative forest management scenarios for both future yields and biodiversity conservation.

7.2 Thesis outline

In **Chapter 2** the actual responses in population dynamics of saplings (2-5 cm DBH) and poles (5-20 cm DBH) to selective logging are studied in the Pibiri plots. Differences in responses are compared between species that were classified in three functional groups (pioneers, long-lived pioneers and climax species). Furthermore the short-term (5 to 6 years) effects of logging on composition of functional groups and diversity is examined for plots in Pibiri and plots in the Northwest of Guyana. Additionally, in this chapter the suitability of wood density as proxy for maximum growth rates is evaluated.

Chapter 3 gives the description, parameterisation and evaluation of a spatially-explicit individual based tree dynamics model. The model is based on the Pibiri plots and is used to evaluate long-term effects of different logging scenarios (combinations of various felling cycles, minimum felling DBH and harvest intensities) in chapter 4. The model simulates the key demographic processes in tree populations: growth, mortality and recruitment. The rates and/or probabilities of these processes depend mainly on a competition index (proxy for light availability). Recruitment is modelled as a probability of the appearance of new trees at the minimum size threshold of 2 cm DBH. Another version of the model with more mechanistic modelling of tree recruitment is presented in a partner project (van Ulft 2004a). Because that version did not yet give realistic projections of the future of the forest that mechanistic version is not used in this thesis.

In **Chapter 4** several alternative scenarios of selective logging for sustainable timber harvesting are evaluated using the model described in chapter 3. The long-term effects on both functional group composition and sustained yields are determined and compared between the scenarios.

In **Chapter 5** a new modelling approach is presented for the simulation of growth of juvenile trees (< 2cm DBH). This approach includes both auto-correlation in growth and variation resulting from stochastic processes that affect net realised growth, like reductions in stem height by falling debris and herbivory and subsequent resprouting. Additionally the significance of this auto-correlation and stochastic variation for the simulation of tree recruitment is evaluated. This approach was subsequently implemented to simulate the growth of seedlings in a simulation model that includes a mechanistic regeneration module with seed production, dispersal and germination as described in van Ulft (2004a)

In the final chapter the main results from the previous chapters are summarised and discussed. Additionally the implications of the results for sustainable forest management are evaluated.

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Chapter 2

Responses of tree populations and forest composition to selective logging in Guyana

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Abstract

Tropical rainforests in Guyana are characterised by small-scale disturbance regimes. As a result, tree communities are dominated by shade-tolerant climax species that are adapted to these low and infrequent disturbance events, while pioneers are hardly present. Selective logging in these forests increases the disturbance intensity and was expected to affect population dynamics of different species differently and to change species composition and increase diversity conform the predictions of the intermediate disturbance hypothesis (IDH) for forests with low disturbance intensity.

We studied the responses in population dynamics of saplings (2-5 cm DBH) and poles (5-20 cm DBH) of three functional groups (pioneer, long-lived pioneer and climax) to logging in plots in Pibiri, Central Guyana. Additionally we examined effects of logging on functional group composition and tree diversity in Pibiri (6 years data) and Northwest Guyana (5 years data) in plots with harvest intensities ranging from 0 (control) to 16 trees ha^{-1}. The classification of species into three functional groups was based on their wood density and seed mass. Wood density is shown to be a good predictor of a species' potential maximum growth rate.

In Pibiri, 6 years after logging light conditions were still positively related to harvest intensity. All groups showed increased growth rates with increased light availability. In the higher light classes the growth rates of pioneer poles and saplings were higher than for the other two groups. Especially, highly increased recruitment rates (47% yr^{-1}) in high light climate resulted in fast net population gain rates for pioneer saplings (44 % yr^{-1}) in high light conditions.

In the Northwest, the abundance of pioneer saplings increased from 1% to 7% in logged plots and of pioneer poles from 2% to 8%, while in Pibiri only pioneer saplings increased from 0% to 6.2% with increasing harvest intensity. In all cases the increased relative abundance of pioneers was at the expense of relative abundances of climax species. In both forest areas, tree α-diversity of saplings, as measured by Fisher's α, significantly increased with increasing harvest intensity.

The results of this study are consistent with the predictions of the IDH for forests at the low intensity end of the disturbance range. Logging increased light availability and created more suitable habitat conditions for successful regeneration of pioneer species that were previously virtually absent. From the trends that we found we made predictions for longer-term effects of logging. Long-term monitoring studies or studies with simulation models are needed to test further hypotheses on the long-term effects of logging.

1 Introduction

In tropical rain forests there is a continuous, dynamical pattern of small and larger disturbances caused by falling trees and branches. Consequently the forest is a mosaic of patches with different environmental conditions. Different tree species are assumed to possess life history traits that are adapted to different degrees and different phases of disturbance. Traditionally, tree species can be grouped, according to their adaptations, into two functional groups, namely pioneers and climax species (Swaine & Whitmore 1988, Whitmore 1989, ter Steege 2003b), while in other classifications also an intermediate group (*e.g.* long-lived pioneers, late secondary species) is distinguished (Finegan 1996, Peña-Claros 2001). These classifications are based on differences in combinations of plant morphological and physiological traits, such as seed size, dispersal syndrome, size at maturity, and photosynthetic capacity. The inter-specific differences in traits and trade-offs among traits (Veneklaas & Poorter 1998, Brown *et al.* 1999) result in differences in light requirements for processes such as germination, growth and mortality in the various life stages and affect the population dynamical rates of these processes.

The life history traits are assumed to give the various species advantages in a certain part of the spectrum of the spatial and temporal environmental variation that exists in the forest. The existence of species with different suites of life history characteristics allows partitioning of resources in the forest, thus contributing to coexistence of species. Similarly, it may explain the spatial and temporal variation in abundance and composition of different functional groups.

Logging is a source of disturbance that is additional to the natural disturbance regime. Depending on the extent and intensity of the logging operation, logging may create more and larger gaps in the forests when compared to natural disturbance (van der Hout 1999). While it is generally assumed that logging affects the tree species composition and population structure of the forest, the direction of the effects of logging on forest communities is not consistent among different forests and different species groups, though it is likely that its effects interact with those of natural disturbance (Putz *et al.* 2000).

One of the theories describing the relation between disturbance and diversity is the intermediate disturbance hypothesis (IDH) (Connell 1978, see also Sheil & Burslem 2003 and Chapter 1). According to this hypothesis diversity is highest at an intermediate level of disturbance and lowest at the extremes of the disturbance gradient through exclusion of species with certain life histories. This would mean that, depending on its intensity, logging in forests with low natural disturbance regimes will increase diversity, while it will decrease diversity in forests with intermediate to high natural disturbance regimes.

The tropical rain forests of Guyana have been cited as an example of low-dynamics forests, generally characterised by small-scale disturbance events caused by tree falls (Hammond & Brown 1995, ter Steege & Hammond 2001). In a survey of natural tree fall gaps in Central Guyana, van Dam & Rose 1997) estimated annual rate of gap formation at 0.4% of the area, which is well below the rates found in other forests (*e.g.* Hartshorn 1990, van der Meer & Bongers 1996). So far, in most of the forested area of Guyana logging has been selective and at a rather restricted scale (van der Hout 1999 compared with Putz *et al.* 2000), though logging is shown to create more larger gaps than natural disturbance (van der Hout 1999). It is interesting therefore to investigate the population dynamical response of a number of easily characterised functional groups to logging and whether logging leads to increased diversity as suggested by the IDH.

We do this by analysing recruitment, growth and survival patterns of trees classified into three life history strategies (pioneer, long-lived pioneer and climax). We used functional groups because in tropical forests most tree species are rare and just a few are abundant enough to measure population dynamics at the species level. Our classification is based on two morphological parameters, wood density and seed mass, which we believe are predictors of species' responses to disturbance in terms of recruitment, survival and growth. Wood density and seed mass have an advantage over population dynamical characteristics, as they are instantaneous and relatively easy to obtain.

Seed mass is correlated with recruitment success and early survival of a species. Climax species are characterised by large and heavy seeds, while pioneer species generally have many small and light seeds (Foster & Janson 1985, Hammond & Brown 1995, Boot 1996, Rose & Poorter 2003, ter Steege 2003b, but see Grubb 1996). Wood density is used as a proxy for maximum potential diameter growth rate (ter Steege 2003b). The large differences in wood density between species are mainly due to differences in wood porosity (Winstead 1972, Barajas-Morales 1987, Suzuki 1999). As a consequence, per unit of assimilated carbohydrates, species with a relatively low wood density will be able to grow faster in diameter than species with a high wood density. Although the relation between wood density and or diameter growth rate seems to be quite obvious and is often assumed (Swaine & Whitmore 1988, Köhler *et al.* 2000, ter Steege & Hammond 2001) it is hardly demonstrated (but see ter Steege *et al.* (2003) and Verburg & van Eijk-Bos (2003b)). We test the relation between maximum potential growth rate and the wood density of tree species for which we expect a negative relationship.

If light availability increases with increasing logging intensity we hypothesise that this will positively affect growth, survival and recruitment in all functional groups. However, we further anticipate that pioneer species show the strongest response to increased light availability in terms of growth, survival and recruitment, and therefore we expect that this group will increase in relative abundance with increasing logging intensity. Because the natural disturbance regime in the forests we studied is low, we finally hypothesise that, in line with the IDH, tree species diversity for the smaller size classes (*i.e.* trees < 20 cm diameter at breast height (DBH)) in our forests will increase with increasing logging intensity. We expect that the time since logging of maximum six years in this study is too short to find effects on the larger size classes.

2 Methods

2.1 Research areas

To test our hypotheses we used permanent sample plot (PSP) data from two different areas in Guyana. The first set comes from the Barama Company Ltd.'s (BCL) timber concession in the Northwest district of Guyana (henceforth referred to as Northwest-data) around Port Kaituma (7°44' N, 59°52' W). The second data set originates from 12 experimental sample plots in the West-Pibiri compartment (henceforth referred to as Pibiri data) of Demerara Timbers Ltd. 's concession approximately 50 km south of Mabura Hill (5°02' N, 58°37' W) (van der Hout 1999). An important difference between the two areas is that the plots in the Northwest have been selectively logged without special precautions to reduce the impact of the logging operation, while the Pibiri plots have been logged with reduced impact logging techniques. Possible differences between these two methods are no direct subject for this study, but may be relevant.

2.1.1 Northwest plots

In the Northwest, PSP were established and inventoried in advance of the logging operations of BCL (ECTF 1994). Thereafter the area, along with the plots, was logged within one year after the plots were set up and inventoried. Some of these plots were "missed" by the harvesting operation and will be used as (unplanned) non-harvested control plots. The trees in these plots were re-measured on a yearly basis starting from approximately 1 year after logging (ECTF 1994). We used 56 PSP that were re-censused during 2-6 years after logging for growth analyses, while the results on the diversity and composition are based only on those 37 (7 unlogged and 30 logged) PSP for which 6 years of data were available. In table 1 the measurement thresholds and sampling intensities are shown.

In the PSP the logging intensity ranged from 0 to 16 trees ha^{-1}. *Catostemma commune* is the most important merchantable species in the concession and accounts for approximately 80% of the harvested trees (ECTF 2000).

The most abundant species in the plots, based on individuals larger than 5 cm diameter at breast height (DBH, *i.e.* diameter at 1.30m height), are *Eschweilera sagotiana* (Black Kakaralli, 18.2%), *Tovomita spp.* (Awasokule, 10.9%), *Alexa imperatricis* (Haiariballi, 9.5%), *Licania guianensis* (Kauta, 8%), *Protium decandrum* (Kurokai, 4.4%), *Rollinia exsucca* (Black Maho, 4.4%), *Pentaclethra macroloba* (Trysil, 4.3%) and *Catostemma* *commune* (Swamp Baromalli, 3.4%). Together these 8 species account for slightly more than 60% of the individuals larger than 5 cm DBH.

The soil types in the area are mainly well-drained red-yellow podzolic soils and red-yellow latosols (Gross-Braun *et al.* 1965). The average annual rainfall is 2600 mm (ECTF 2000).

2.1.2 Pibiri plots

The Pibiri experimental sample plots were set up in 1993, considering 4 different intensities of reduced impact logging (see van der Hout 1999, 2000): low intensity reduced impact logging (4 trees ha^{-1}), moderate intensity (8 trees ha^{-1}), high intensity (16 trees ha^{-1}), and a control without intervention. The experiment was set up as randomised block design in three blocks with 4 treatments. Reduced impact logging was carried out in 1994. The trees in the plots were re-censused at one (1995), three (1997) and six years (2000) after logging. In table 1 the measurement thresholds and sampling intensities are summarised.

The plots are situated in mixed Greenheart forest (Ek 1997, van der Hout 1999), dominated by *Tapura guianensis* (Waiaballi, 10.4%), *Oxandra asbeckii* (Karishiri, 7.8%), *Catostemma fragrans* (Sand Baromalli, 6.5%), *Chlorocardium rodiei* (Greenheart, 6.3%), *Lecythis confertiflora* (Wirimiri Kakaralli, 5.8%), *Mora gongrijpii* (Morabukea, 3.6%), *Eschweilera sagotiana* (Black Kakaralli, 3.3%) and *Licania heteromorpha* var. *perplexans* (Kairiballi, 3.2%). Together these 8 species account for just over 45% of the individuals larger than 5 cm DBH.

The soils belong to the brown sand series with a moderate to high percentage of clay (Ferralsols) (Van der Hout, 1999). The average annual rainfall in this area in the period 1996-2000 was 2772 mm (van Dam 2001).

2.2 Measurements

In both areas, at all censuses the DBHs of three size classes (large trees, poles and saplings) were measured at the same point of measurement as in previous years and mortality and recruitment (in-growth into size class) were recorded.

Table 1 Minimum measurement limits for trees, number and size of subplots and total sampled area per, plot for each size class in the Northwest and Pibiri experiment.

Area	Size class	Minimum measurement limits	Number (size) of subplots per plot	Sample area per plot (ha)
Northwest	Large trees	20 cm DBH	25 (20 x 20 m)	1
	Poles	5cm DBH	5 (20 x 20 m)	0.2
	Saplings	1.5 m height	1 (20 x 20 m)	0.04
Pibiri	Large trees	20 cm DBH	49 (20 × 20 m)	1.96
	Poles	5 cm DBH	25 (10 × 10 m)	0.25
	Saplings	2 cm DBH	25 (5 × 5 m)	0.0625

Only in the Pibiri plots direct data on light availability were available in the form of Dawkins' crown illumination index (CII) values (Dawkins & Field 1978, Clark & Clark 1992). This index is determined visually on an ordinal scale (1: crown receives no direct light, 2: only lateral direct light, 3: partly direct overhead light, 4: full overhead light and 5: Emergent, crown fully exposed vertically and laterally at least within the 90º inverted cone subtended by the crown base). At the second (1997) re-measurement, CII values were only determined in the centre at 2m height of the subplots in which poles and saplings were measured while at the third (2000) re-measurement CII values were determined for all individuals. Because many smaller individuals in the understorey were often assigned CII class 2, for the third re-measurement this class was subdivided into three subcategories: low, medium and high light, which also has been done in other studies (Clark & Clark 1992, Zagt 1997, Poorter & Arets 2003). If not stated differently, we used the 2000 CII values.

Because direct measurements for light conditions were not available for the trees in the Northwest plots we restricted the analyses of responses in population dynamics (*i.e.* growth, mortality and recruitment) of the three functional groups in relation to light availability to Pibiri. We focused on the size classes of the future, saplings and poles, because we expected to find no effects of logging on population dynamics of the large trees within the short time span we studied after logging. For the analyses on the relationship between wood density and growth rate and the effects of logging on functional group composition and diversity we used the data from both areas.

2.3 Functional groups

We classified all species into three functional groups (pioneers, long-lived pioneers and climax species) based on differences in the functional characteristics wood density and seed mass. The wood density refers to the air-dry density (g cm^{-3}) at 12% moisture content (*i.e.* specific gravity) that we derived from ter Steege (2000a) with additions taken from CTFT (1989), Fanshawe (1961) and Gérard *et al.* (1996). We used seed mass data from Hammond & Brown (1995).

A 3-means cluster analysis with wood density and seed mass class, of all tree species in Guyana with known values for these two parameters, resulted in the classification as shown in Table 2. Except for one species, all species classified as climax species have seed mass $\geq$0.1 g.

In the Pibiri data, we were able to classify 161 out of 189 (85.2 %) species, while in the Barama data this was 134 out of 147 (91.2 %) species. These represented 1501 out of 1682 saplings (89.2 %) and 2988 of 3188 poles (93.7 %) in Pibiri and 4719 out of 5351 saplings (88.2 %) and 6796 out of 7075 poles (96.1 %) in the Northwest (in 37 plots with 7 censuses). The species that could not be classified were left out from all analyses, except for the calculation of the effects of logging on relative abundances of the functional groups.

Table 2 Limits for wood density (g cm^{-3}) and seed mass (g) for the three functional groups.

Functional group	Wood Density (g cm^{-3})	Seed Mass (g)
Pioneers	< 0.8	< 0.1
Long-lived pioneers	< 0.8	≥ 0.1
Climax	≥ 0.8	all

2.4 Light availability and logging

To test whether increased logging intensity was associated with increased light availability, we determined, for each size class, the relative frequency distribution of individuals over CII classes for plots with increasing harvest intensity. We tested whether the distribution of individuals shifted towards higher CII classes if harvest intensity was higher using χ^2 analyses in the EcoSim statistical package (Gotelli & Entsminger 2001). This compares the χ^2 deviation statistics between expected and observed distributions with those between the expected and 1000 randomly generated distributions. The null hypothesis that the frequency distributions of individuals over CII classes are equal between the harvest intensities is rejected if the χ^2 deviation statistic for at least 95 percent (at α=0.05) of the random distributions is smaller than that of the observed distribution.

2.5 Tree growth

For individual trees with at least two DBH measurements available, we regressed DBH on date of measurement to obtain an estimator for the annual DBH growth rate. We omitted individual trees with conditions that may have had an influence on growth (*i.e.* trees that died in the course of the period, trees with rotten bark, trees with damaged bark, stem or crown, and so forth) and species with fluted stems (3 spp.). Additionally, we rejected data of trees with aberrant growth trends that were obviously caused by measuring or recording errors.

To test the relation between wood density and potential maximum growth rate we used linear regression analyses on large trees and poles in the Pibiri and Northwest data. For the Northwest we used data from all 56 plots. We defined the maximum potential growth rate of a species as growth that is not limited by environmental factors, which we estimated by taking the 90-percentile of the growth rate distribution of species. In that case we expect the growth rate to be limited only by the density of the added wood and photosynthetic capacity, not by shading by neighbours. The average growth rate is strongly affected by poor growth of suppressed individuals and therefore is not a reliable measure for maximum potential growth rate. For Pibiri, we conducted this analysis twice: for all individuals and for individuals with CII 4 and 5, excluding light-suppressed individuals. In all cases we only included species with more than 10 individuals.

We tested for overall differences in growth rates between the functional groups for poles and saplings separately, using Kruskal-Wallis tests. In addition we also tested, for both size classes separately, the effects of light availability on mean growth rates using Kruskal-Wallis tests. First we tested whether, *within* each functional group, mean growth rates increased with increasing CII. Thereafter we tested whether, for individuals with the same CII, mean growth rates differed *between* the functional groups. Because pioneer poles and saplings had only sufficient (but still low) numbers of individuals in CII 2 and 3, we excluded the data from the other two CII classes of the pioneers. Therefore we used for the pioneers Mann-Whitney tests to test the differences in CII classes within the group and was the pioneer group only included in the Kruskal-Wallis tests between the groups for CII 2 and 3. Because for saplings only climax species had individuals growing with CII 4, this light class was not included in the analyses for saplings

If significant differences in growth existed according to the test, we did multiple comparisons between the groups using a Dunn post hoc test for Kruskal-Wallis.

2.6 Mortality and recruitment patterns

We analysed the mortality, recruitment and net gain rates (*i.e.* the sum of mortality and recruitment) of the three functional groups in relation to light availability over a period of 1 to 6 years after logging. A positive value of the net gain rate implies a positive population growth rate over the measurement period, while a negative rate means that the number of individuals in the population decreased. To determine the effect of light availability on the recruitment and mortality rates of the saplings of the different functional groups, we calculated their rates for each CII class. We used the CII values assigned to subplots of the 1997 census. For the poles, which had no CII values assigned to subplots in 1997, we used the CII from the 2000 census. For the individuals that had died before that we used the 1993 CII. The three blocks (see section Pibiri plots in methods) are used for replication of the mortality, recruitment and net gain rates.

We quantified the mortality rates (m) per functional group according to equation (1) as postulated by Sheil *et al.* (1995),

$$m = 1 - \left(\frac{N_0 - N_m}{N_0} \right)^{\frac{1}{t}} \tag{1}$$

where N_0 is the total numbers of stems of the particular functional group at the beginning of the time interval t, and N_m is the number of recorded dead trees during the interval.

To be able to directly compare the mortality and recruitment rates, we calculated the recruitment rate (r) in a way that is equivalent to that of the mortality rates (Sheil *et al.* 2000) as,

$$r = 1 - \left(1 - \frac{N_i}{N_t} \right)^{\frac{1}{t}} \tag{2}$$

where N_t is the total number of stems at the end of the time interval t and N_i is the number of recorded recruits (*i.e.* ingrowths) in the particular size class during interval t.

We calculated mortality and recruitment rates for the intervals 1995-1997 and 1997-2000. The mean rates of these two intervals were used as the rates for the whole interval. We statistically tested the differences in effects of light availability on recruitment, mortality and net-gain rates of the three groups, using two-way ANOVA and Student-Newman-Keuls (SNK) post hoc tests.

2.7 Functional group distributions

To determine whether different functional groups were associated with different light conditions we examined the frequency distributions of poles and saplings of each functional group over CII in Pibiri. We tested for differences between functional groups using χ^2 analyses with the EcoSim statistical software as above (Gotelli & Entsminger 2001).

2.8 Shift in functional group composition

For the logged and unlogged plots in the Northwest we produced, per size class, a time series of change in functional group composition by calculating the relative abundances of the functional groups before logging and for each year during the first 5 years following logging. We could only make a distinction between logged and unlogged plots because the exact harvest intensities in trees ha^{-1} were not known for most of the plots in the Northwest. For Pibiri we determined per size class the relative abundance of functional groups for each harvesting treatment before logging, just after logging and 2 and 6 years after logging.

For the Northwest plots, for each size class we tested shifts in functional group composition using G-tests on absolute distributions for unlogged and logged plots. For the Pibiri plots we did the same for each harvesting treatment (including the unlogged control).

2.9 Diversity

We used Fisher's alpha (Fisher *et al.* 1943, Condit *et al.* 1996), which is sample size independent (Rosenzweig 1995), to quantify the tree species alpha-diversity per size class for each plot for the pre-logging census ($FA_{(0)}$) and the last available post-logging census ($FA_{(al)}$), *i.e.* five years in the Northwest and six years in Pibiri. To determine the response of Fisher's alpha to logging we did regression analyses of the ratio $FA_{(al)}/FA_{(0)}$ on logging intensity. We used the percentage basal area lost as a measure for harvest intensity, defined as the percentage of the basal area of all trees >20 cm DBH present before logging that is lost due to the logging operation (measured at the first census after logging).

We did all statistical analyses, except the χ^2, G and Dunn post hoc tests, using the SPSS (2001) statistical software package. Dunn post hoc tests for Kruskal-Wallis tests and G tests were carried out using a spreadsheet.

3 Results

3.1 Light availability and logging

In Pibiri, 6 years after logging, the proportions of individuals in higher light climates (*i.e.* higher CII values) increased with increasing harvest intensity (figure 1). The frequency distributions of poles and saplings over CII classes were significantly different between most harvest intensities (figure 1, χ^2 tests at $P<0.005$ for all differences), except between plots with 4 and 8 trees ha^{-1} logged for the poles and between the control and 4 trees ha^{-1} logged plots for the saplings.

3.2 Tree growth

The maximum potential growth rate of species was significantly negatively correlated with the specific wood density (figure 2, Northwest: $R^2=0.23$, n=74, $P<0.001$ and Pibiri: $R^2=0.10$ n=66, $P<0.01$, based on 90 percentile of growth). When we only used individuals with CII > 3 (*i.e.* individuals that grow in high light conditions), the amount of explained variance more than doubled to 25 percent (figure 2, $R^2=0.25$, n=23, $P<0.05$, Pibiri plots only).

Mean growth rates, not adjusted for differences in CII, of pioneer poles and saplings were much higher than for long-lived pioneer and climax species, but were accompanied by high standard errors and based on small numbers of individuals (Table 3). Only the mean growth rates of long-lived pioneer and climax poles (Dunn-test, Q=4.64, $P<0.01$) and pioneer and climax saplings were significantly different (Dunn-test, Q=2.81, $P<0.05$).

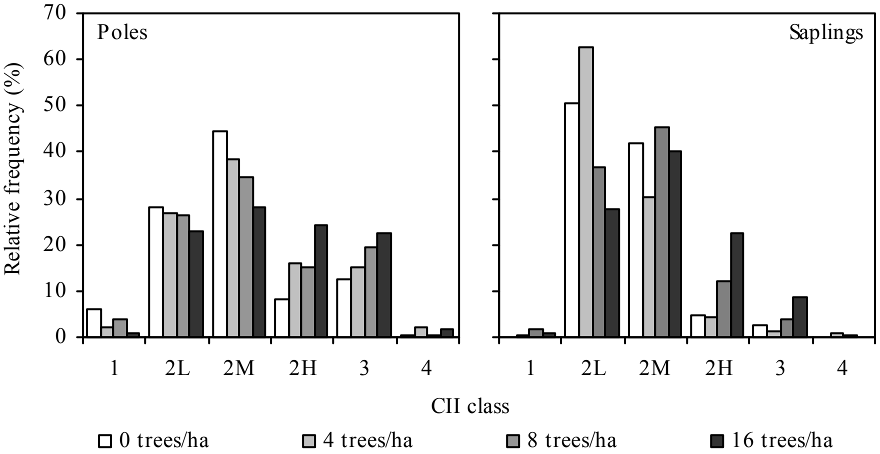

Figure 1 The relative frequency distribution of Crown Illumination Index (CII) for poles and saplings in plots with different logging intensities (0, 4, 8 and 16 trees ha^{-1} - see legend in poles figure) in Pibiri, 6 years after logging. With increasing logging intensities the frequency distributions for poles and sapling shifted significantly to lighter CII classes (χ^2-tests, $P<0.001$).

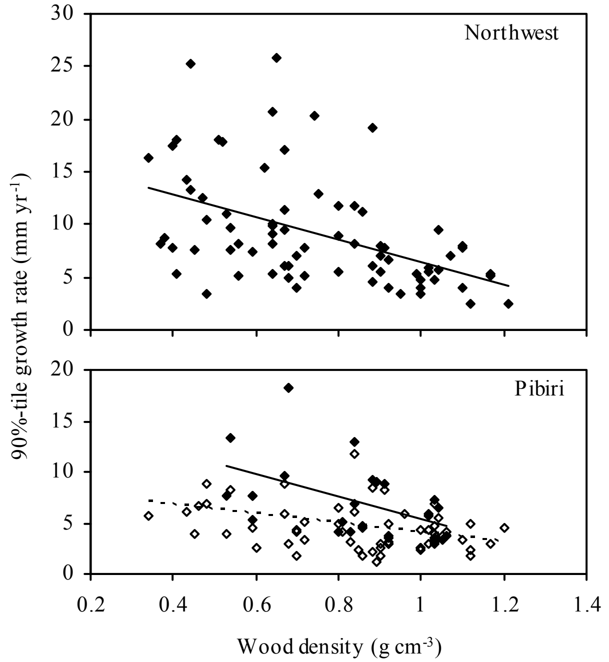

Figure 2 The relation between wood density (g cm^{-3}) and 90-percentile growth rates of tree species in the Northwest and Pibiri plots. The Northwest figure is based on all species with more than 10 individuals (R^2=0.23, n=74, P<0.001). In the Pibiri figure, open symbols with dashed trend-line are all species with more than 10 individuals (R^2=0.10 n=66, P<0.01), the closed symbols with solid trend-line are based on individuals with CII > 3 for species with more than 10 individuals (R^2=0.25, n=23, P<0.05).

The mean growth rates of poles and saplings of all functional groups increased with increasing CII class (Table 4). Pioneer poles with CII 2 grew significantly faster than those with CII 3 (Mann Whitney U=6, P<0.05) but there were no significant differences within the pioneer saplings. For both long-lived pioneer and climax poles and saplings, the growth rates were significantly different between all CII classes, except between CII 1 and CII 2 for the poles of both groups (Kruskal-Wallis tests, all P<0.001, see table 5 for comparisons with Dunn test).

For poles with CII 1, long-lived pioneers grew significantly faster than climax species (Mann-Whitney, U=285, P<0.05), but there were no significant differences for the saplings.

Table 3 Mean diameter growth rates ± standard error (s.e.) (mm yr^{-1}) and sample sizes (n) per size class, per functional group in all Pibiri plots. Within each size class, values of mean growth rate with different letters are significantly different (Dunn test at P<0.01 for poles and P<0.05 for saplings).

Functional group	Poles growth ± s.e. (mm yr^{-1})		n	Saplings growth ± s.e. (mm yr^{-1})		n
Pioneers	3.27 ± 0.91	ab	19	3.5. ± 1.12	a	9
Long-lived pioneers	1.73 ± 0.07	a	702	0.96 ± 0.06	b	364
Climax	1.38 ± 0.03	b	1839	0.81 ± 0.04	b	822

Table 4 Mean diameter growth rates ± standard error (s.e.) (mm yr^{-1}) and sample sizes (n) per size class per functional group among individuals with different Crown Illumination Index (CII) classes in Pibiri. Growth rates based on less than three individuals are not used for the analyses.

Functional group	CII	Poles growth ± s.e. (mm·yr^{-1})	n	Saplings growth ± s.e. (mm·yr^{-1})	n
Pioneers	1	0.01	2	0.51	1
	2	0.70 ± 0.37	6	2.10 ± 1.07	3
	3	4.29 ± 1.32	9	4.49 ± 1.70	5
	4	9.69	2	-	0
Long-lived pioneers	1	0.63 ± 0.23	18	0.47 ± 0.05	104
	2	1.42 ± 0.06	520	0.98 ± 0.08	164
	3	2.76 ± 0.20	147	1.46 ± 0.16	96
	4	3.68 ± 0.68	17	-	0
Climax	1	0.22 ± 0.04	52	0.41 ± 0.03	223
	2	1.15 ± 0.03	1383	0.74 ± 0.04	386
	3	2.25 ± 0.09	390	1.33 ± 0.09	209
	4	3.14 ± 0.55	15	2.43 ± 0.96	4

The multiple comparisons at CII 2 and CII3 between the functional groups, including the pioneers, showed that growth rates of pioneer poles and saplings at CII 2 were significantly higher than those of the climax poles (Dunn test, Q=4.36, P<0.001) and saplings (Dunn test, Q=3.01, P<0.001). There were no significant differences for CII 4.

3.3 Mortality and recruitment patterns

For the saplings in Pibiri, there was a significant effect of functional group (F=6.85, d.f.=2 and P<0.01) and CII (F=3.86, d.f.=2 and P<0.05) on recruitment rates but not mortality rates (figure 3). Pioneers had a significantly higher recruitment rate (SNK, P<0.05) than the other

Table 5 Significance levels (*: P<0.05, **: P<0.01 and n.s.: not significant) of differences in mean growth rates (see table 4) between CII classes within each functional group. Pioneers only have sufficient individuals for CII 2 and CII 3. Comparisons within the pioneers were done with Mann-Whitney tests and within the other groups with Dunn post-hoc tests.

Functional group	CII	Poles			Saplings	
	vs	2	3	4	2	3
Pioneers	2	-	*		-	n.s.
Long-lived pioneers	1	n.s.	**	**	*	**
	2	-	**	**	-	**
	3		-	*		-
Climax	1	n.s.	**	**	**	**
	2	-	**	**	-	**
	3		-	**		-

two groups, and subplots with CII 3 had significantly higher recruitment rates than subplots with lower CII values.

The ANOVA for net gain rate of the saplings (figure 3) showed a significant interaction between functional group and CII values (F=4.69, d.f.=4 and P<0.05). From this we can conclude that the effect of CII of the subplot is different for the different functional groups. Net gain rate was significantly higher (P<0.05) for the pioneers in subplots with CII 3 than for any other combination of functional group and CII (SNK, P<0.05).

The recruitment and mortality patterns of the poles were less clear (figure 3). There were no pioneers and only few long-lived pioneer and climax poles that had a CII value of 1 or 4. Recruitment and death of a few individuals will in that case have relatively large effects on the rates. For recruitment and net gain rates there were significant interactions between functional group and CII values (recruitment: F=2.80, d.f.=6, P<0.05 and net gain rate: F=3.92, d.f.=6, P<0.01). We found no significant differences in mortality rates. Pioneer poles with CII 2 had a significantly higher recruitment rate (SNK, P<0.05) than any other

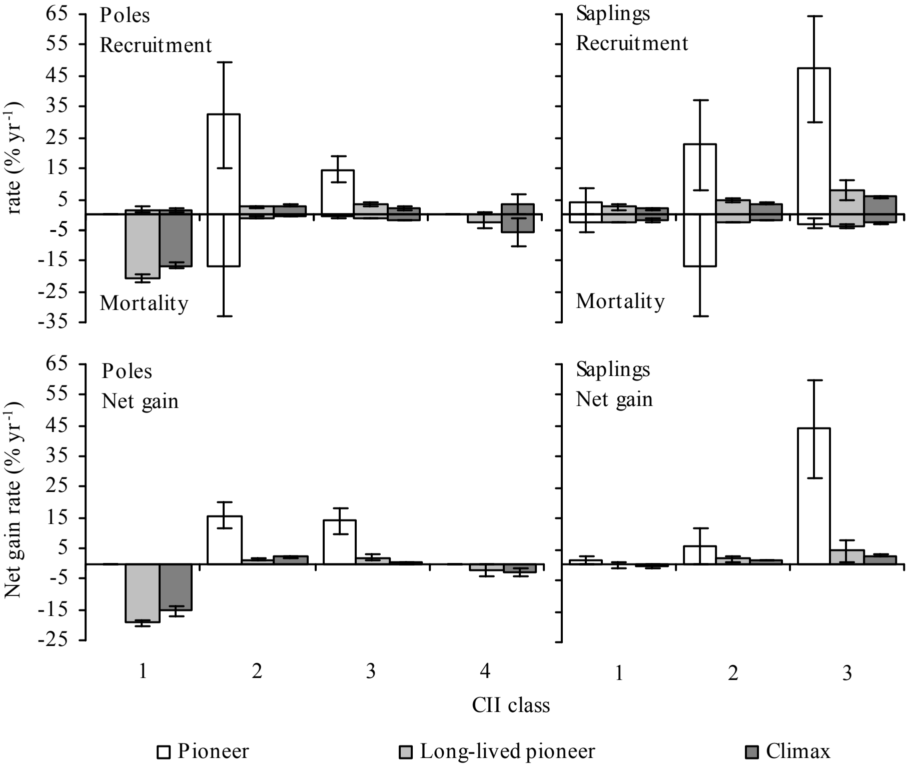

Figure 3 Mean mortality, recruitment and net gain rates (% yr^{-1}) for pioneer, long-lived pioneer and climax poles and saplings at different CII classes. Error bars are standard errors. Mortality rates are represented as negative values. The net gain rate is the sum of the recruitment and (negative) mortality rates.

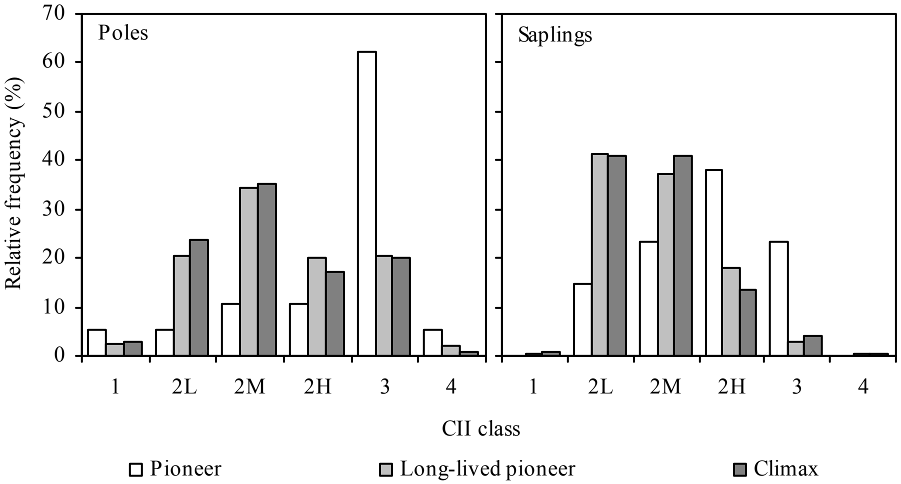

Figure 4 The relative frequency distributions of CII for pioneer, long-lived pioneer and climax poles and saplings in Pibiri. In both size classes the distributions of the pioneers significantly differed from that of the long-lived pioneers (poles: χ^2=15.7, P<0.005 and saplings: χ^2=15.25, P<0.005) and climax species (poles: χ^2=17.7, P<0.001 and saplings: χ^2=16.11, P<0.005).

combination of functional group and CII. Pioneer poles with CII 2 and 3 had significantly higher net gain rates (SNK, P<0.005) and long-lived pioneer and climax poles at CII value 1 had significantly lower (negative) net gain rates than the other combinations of functional group and CII.

3.4 Functional group distributions

The distributions of both poles and saplings over CII classes were significantly more towards higher CII values for pioneers than for long-lived pioneers (figure 4, poles: χ^2=15.7, P<0.005 and saplings: χ^2=15.25, P<0.005) and climax species (figure 4 poles: χ^2=17.7, P<0.001 and saplings: χ^2=16.11, P<0.005). The distributions for long-lived pioneers and climax species were almost identical.

3.5 Shift in functional group composition

In the Northwest plots, the relative abundance of saplings of pioneer species significantly increased over the first three years after logging from 1% to 7%, at the expense of the relative abundance of saplings of climax species, which decreased in the same period from 51% to 47% (G-test on absolute abundances: G=454.7, d.f.=9, P<0.001, figure 5). After three years, the relative abundance of pioneer saplings decreased again (figure 5), which was due to outgrowth to the poles size class (compare with the saplings in figure 5). The relative abundances of saplings of the three functional groups did not shift in the non-logged plots (figure 5). Delayed by one year, a similar trend was found for the poles, where the relative abundance of pioneers increased from 2% to 8% and that of the climax species decreased from 61% to 58% (G-test on absolute abundances: G=245.9, d.f.=9, P<0.001, figure 5). This increase was caused by in-growth from the sapling size class (see above).

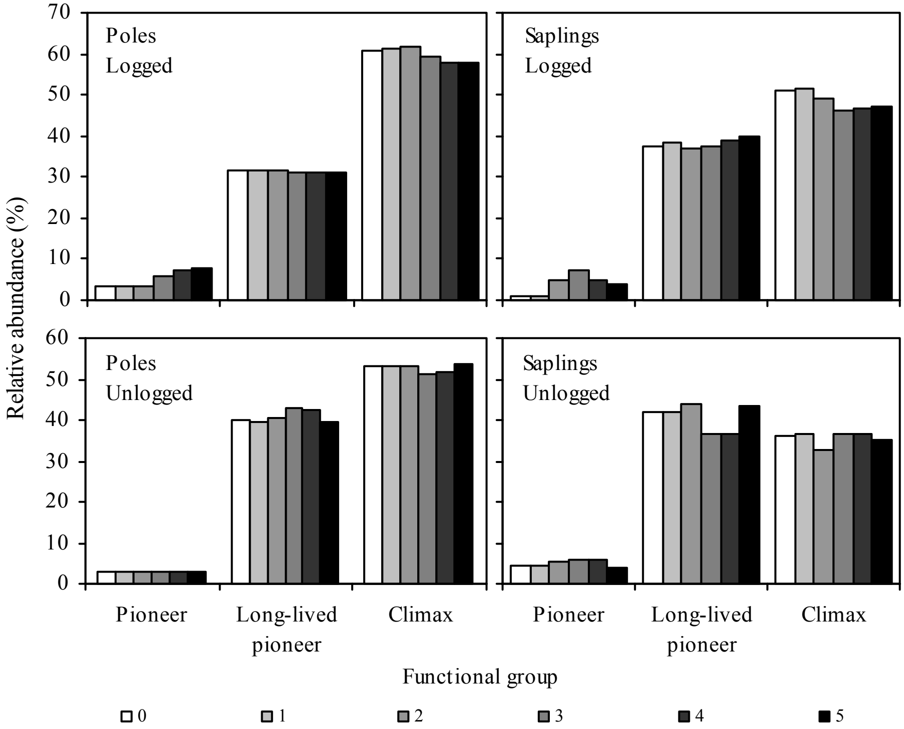

Figure 5 Time series of relative abundances of pioneer, long-lived pioneer and climax poles and saplings since logging (see legend in figure, 0: initial inventory and 1-5: one to five years after plots were set-up) for logged and unlogged plots in the Northwest. Logged plots have been harvested just after the initial inventory. In the logged plots the abundance of the pioneers increased significantly at the expense of the climax species (G-tests, all $P<0.001$) while in the unlogged plots there were no significant shifts in abundance between the functional groups.

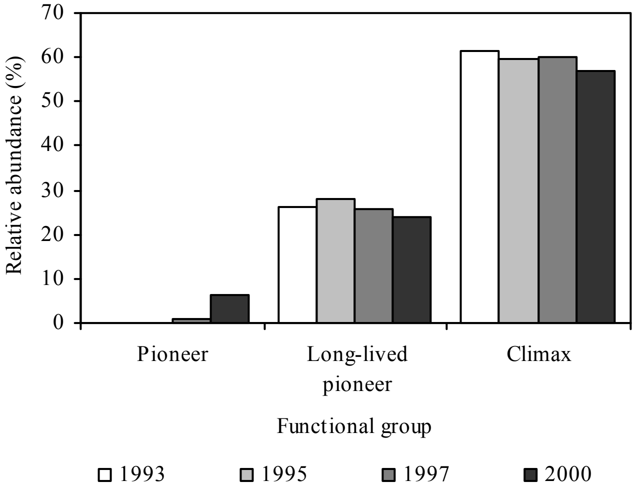

Figure 6 The relative abundances of pioneer, long-lived pioneer and climax saplings over years (see legend, 1993: before logging, 1995: just after logging) in the Pibiri plots with a harvest intensity of 16 trees ha^{-1}.

In the Pibiri plots the relative abundance of the pioneer saplings in the plots that had a harvest intensity of 16 trees ha^{-1} significantly increased at the expense of that of climax species (G-test on absolute distributions: G=41.1, d.f.=9, P<0.001, figure 6). In these plots, within 6 years after logging the relative abundance of pioneer saplings increased from 0% to 6.2% and the relative abundance of saplings of climax species decreased from 61.5% to 57%. For the saplings in the other logged PSPs the relative abundances of pioneers slightly increased from 0.4% to 1.2% in plots with harvest intensity 4 and from 0.6% to 1.9% in plots with harvest intensity 8, but these shifts were not statistically significant. Functional group composition for saplings in the unlogged plots and for poles in all treatments remained more or less constant over years.

3.6 Diversity

The ranges in $FA_{(0)}$ and $FA_{(al)}$ for poles and saplings in 37 plots in the Northwest and the Pibiri plots are presented in table 6. In both the Northwest and Pibiri plots the $FA_{(al)}/FA_{(0)}$ ratio for the saplings was positively related to logging intensity (figure 7, Northwest: N=37, R^2=0.28, and Pibiri: N=12, R^2=0.79, both at P<001, logging intensity expressed as %basal area lost). There was also a weak positive relation between logging intensity and $FA_{(al)}/FA_{(0)}$ ratio for the poles in the Northwest (figure 7: N=37, R^2=0.16 at P<0.05) and a weak negative relation for the poles in Pibiri (figure 7: N=12, R^2=0.34, P<0.05). In both areas the $FA_{(al)}/FA_{(0)}$ for trees were not related to percentage basal area lost (data not shown).

Table 6 Ranges in $FA_{(0)}$ and $FA_{(al)}$ for poles and saplings in 37 plots in the Northwest and the Pibiri plots.

Area	Poles		Saplings	
	$FA_{(0)}$	$FA_{(al)}$	$FA_{(0)}$	$FA_{(al)}$
Northwest	6.4 - 15.9	7.0 - 15.9	5.6 - 13.8	6.0 - 16.6
Pibiri	15.8 - 29.7	14.2 - 31.4	11.2 - 29.2	11.35 - 28.0

4 Discussion

4.1 Population dynamics

The tree-communities that we studied appear to be adapted to low intensity and infrequent disturbance events and contain many species that are able to establish, survive and grow (slowly) in small gaps and the shaded forest understorey. As expected, light availability in the forest increased with increasing logging intensity. From the differences in the CII distributions of poles and saplings between the various treatments in Pibiri we can conclude that six years after logging there are still significant effects of logging on light availability in the forest. In general the growth rates of all three functional groups increased with increasing light availability, suggesting a positive effect of logging on growth rates of all species, conform our hypothesis. Increased light availability showed a clear positive effect on the recruitment (in-growth) rates of the pioneer saplings. This may be explained by the faster

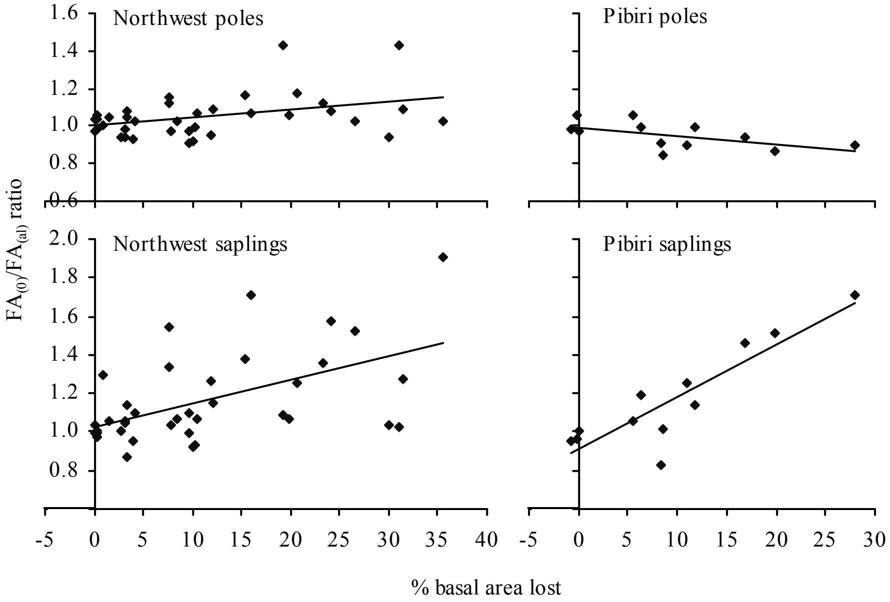

Figure 7 Relation between $FA_{(al)}/FA_{(0)}$ and the percentage basal area lost after logging, for poles and saplings in PSPs in the Northwest and Pibiri. $FA_{(0)}$ is Fisher's alpha before logging and $FA_{(al)}$ is Fisher's alpha at the last available post-logging census, *i.e.* five years in the Northwest and six years in Pibiri. In the Northwest, % basal area lost explained 16% of the variance in the ratio for poles ($n=37$, $R^2=0.16$ at $P<0.05$) and 28% of the variance in the ratio of saplings ($n=37$, $R^2=0.28$ at $P<0.001$). In Pibiri it explained 34% of the variance in the ratio for poles ($n=12$, $R^2=0.34$ at $P<0.05$) and 79% of the variance in the ratio for saplings ($n=12$, $R^2=0.79$ at $P<0.001$).

growth at higher light availabilities, enabling new recruits to reach the minimum sapling size-class limit faster. The relative frequency distributions of CII classes of poles and saplings (figure 3) showed that pioneers occur relatively more often in high light conditions than individuals of the other two groups.

Brokaw 1985) found that pioneers need gaps larger than 150 m^2 for successful regeneration in Panama, while others (Ek 1997, van der Hout 1999 and Rose 2000) suggest that no major pioneer proliferation occurs in gaps below 300-400 m^2, based on data in Guyana. In a review, Rose & Poorter (2003) show that large seed mass is associated with high survival in shade and slower relative growth rate in high light conditions. Only in large gaps (high light) where pioneers are able to germinate and realise higher growth and survival rates they are able to outcompete seedlings of large seeded species that are already present before gap creation (Boot 1996, ter Steege & Hammond 1996, Rose & Poorter 2003, ter Steege (2003b).

In Pibiri logged forest had more and larger gaps than unlogged forest in the same area (van Dam & Rose 1997, van der Hout 1999). Based on data in van Dam & Rose 1997) we estimate that in a forest area of 1 ha approximately every 15 years a gap > 150 m2 is formed (Brokaw 1985 found 5.3 yr), while only once every 45 years this is a gap > 300 m^2. Disturbance intensity and frequency in these forests should be regarded low when compared to other forests (*e.g.* Hartshorn 1990, van der Meer & Bongers 1996, van der Hout 1999). In logged forest, both the frequency of large gaps and the total area in large gaps is larger than in unlogged forest (van der Hout 1999), providing more opportunities for pioneers for successful regeneration.

The increased recruitment success and high growth rates of pioneer seedlings compared to the other groups in high light conditions was in our study expressed as the much higher recruitment and population gain rates of the pioneer saplings in subplots with high light conditions. Since the survival rates of saplings and poles (except at low light) are generally high (> 95% if low light for poles is omitted, see also Clark & Clark 1992, Welden *et al.* 1991), we expect that many of the new pioneer recruits that we found in the saplings and poles classes will be able to reach maturity, which is among other factors import for these species to maintain themselves in the community.

4.2 Functional groups

At both sites, the 90-percentile growth rate was significantly related to wood density, with high growth rates associated with low wood density. In the Northwest, wood density of species accounted for 23% of the variation in 90-percentile growth rate and in Pibiri the wood density explained 25% of the variation in 90-percentile growth rates of individuals growing in high light conditions. The amount of explained variance is in the same order as found by ter Steege *et al.* 2003 (ter Steege *et al.* 2003) and Verburg & van Eijk-Bos (2003a, 2003b). Based on these results we conclude that species-specific wood density can be used as a predictor of a species potential growth rate. Other studies (Williamson 1975, Augspurger 1984) show that wood density is positively related with other measures for the shade tolerance of tree species.

Species that we classified a-priori into three functional groups based on differences in two plant traits, wood density and seed mass, could indeed be distinguished in their functional response to light availability as generally (*e.g.* Brokaw 1985, Brokaw 1987, Clark & Clark 1992, Poorter 1999, Poorter & Arets 2003) found for pioneer, long-lived pioneer and climax species. For another study in Guyana (ter Steege *et al.* 2002) that used an almost identical classification of species into functional groups (only subdivision of wood density at 0.7 vs. 0.8 in this study) was found that all species cited in literature as pioneers had wood densities < 0.7 g cm^{-3}. Hence our classification is comparable with more subjective classifications used in other studies.

4.3 Functional group composition

In Pibiri the relative abundance of pioneer saplings increased with increasing harvest intensity. In the Northwest there was an effect of logging on relative abundance of pioneer saplings and poles. Because we pooled all logged plots in the Northwest, the changes in relative abundance are based on an average response across the whole range of harvest intensities. The results from both areas are consistent with our expectations and other studies on effects of logging on composition (Silva *et al.* 1995, Verburg & van Eijk-Bos 2003a, 2003b).

The timing and magnitude of the changes in functional group composition after logging differed between the two study areas. In the Northwest, there was already a notable increase in abundance of pioneer saplings within 2 to 3 years after logging, while in Pibiri this was seen after 4 to 6 years. Further, the relative abundance of pioneer poles in the Northwest increased within 5 years since logging, but in Pibiri this was not as yet the case within 6 years since logging. These differences are associated with a difference in mean pioneer growth rates between the two areas (data not shown, but compare the two graphs in figure 2), which will probably also be the case for the saplings. Furthermore, the minimum size limit of saplings was lower in the Northwest plots than in Pibiri (table 1). Hence in the Northwest recruits of the pioneer species would have been able to achieve sapling size more quickly than in Pibiri. Differences in growth rates are most likely due to differences in nutrient availability between the soil types in the two areas (Gross-Braun *et al.* 1965).

Even though the relative abundance of pioneer species increased after logging, they still remain rather scarce (between 6% and 8% of sapling or pole stems, depending on research area and size class). In the forests studied, pioneers are almost absent (see also ter Steege & Hammond 2001 and ter Steege *et al.* 2002), most likely due to a lack of suitable sites for regeneration (see above), consequently leading to reduced density of seed rain and soil seed bank. Therefore the seeds have to come from adult pioneers standing along (logging) roads and old log-markets further away. Consequently distances may be too long for proliferate colonisation of the logging gaps, in spite of the small and well-dispersed seeds of pioneers.

4.3 Diversity

The sapling diversity increased with increasing harvest intensity. The diversity of poles increased in the Northwest with increasing harvest intensity, while it decreased slightly for poles in Pibiri. This difference between sites may be explained similarly as for composition by the fact that in Pibiri growth rates of new recruits were too low to reach the poles size limit yet.

Increased diversity after disturbance is consistent with the predictions of the IDH with respect to effects of disturbance on diversity in forests with a few dominant species and low intensity natural disturbance regimes. We did not find, however, the humpbacked relationship between disturbance and diversity (figure 7) as predicted by the IDH (Connell 1978 and see Chapter 1) that was found in a forest with similar compositional and disturbance properties (ter Steege *et al.* 2000) in French-Guiana (Molino & Sabatier 2001). In this study in French-Guiana, Molino & Sabatier (2001) found that diversity was highest in logged forests with an intermediate abundance of pioneers (around 30%), which was used as an estimator for disturbance regime. The cumulative basal area lost for trees > 10 cm DBH over a 8 years period (including logging) at that site varied from 0 to 24.6 m^2 ha^{-1}. Since the highest pioneer abundance found in our study was not higher than 8% and the cumulative basal area lost (during 7 years period in Pibiri) did not exceed 11 m^2 ha^{-1}, the disturbance levels in our study appear to be too low to find an optimum effect of disturbance on diversity. The change in diversity after increased disturbance in our case would then still be in the ascending trajectory (arrow ① in figure 1 in Chapter 1) towards optimum diversity. If logging increases disturbance beyond this point, diversity would be expected to decrease again.

Some studies that determine the effect of large-scale disturbance events (of which logging is an important example) on tree species diversity only take into account trees with large DBH (*i.e.* typically 10-20 cm DBH and larger) combined with relatively short monitoring periods since logging (Cannon *et al.* 1998, Webb & Peralta 1998). Based on 90-percentile growth rates from functional groups in this study (Table 7) we calculated that the minimum number of years for a sapling of 2 cm DBH to reach 20 cm DBH is approximately 20 years (Table 7), while the times needed by species of the other two groups are even longer. Hence, effects of recruitment of new species after disturbance cannot be found in the composition and diversity of trees larger than 20 cm DBH until more than 20 years after disturbance. Studies that find no effect of disturbance on diversity may not be long enough in relation to the size classes that are considered. Although Cannon *et al.* 1998) found that diversity of trees >20 cm DBH increased within 8 years since selective logging on Borneo it appeared that these results were most likely caused by older disturbance events (Sheil *et al.* 1999).

Recently the role of disturbance as explanation for the maintenance of species diversity in tropical forests has been disputed (Hubbell *et al.* 1999, Brokaw & Busing 2000). Hubbell *et al.* 1999) found that although patches with light gaps contained more species than undisturbed forest, this was entirely attributed to increased stem densities. They argued that recruitment limitation, a chance process that explains why the species that is the best competitor in certain environmental conditions does not occupy all sites with those conditions, offers a better explanation for maintenance of diversity. Our results and other studies (Cannon *et al.* 1998, Magnusson *et al.* 1999, Molino & Sabatier 2001, Sheil 2001) show, however, that disturbance plays an important role in determining tree diversity at least on the scale of one to several ha.

Table 7 90-percentile annual DBH growth rates (mm yr^{-1}) for pioneer, long-lived pioneer and climax poles and saplings. For the pioneer saplings the sample size was insufficiently large for calculation of 90-percentile annual growth rates, therefore we used for these the maximum growth rate. The amount of years needed to grow from 2 to 20 cm DBH was estimated using the 90-percentile annual growth rates, assuming that these stay constant over time and within a size class.

Functional group	90-percentile growth rate (mm yr^{-1})		Years needed to grow
	Poles	Saplings	from 2 to 20 cm DBH
Pioneer	9.9	10.8	20
Long-lived pioneer	3.7	2.1	64
Climax	3.3	1.9	72

4.4 Long-term effects

Although in this study we report on effects over relatively short periods after disturbance the results and trends we found can be used to make predictions about future developments in composition and diversity. We propose that pioneers will further increase their relative abundance if logging will be repeated in the same area within the lifespan of the pioneers that have recruited after the first logging (estimates of the maximum life spans of typical pioneer species are *e.g.* 54 yrs for *Cecropia sciadophylla* and 69 yrs for *Miconia punctata*, Korning & Balslev 1994). In that case the distances from pioneer seed sources (*i.e.* the new recruits from the past logging event) to newly formed gaps will become smaller and may result in more effective colonisation of the area. If this happens repeatedly over long time, the proportion of pioneers within the forest will gradually increase while the abundance of the climax species that are typical for the primary forest as it is now, will further decline due to their inferior colonisation of the large number of large gaps in relation to pioneers. As a consequence, we expect that tree diversity in these forests will decrease towards low diversity at the high intensity disturbance end of the range (*i.e.* arrow ③ in figure 1 in Chapter 1). If logging is only limited to this one occasion, or the time till the next disturbance event is longer than the lifespan of the newly recruited pioneers, we expect that the tree community will completely recover from this single perturbation of the disturbance regime and will return to its previous state.

Either long-term monitoring or studies with simulation models are needed to test these and other hypotheses on long-term effects of different management regimes (*e.g.* logging intensities, times between logging events and total number of logging events in the same area) and large-scale natural disturbance events on species composition and diversity. Because long-term monitoring data are rather sparse for most areas (but see *e.g.* Burslem & Whitmore 1999, Sheil 2001 and ter Steege *et al.* 2002), often not long enough (as discussed before) and don't allow for much flexibility in testing different management and disturbance regimes, simulation models should be regarded as the most promising tools to get more insight in the longer-term effects of high intensity disturbance on species composition and diversity.

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Chapter 3

A spatially explicit individual-based tree dynamics model for a tropical rain forest community in central Guyana

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Abstract

In this chapter we present a model of forest dynamics in central Guyana with which the effects of alternative forest management regimes can be evaluated on timber yields, forest structure and forest composition. The model is implemented within the SYMFOR modelling framework, which is spatially explicit and individual-based. We used 9 functional groups (pioneers, long-lived pioneer and climax species divided in 3 classes of adult stature each) to model key demographic processes. Diameter growth rates of individual trees were modelled as function of tree diameter and a distance and size dependent competition index. Natural mortality probability was modelled as a logistic function of competition index and also the probability of recruitment, defined as the in-growth of trees with a diameter of 2 cm, was based on the competition index. The functions in the model were parameterised based on measurements of all trees that have a diameter greater than 2 cm from 15 experimental sample plots in central Guyana that were experimentally logged using reduced impact logging.

Long runs (1000 years) of the model without simulation of management scenarios showed that the abundance of some of the functional groups changed over time. All simulated stem densities, however, remained within the range as found in the field data. Within 250 years all groups had reached a stable state. Sensitivity analysis showed that the model is rather robust for changes in tested model components (growth, mortality, recruitment and three parameters that directly affect these components). Exceptions were the pioneer groups, which showed very large changes in abundance and basal area. Model results were, however, most sensitive to mortality and recruitment, which are also the components that had the highest uncertainty. The model can be used to guide ongoing discussions on the improvement of forest management, regulation and certification in Guyana.

1 Introduction

Throughout the tropics, rain forest trees are selectively harvested at an increasing rate and scale (FAO 2000, van der Hout 1999). In Guyana, situated in the northeast of South America, an estimated 160,000 ha is selectively harvested annually (FAO 2000). Although generally the intensity of selective logging is rather low, damage to the residual forest may be considerable (Johns 1988, van der Hout 1999). For sustainable forest management, information is required describing the long-term consequences of current logging practices for future timber yields and for ecological functioning of exploited forests. An important difficulty in obtaining this information is that tropical trees often are slow-growing and long-lived organisms that may live for several hundred of years (*e.g.* Lieberman & Lieberman 1987, Korning & Balslev 1994, Fichtler *et al.* 2003, Laurance *et al.* 2004b).

There are several ways to study and predict the long-term effects of forest management regimes and large-scale natural disturbance events, on future forest structure, composition, diversity and economic value. The first option is the long-term monitoring of managed forest (*e.g.* ter Steege *et al.* 2002). For most forests, however, these studies are limited as long-term post-harvest monitoring data are scarce for tropical forests. An alternative is the use of forest simulation models that are parameterised with short-term sample plot data to simulate the key demographic processes in tree populations, *i.e.* growth, mortality and recruitment. Such simulation models can be used for scenario studies to evaluate the impact of different forest management regimes on timber production and species composition. These scenario studies also allow much more flexibility in testing different management and disturbance regimes than long-term monitoring.

In this paper we describe, parameterise and evaluate a simulation model for a forest in Guyana. Our objective is to create a model that can evaluate future timber yields, community structure and community composition of forests subjected to alternative logging regimes. A wide variety of approaches exists to model tree population dynamics in forest ecology and forestry (*e.g.* Vanclay 1994, Liu & Ashton 1995, Peng 2000, Porté & Bartelink 2002). Not all approaches, however, are suitable to simulate the considerable environmental changes caused by logging and their effect on community characteristics such as structure and composition (Boot & Gullison 1995). Models that cannot explicitly simulate changes in structure and environment are generally only valid under conditions for which they were calibrated (*e.g.* matrix models) and consequently these models lack flexibility in testing scenarios for which field data do not exist. Furthermore, matrix models generally only take into account one specific commercial species. Although these models may reveal important information on the consequences of logging for specific species (*e.g.* Zagt 1997), they cannot be used to determine the consequences of logging on community structure and composition. In spatially explicit individual-based models (*e.g.* Pacala *et al.* 1996, Deutschman *et al.* 1997, Liu & Ashton 1998, Chave 1999, Gourlet-Fleury & Houllier 2000, Phillips *et al.* 2003, 2004b), individual trees that occupy a unique spatial position are the units of modelling. In these models spatial variation is not averaged over large areas, making them able to explicitly simulate changes of structure of the forest.

We implemented the model described in this paper in SYMFOR, a software framework for spatially explicit individual-based ecological and management models for species-rich tropical forests (Phillips & van Gardingen 2001a, 2001b, Phillips *et al.* 2002b, 2003, 2004b). Previous models within SYMFOR have been implemented successfully for a Dipterocarp forest in Indonesian Borneo (Phillips *et al.* 2003) and forests in Guyana (Phillips *et al.* 2002a, 2002b) and Brazil (Phillips *et al.* 2004b) to evaluate sustainability of alternative management scenarios (van Gardingen *et al.* 2003). The model presented here is based on data from a tropical rain forest in central Guyana. Another version of this model was previously developed for this area (Phillips *et al.* 2002b). The current model is, however, based on more data. The functional groups are based on ecological characteristics of the species and are now comparable with classifications used in other studies in Guyana (*e.g.* ter Steege & Hammond 2001, ter Steege *et al.* 2002, chapter 2). Further, the model includes smaller saplings that show a stronger response to disturbance and logging. Different functions were derived for most processes and size relationships of DBH on height and crown dimensions were parameterised and, finally, a competition index was used that is better associated with light availability. The model can be used by forest managers and other stakeholders to evaluate the effects of logging and to provide optimum silvicultural prescriptions (*e.g.* felling cycle, harvest intensity and minimum felling diameter) for sustainable management.

2 Model description

2.1 General

The ecological model that we describe here was implemented in the SYMFOR framework (for more details see Phillips & van Gardingen 2001a, Phillips *et al.* 2003, 2004b: http://www.symfor.org). SYMFOR is programmed in the object-oriented programming language C++. Ecological models within SYMFOR are developed to represent the three main demographic processes in populations of forest trees, namely, *growth*, *mortality* and *recruitment*. The rates of these processes for individual trees depend on their own size and on competition with other trees. Competition among individuals is represented as a competition index that is explicitly derived from the data. The model is individual-based and spatially explicit, meaning that all trees are individually represented and occupy a unique spatial position in the simulated forest stand. The SYMFOR framework was designed to run with an annual time-step. To avoid edge effects, it uses plot wrapping for all spatial processes (*e.g.* competition index and tree fall). This means that a plot is simulated as a torus and thus that each border of a plot is connected to the opposite border.

Our choices of form of particular functions in the model were based on the data from which the functions were developed in combination with descriptions in literature and expert knowledge. For all functions we opted for the most parsimonious alternatives and we only included detail where it was justified by the data. The used variables and parameters are summarised in appendix I, at the end of this chapter.

Before turning to describing the main functions for growth, mortality and recruitment it is necessary to explain the treatment of species in the model.

2.2 Functional groups

Since most tree species in the forest are very rare (chapter 1 & 2), it is not possible to parameterise the functions in the ecological model separately for all species. Therefore we objectively classified species into functional groups with similar ecological characteristics. Tropical trees are often classified depending on the stage of succession in which they appear in the forest (*e.g.* Swaine & Whitmore 1988, Finegan 1996), which is related to the light demand of the species. The basis of many classifications is the dichotomy between pioneer and climax species (Swaine & Whitmore 1988). Pioneers are fast growing and light demanding species that appear early in succession while climax species grow slower and are more shade-tolerant that appear late in the succession. Individuals of an intermediate group of long-lived pioneers show up later than the pioneers and live for a prolonged period of time (Finegan 1996). Our classification was objectively based on differences in three morphological characteristics: wood density, seed mass and adult stature, which we consider to be predictors of species' responses to disturbance in terms of growth, recruitment and survival (see Favrichon 1994, Finegan 1996, ter Steege & Hammond 1996, ter Steege & Hammond 2001).

Wood density is a good proxy for maximum potential growth rate (Verburg & van Eijk-Bos 2003, ter Steege *et al.* 2003, Verburg *et al.* 2003, chapter 2). Seed mass is correlated with recruitment success and early survival of a species (*e.g.* Foster & Janson 1985, Hammond & Brown 1995, Boot 1996, Rose & Poorter 2003, van Ulft 2004, but see Grubb 1996). Adult stature is a measure for environmental conditions that are needed for a tree to reproduce and timing of reproduction, *i.e.* trees in the forest understorey need less light and will start reproducing earlier than canopy or emergent species. It is also related to shade tolerance and growth (Swaine & Whitmore 1988, Davies & Ashton 1999). We used wood density and seed mass to quantify three life history strategies (pioneers, long-lived pioneers and climax species) as was done in chapter 2 and we subdivided these life history groups in three subgroups each, depending on adult stature (small, medium and tall stature, which relate to understorey, canopy and emergent positions in closed forests). This combination of life history and adult stature groups resulted in nine functional groups (table 1). A complete list of the classification for all species present in the dataset is provided in appendix A at the end of this thesis.

Table 1 Classification of the 9 functional groups. WD: Wood density (Low: < 0.8 g cm^{-3}, High: ≥ 0.8 g cm^{-3}), SM: Seed Mass (Low < 0.1 g, High: ≥ 0.1 g), TH: maximum Tree Height (small (understorey): < 25 m, medium (canopy): 25 – 35 m, tall (emergent): ≥ 35 m). Ns$_{pecies}$: number of species occurring in the Pibiri sample plots for each functional group, see appendix A for an overview of species per functional group. Column AG refers to the corresponding classification into super-groups used for the allometric relationships (allometry groups). This classification of allometry groups was based only on wood density and maximum tree height.

Functional group		WD	SM	TH	$N_{species}$	Coding	AG
Pioneers	small	Low	Low	< 25	13	P1	1
	medium	Low	Low	25 - 35	5	P2	2
	tall	Low	Low	≥ 35	5	P3	3
Long-lived pioneers	small	Low	High	< 25	14	LP1	1
	medium	Low	High	25 - 35	31	LP2	2
	tall	Low	High	≥ 35	21	LP3	3
Climax	small	High	All	< 25	29	C1	4
	medium	High	All	25 - 35	49	C2	5
	tall	High	All	≥ 35	18	C3	6

In this way all known tree species occurring in the data used for parameterisation could be classified. 99.2% of individuals in the database had species information recorded and were classified into the functional groups Individuals of unknown species were omitted for parameterisation, while for model simulations they were randomly distributed over the functional groups.

2.3 Allometric functions

The SYMFOR framework requires estimates of the dimensions of individual trees (figure 1a) to simulate processes such as damage caused by falling and logged trees (figure 1b) and to calculate the competition index. In previous SYMFOR models (Phillips *et al.* 2003, Phillips *et al.* 2004b) allometric relations were generic and the coefficients and assumptions used were based on anecdotal experience. In the current model all allometric relations were parameterised using field data.

We described the relation between height, H (in meters), and diameter at breast height (DBH, *i.e.* diameter at 1.3 meters height), D (in cm), of functional groups using an asymptotic relationship with 3 parameters that determine the shape of the function, as presented by Thomas (1996),

$$H = h_2 \cdot (1 - \mathrm{e}^{-h_0 \cdot D^{h_1}}) \tag{1}$$

where h_0 and h_1 are functional group specific parameters that determine the curving and h_2 is a parameter that determines the asymptote, *i.e.* the height at infinitely large DBH.

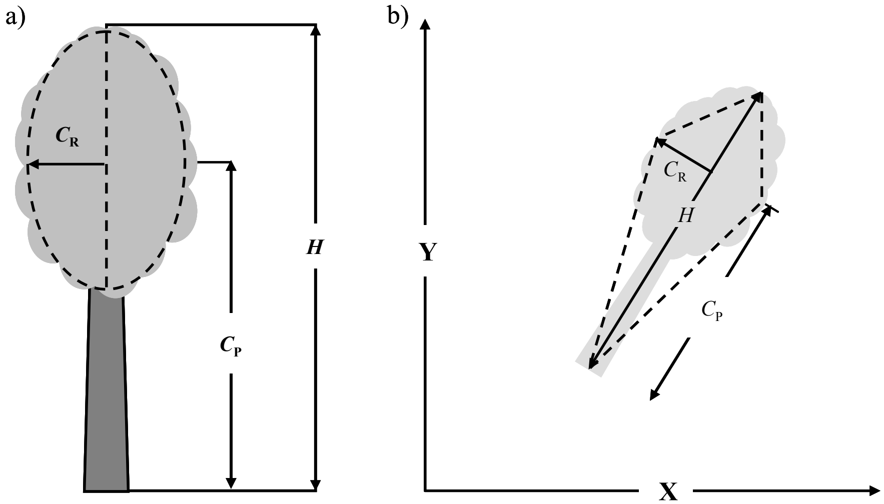

Figure 1 Graph a) shows the allometric properties of individual trees: H is the total tree height, C_p is the crown-point, *i.e.* the height at which the crown is widest, and C_R is the radius of the crown. Graph b) shows schematically the damage area associated with a tree that falls in a random direction (x, y). The allometric properties of the falling tree determine the sizes of the kite-shaped damage area. Other trees that are standing within this damage area and that are smaller than the falling tree have a probability M_D to get killed.

We assumed that the radius of a tree's crown, C_R (in meters: figure 1), is a circular cross-section. We modelled it using a relationship with tree DBH (D, in cm),

$$C_R = \left(\frac{c_0}{D} + \frac{1}{c_1} \right)^{c_2} \tag{2}$$

where c_0, c_1 and c_2 are functional group specific parameters.

The "crown-point", C_P (figure 1) of a tree is the height at which the tree has maximum crown width. We modelled this using a simple linear relationship with tree height, H (m),

$$C_p = f_c H \tag{3}$$

where f_C is a functional group specific parameter.

2.4 Competition index

All demographic rates in the model are regulated through an asymmetric competition index that gives a measure for the level of competition that a tree experiences from its neighbouring trees. We based this index on the assumptions that an individual experiences stronger competition for light (but also other resources) as more and taller neighbours are standing closer by, and that stronger competition, *i.e.* a higher competition index, means less resource availability. Because in the understorey of tropical forests particularly light is a limiting resource (*e.g.* Chazdon & Fetcher 1984, Nicotra *et al.* 1999) and because forest management activities mainly affect aboveground biomass, this index should focus on aboveground competition. Other studies show that the best prediction of growth rates is obtained with distance and size dependent competition indices (*e.g.* Gourlet-Fleury 1998, Moravie *et al.* 1999, de Graaf 2001, Phillips *et al.* 2003).

The competition index (C_d) that we implemented consists of two parts,

$$C_\mathrm{d} = G + O \tag{4}$$

The first part (G) describes the competition effect caused by neighbouring trees larger than 20 cm DBH, for which we know exact positions in the forest. It is based on the canopy closure index (G) as defined by Lieberman *et al.* (1989, 1995),

$$G = \sum_{j=1}^{n} \left(\frac{H_j - H_i}{d_{ij}} \right) \text{ if } (H_j > H_i \text{ and } D_j \geq 20 \text{ cm}) \tag{5}$$

where n is the number of taller neighbours j within a radius of 15 m with height H_j and DBH D_j, H_i is the height of the subject tree i and d_{ij} is the distance between the top of the subject tree i and the top of its jth taller neighbour. Distances to trees with a DBH less than 20 cm DBH are calculated by assuming they were positioned in the centre of the subplot, since co-ordinate position data were not available.

The second part (O) of the competition index C_d is based on the sum of the height differences with overtopping neighbours less than 20 cm DBH that are standing in the same subplot as the subject tree. This was standardised for subplots of 25 m^2,

$$O = \sum_{k=1}^{n} \left(\frac{25}{a_\mathrm{p}} \left(H_k - H_i \right) \right) \text{ if } (H_\mathrm{k} > H_i \text{ and } D_k < 20 \text{ cm}) \tag{6}$$

where n is the number of taller neighbours k within the same subplot with height H_k, H_i is the height of tree i and a_p is the area of the subplot.

In the growth model both DBH and competition index were used to estimate a tree's growth rate. From a statistical point of view, both explaining factors should be independent from each other. Obviously, DBH and competition index are not independent from each other, as larger trees generally will have fewer neighbours that are taller, and thus experience less competition than smaller trees. Therefore we additionally converted the size dependent competition index, C_d, into a size independent competition index, C. We modelled the relationship between competition index (C_d) and DBH (D) using a Weibull probability density function (Equation 7) and then subtracted the calculated $\hat{C}_\mathrm{d}$ from the observed C_d for each data point,

$$\hat{C}_\mathrm{d} = b_0 \left(\frac{(b_1 D^{(b_1-1)})}{{b_2}^{b_1}} \exp(-((D/b_2)^{b_1})) \right) \tag{7}$$

where b_0 is a scaling parameter and b_1 and b_2 are parameters for the Weibull probability density function.

$$C = C_\mathrm{d} - \hat{C}_\mathrm{d} \tag{8}$$

The calculated competition index $\hat{C}_\mathrm{d}$ represents the average competition experienced by a tree of diameter d. Hence a tree with $C = 0$ would experience average competition for a tree of its DBH, while a highly positive value of C would indicate that the tree experiences much more competition than average for its DBH and *vice versa* for highly negative values.

2.5 Growth model

Growth rates of trees, in terms of rates of change in DBH, are generally non-linear and are typically highest at intermediate sizes. To represent this humpbacked pattern, we used the Hossfeld IV equation for the part of the growth function that describes the effect of initial DBH on growth (part in between square brackets in Equation 9, see Zeide 1993). The total diameter increment, I (cm year^{-1}), for individual trees in a given year depends on its initial DBH (D) at the start of a given year and size- independent competition index (C) as follows:

$$I = \left[\frac{a_1 a_2 D^{(a_2-1)}}{\left(a_1 + \left(D^{a_2}/a_0\right)\right)^2} \right] - a_3 C + a_4 \tag{9}$$

where a_0, a_1, a_2, a_3 and a_4 are model parameters.

2.6 Natural mortality model

The natural mortality model describes the probability that a tree dies as a result of natural causes like resource deficiency, diseases or senescence. Trees that experience more competition from neighbouring trees and thus receive less light will have a lower carbon balance and consequently a higher probability to die from natural causes. Many studies often find higher mortality probabilities for smaller trees. Including DBH in the natural mortality model was not found to significantly increase the amount of variation in mortality probability already explained by competition index. Decreasing mortality probability with increasing size, however, is implicitly already incorporated in the absolute competition index C_d because bigger trees experience less competition. Therefore we derived the following logistic function for annual natural mortality probability (M) in relation to competition index integrated in the approach proposed by Sheil *et al.* (1995) to get true annual mortality probabilities:

$$M = 1 - \left(\frac{e^{(m_0 C_d + m_1)}}{1 + e^{(m_0 C_d + m_1)}} \right)^{\frac{1}{t}} \tag{10}$$

where m_0 and m_1 are functional group specific parameters, C_d is the competition index and t is the length of the census intervals used for parameterisation (years).

Test simulations showed that the maximum diameters that trees obtained exceeded those found in the data. This can be explained by the fact that the model does not include DBH in the mortality function. Consequently the model cannot capture mortality caused by senescence of large (and old) trees. Yet, even when DBH was included to the mortality function no additional mortality was apparent. Probably this was obscured by the accumulative effect of both the rarity of large trees and the infrequency of mortality, which results in a poor representation of mortality of large (senescing) trees in the data.

To prevent trees from becoming unrealistically big and infinitely old in model simulations, we arbitrarily increased mortality for trees that have a DBH larger than the 95 percentile of DBH (D_{95}) for each functional group. This additional mortality value increases linearly with DBH from 0 at D_{95} to m_2 at the maximum DBH ($D_{\max}$). Consequently the probability of additional mortality increases faster with increasing DBH when the difference between D_{95} and $D_{\max}$ is smaller. Parameter m_2 was set to 0.1 as this value gave good results during subsequent test simulations.

2.7 Damage mortality

In SYMFOR, trees that die have a certain probability (M_F) to fall in a random direction. Falling trees cause damage and associated mortality to a certain proportion (M_D) of trees that are smaller and within its damage area, *i.e.* smaller trees within the damage area have a probability M_D to get killed. In the model the damage area has a kite-shape that is determined by the falling tree's height, crown radius and crown-point (figure 1b). The damage mortality probability is not directly related to the size of the falling tree, but smaller trees will have a higher probability that a falling tree is bigger than itself. Consequently, in the simulated forest the overall chance of being killed by falling trees decreases with increasing size.

2.8 Recruitment model

To be able to include the ecological processes of seed dispersal and germination specific data are needed (*e.g.* Chave 1999, van Ulft *et al.* 2004) that are not readily available from most sample plots. Therefore we used an alternative approach that was similar to that used in other recruitment modules implemented in the SYMFOR framework (Phillips *et al.* 2003, Phillips *et al*. 2004b). The recruitment model describes the appearance of new trees at the minimum DBH threshold of 2 cm DBH in which the probability of a new tree becoming established in a grid-square is described as a function of competition index in that grid-square. We modelled annual probability of recruitment (F) as a function of growth rate of the potentially recruiting tree of 2 cm DBH in the particular grid-square scaled to 25 m^2, which is the area of the subplots used for calibration, according to equation

$$F = \frac{a_\mathrm{p}}{25} \cdot \mathrm{e}^{(r_0 I' + r_1)} \tag{11}$$

where r_0 and r_1 are parameters, a_p is the area of the simulated grid-squares and I' is the predicted growth rate for a ‘virtual’ tree of 2 cm DBH at a randomly selected location within the grid-square, calculated using equation (9). Because of the exponential nature of this function, it should not be extrapolated beyond values of growth used in calibration. Therefore, if in model simulations I' exceeds the maximum growth rate that was used in the parameterisation (I'_{max}), I' is set to I'_{max}.

In an area of forest that has been subjected to severe damage caused by disturbance through for instance tree fall or logging (log extraction and skid-trails), no saplings of 2 cm DBH can be expected to recruit within a time period shorter than the time needed for seedlings to grow to 2 cm DBH. Therefore we included a parameter T_i, which represents the time required for a tree to grow from seed to 2 cm DBH for recruitment in those damage areas that are cleared of seedlings. In chapter 5 the importance and consequences of variation in growth rates of juvenile trees for the time needed to recruit to 2 cm DBH is shown. This variation in growth allowed some juveniles to recruit faster to 2 cm DBH and this had important consequences for forest dynamics (chapter 5). For that reason we also included the resulting variation in time needed to recruit to 2 cm DBH as found in chapter 5 in parameter T_i. In the simulations, parameter T_i is randomly drawn from a normal distribution using,

$$T_i = t_\mu + z \cdot t_\sigma \tag{12}$$

where t_μ is the average with t_σ standard deviation of time (years) needed to recruit to a DBH of 2 cm and z is the normal deviate that is randomly drawn from a standard Gaussian distribution.

2.9 Small tree data generation

Because trees between 2 and 20 cm DBH were only inventoried in sub-samples of experimental plots, at the start of each simulation these trees have to be generated in the simulated forest. For each functional group a parameter N_t represents the number of trees per hectare within the range of 2 to 20 cm DBH that have to be generated at random locations in the simulated plot. The location of each tree is checked to ensure that its stem does not overlap with other trees. If the stem overlaps with another tree, a new position is selected and checked again.

The diameter of the generated tree is estimated to fit a double exponential probability function (Q) that is based on the size distribution of trees between 2 and 20 cm DBH,

$$Q = g_0 \cdot e^{-g_1(D-2)} + g_2 \cdot e^{-g_3(D-2)} \tag{13}$$

where g_0, g_1, g_2 and g_3 are parameters describing the shape of the function and D is the DBH.

This probability was scaled between 1 at 2 cm DBH and 0 at 20 cm DBH. Subsequently a value for Q is randomly drawn between 0 and 1 and through the inverse of equation 13 this provides the DBH for a newly generated tree. Because the inverse of equation 13 cannot be analytically inferred, we implemented an iterative approach.

After the diameter is assigned, the competition index, C_d, of the newly created tree is calculated and compared against the maximum competition index (C_d^+) for trees of the same functional group and size class as occurring in the data. If the C_d of the newly created tree exceeds C_d^+ of the data, the tree is deleted and its creation will be attempted again from the beginning of the generation sequence. If after 10 attempts no suitable position could be found, this tree is omitted. This part was implemented to prevent that trees would be generated on positions where they would normally not occur because of unfavourable light conditions.

3 Data and parameter estimation

3.1 Research area and data

For model parameterisation we used data from 15 experimental sample plots (ESP) in the West-Pibiri compartment of Demerara Timbers Ltd.'s logging concession in Central Guyana (5°02' N, 58°37' W), approximately 250 kilometres south of Georgetown, Guyana's capital (van der Hout 1999). Each ESP measures 140 x 140 m (1.96 ha). Table 2 summarises the measurement thresholds and sampling intensities of different size classes of trees. The plots were set up in 1993 and harvested in 1994, with five different intensities of experimental reduced impact logging (RIL): control without intervention, low intensity RIL (4 harvested trees ha^{-1}), moderate intensity RIL (8 trees ha^{-1}), high intensity RIL (16 trees ha^{-1}) and moderate intensity RIL followed by a post-harvest liberation thinning (see van der Hout (1999, 2000) for more details). Reduced impact logging was carried out in 1994. Although the different logging intensities are not the direct focus of this current study, they guarantee a wide range of light conditions that match the range from undisturbed to heavily disturbed forests. The trees in the plots were re-censused at one (1995), three (1997) and six years (2000) after logging. At all censuses the DBH of all trees was measured at the same point of

Table 2 Minimum measurement limits for trees, number and size of subplots and total sampled area per plot for each size class for each of the 15 experimental sample plots (ESP).

Size class	Minimum measurement limits	Number (size) of subplots per ESP	Sample area per ESP (ha)
Large trees	20 cm DBH	49 (20 × 20 m)	1.96
Poles	5 cm DBH	25 (10 × 10 m)	0.25
Saplings	2 cm DBH	25 (5 × 5 m)	0.0625

measurement as in previous years and mortality and recruitment (in-growth into size class) were recorded.

The plots are in mixed Greenheart (*Chlorocardium rodiei*) forest (Ek 1997, van der Hout 1999), that is dominated by 8 tree species accounting for nearly 45% of the trees with DBH larger than 5 cm (chapter 2). The soils in this area belong to the well drained brown sand series with a moderate to high percentage of clay (Ferralsols) (van der Hout 1999, van Kekem *et al*. 1995). The average annual rainfall in the period 1996-2000 was 2772 mm (van Dam 2001).

3.2 Parameter estimation

Pioneer species are very rare in the studied forest (chapter 2). Even after classification into functional groups, the three pioneer groups separately had not sufficient data for successful parameterisation of growth and mortality functions. Since the species in these three groups are expected to respond similarly to logging, we combined the three pioneer groups for the parameterisation of the growth function and combined the small and medium sized pioneer groups for parameterisation of the mortality function. In the model these three groups will thus have the same growth and survival properties, but will still differ in allometric relationships.

We estimated the parameters for the non-linear functions for each functional group, with non-linear regression analyses in SPSS 11.1 (SPSS 2001) that uses an iterative approach. Subsequently we calculated the statistical significance of these parameters using a spreadsheet. The mortality model was parameterised with logistic regression analyses on survival using SPSS 11.1 (SPSS 2001). For each function, we produced one set of parameter values for each of the functional groups.

3.3 Allometric functions

We measured DBH, height and crown dimensions for a sub-sample of trees in the ESPs. Height was measured for 5642 trees ranging from 1.3 to 58.3 m high while crown-dimensions were measured for 3629 of these individuals. For trees lower than 12 metres, we measured the height using a telescoping measuring rod or a measuring tape. Heights of larger trees were measured with a hypsometer and 360° transponder (Haglöf Vertex III). Crown-

Table 3 For each allometry group the estimated parameter values h_0, h_1 and h_2 for the dbh - height relationship (Eq. 1). with the associated goodness of fit (R^2), *F* statistic (*: P<0.001) and degrees of freedom (*d.f.*).

Allometry-group	h_0	h_1	h_2	R^2	*F*	*d.f.*
1 (P1 & LP1)	0.053	1.08	33.3	0.90	1853.90^*	2, 429
2 (P2 & LP2)	0.053	1.03	38.5	0.92	5821.80^*	2, 974
3 (P3 & LP3)	0.062	0.86	46.5	0.94	1053.60^*	2, 142
4 (C1)	0.064	1.02	32.1	0.92	6679.63^*	2, 1203
5 (C2)	0.058	0.91	42.3	0.93	17167.20^*	2, 2563
6 (C3)	0.069	0.77	51.6	0.89	1297.88^*	2, 313

radii were measured in four directions, following the four main compass bearings (0°, 90°, 180° and 270°). For each tree, we used the median radius as the crown-radius.

Not all functional groups had enough data available for rigorous parameterisation of the allometry functions. Of the three traits that we used for the classification of functional groups we expect that wood density and maximum height are most important for the allometric relationships. Therefore we combined functional groups with the same combinations of wood density and maximum heights, resulting in 6 groups for the allometry calculations (allometry groups, table 1).

The estimated parameter values for the height function (equation 1) are presented in table 3 and the estimated parameters for crown-radius (equation 2) are shown in table 4. Figure 2 shows these two relationships with DBH graphically.

For calculation of the crown-point, C_P (equation 3), we assumed that the vertical cross-section of the tree crown is an ellipse or circle and thus that the crown-point is halfway the length of the crown. We calculated this crown-point by subtracting half of the crown height (total height minus height of the lowest leaf) from the total tree height. Because the relationship between crown-point and height did not significantly differ between the allometry groups we decided to estimate its parameter, f_C, using all groups together, resulting in the value 0.80 (R^2=99.3, df=3535, P<0.001).

Table 4 For each allometry group the estimated parameter values c_0, c_1 and c_2 for the dbh - crown-radius relationship (Eq. 2) with the associated goodness of fit (R^2), *F* statistic (*: P<0.001) and degrees of freedom (*d.f.*).

Allometry-group	c_0	c_1	c_2	R^2	*F*	*d.f.*
1 (P1 & LP1)	2.11	$3.44 \cdot 10^7$	-0.45	0.31	14.91^*	2, 65
2 (P2 & LP2)	3.61	$1.64 \cdot 10^5$	-0.51	0.43	262.30^*	2, 707
3 (P3 & LP3)	6.45	$2.76 \cdot 10^5$	-0.84	0.61	82.56^*	2, 106
4 (C1)	1.86	4.40	-1.00	0.34	149.00^*	2, 584
5 (C2)	2.36	$1.29 \cdot 10^5$	-0.52	0.48	825.55^*	2, 1793
6 (C3)	7.23	$2.54 \cdot 10^5$	-0.88	0.64	227.50^*	2, 257

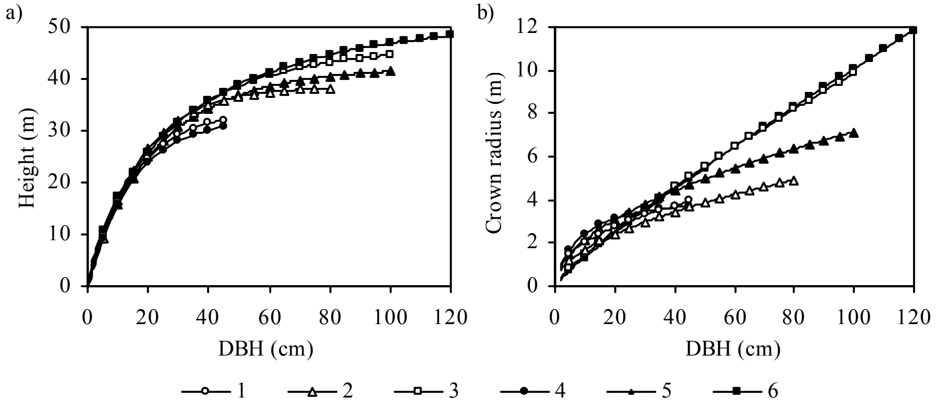

Figure 2 Allometric relationships between dbh (cm) and a) total tree height or b) crown radius for the six aggregated "allometry' groups (see legend). Group 1 is made up from functional groups P1 & LP1, group 2: P2 & LP2, group 3: P3 & LP3 and the groups 4, 5 and 6 represent respectively functional groups C1, C2 and C3.

3.4 Competition index

We determined for each year the competition index of all trees in the data using their position and height. For trees taller than 12 m high, we estimated heights from their DBH using equation 1. No competition index could be calculated for trees taller than 20 cm DBH that were within 15 m of the borders of the 1.96 ha plots, because part of their neighbours within a radius of 15 m were outside the plots and thus unknown. The trees for which no competition index could be calculated were omitted from the analyses in which competition was involved. The parameters in the function that describes the relationship between DBH and absolute competition index C_d (equation 7) are: b_0=479.18, b_1=0.69, b_2=10.08.

3.5 Growth model

We calculated growth rates of individual trees for each of the census intervals in cm year^{-1}. The competition index associated with each growth rate was calculated at the start of each census interval. All combinations of growth rate and associated competition index for each individual were included in the regression analyses that we used for parameterisation of the growth model. Prior to the analyses we inspected the data and we rejected data of trees showing aberrant growth trends that were obviously caused by measuring or recording errors.

The estimated parameter values for the growth function of each functional group are shown in table 5. Growth curves for each functional group based on these parameters for trees experiencing average competition (C=0) are presented in figure 3.

As might be expected, the pioneer groups had the fastest diameter increment rates for trees smaller than 20 cm DBH, while that of the climax species was generally slowest (figure 3). The DBH-height relationships for the smaller trees (<20 cm DBH) were similar for all

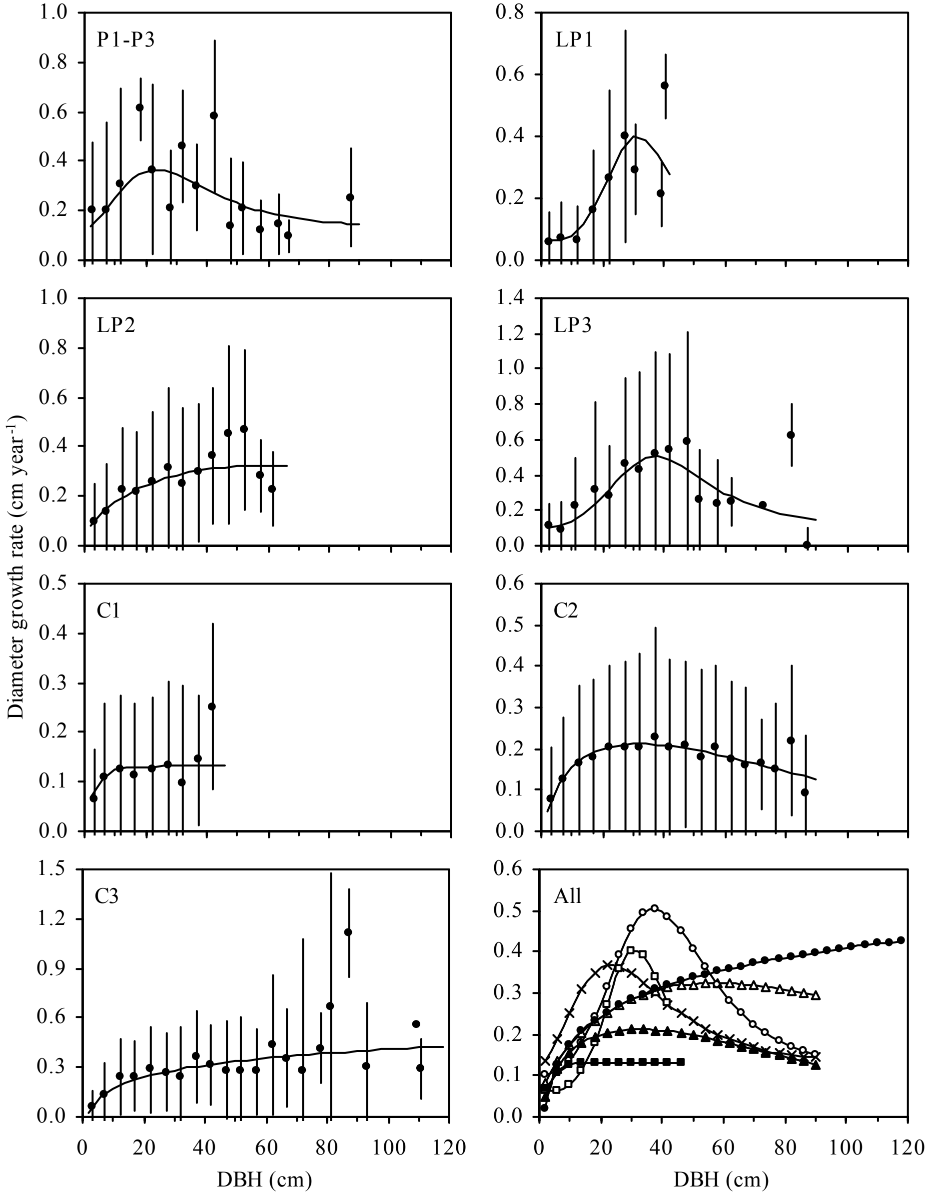

Figure 3 Average diameter growth rate (cm year^{-1}) in relation to dbh for each functional group (P1-C3) separately and for all groups in one graph for comparison (All). The graphs for the separate functional groups show the fitted growth functions at average competition (C=0), together with the observed average growth (dots) and 1 SD (error bars) for dbh classes of 5 cm. The graph with all groups together shows the fitted growth functions at average competition. The legend for this graph is shown at the bottom of the figure.

groups (figure 2), showing that pioneers also grow fastest in height. Parameter a_3 (equation 9, table 5) is associated with the response of growth to competition. A higher value for this parameter means that growth is increasing faster with decreasing competition index C. We

Table 5 For each functional group, the estimated parameter values a_0, a_1, a_2, a_3 and a_4 for the growth function (Eq 9) with the associated goodness of fit (R^2) (*: P<0.005, **: P<0.001), *F* statistic (*: P<0.005, **: P<0.001) and degrees of freedom (*d.f.*).

FG	a_0	a_1	a_2	a_3	a_4	R^2	*F*	*d.f.*
P1-P3	11.23	490.54	2.46	0.0049	0.122	0.06	3.69^*	4, 250
LP1	9.66	$1.21 \cdot 10^6$	4.61	0.0019	0.063	0.25	74.60^{**}	4, 888
LP2	67.38	45.83	1.63	0.0090	0.025	0.09	92.11^{**}	4, 3607
LP3	18.12	$4.13 \cdot 10^4$	3.58	0.0063	0.101	0.10	16.69^{**}	4, 594
C1	-0.37	-58.17	2.29	0.0036	0.132	0.06	62.29^{**}	4, 4427
C2	60.47	12.62	1.38	0.0057	-0.094	0.06	200.36^{**}	4, 12069
C3	$1.04 \cdot 10^6$	0.42	1.04	0.0032	-2.517	0.08	34.67^{**}	4, 1583

might expect that the response to light would be strongest in light demanding pioneer species, but a_3 was highest for the two tallest long-lived pioneer groups (LP2 & LP3), while that of the pioneers had a rather low value (table 5). This can be explained, however, by the fact that in forests, pioneers are usually only found in sites with high light availability. Pioneers intrinsically have a high whole plant light compensation point. Hence, they will die in shaded conditions because reduced photosynthesis cannot compensate for loss of biomass and inherently high respiration rates (*e.g.* Popma & Bongers 1988, Veneklaas & Poorter 1998, Poorter 1999). The average value for competition index, *C*, was -2.2 for pioneers while the average for all groups lies close to 0. This indicates that pioneers indeed occurred at higher light (low competition index) sites in the forest. Because we only measured a small gradient in competition index for pioneers in the field, their response in terms of growth is inevitably limited. As we will see in the section on natural mortality, pioneers indeed showed a very strong increase in mortality probability with increasing competition index (table 6). Thus, more trees with high competition index died in the course of a given census interval and were consequently not included in the growth analysis.

The large amount of residual variation for the total model appears to results from differences among species within a functional group and random effects. These random effects may include measurement error, heterogeneity in nutrient availability, other site specific conditions and unpredictable episodic events like pests and diseases. Additionally trees with damaged crowns will be able to intercept less light, even if they experience little competition, which also adds to variation that cannot be explained by competition index and size.

Another part of the remaining variation may be explained by the abundance of lianas. In the studied forest lianas are very abundant: 39% of all plants in the forest are lianas, while 51% are trees (Ek 1997). They grow up (with) a tree and then spread through the canopy. Consequently lianas compete with trees for available resources and thus can be an important factor reducing tree growth and affecting regeneration and survival (*e.g.* Schnitzer & Bongers 2002, Grauel & Putz 2004). How strong a tree's growth is affected will depend on the number and size of infesting lianas. Further research is necessary to quantify the interactions between trees and lianas before this factor can be included in this model.

3.6 Natural mortality model

We parameterised the logistic function for annual natural mortality probability (M, equation 10) based on observed mortality events for two census intervals: 1993 to 1997 and 1997 to 2000, in combination with the competition index for each tree. The competition index was calculated for the initial situation of each census interval (when the trees were still alive). The time interval, t, between the censuses was approximately the same for the two census intervals and was 3.5 years per interval.

The estimated parameter values for the natural mortality function of each functional group are shown in table 6. In the logistic regression, competition index did not explain significantly additional variation for four functional groups (P3, LP1, LP3 and C1) for which only the constant parameter m_1 was statistically significant. In these cases parameter m_0 was set to zero. Consequently, for these four functional groups natural mortality probability became a constant value, independent of competition index (and therefore size). In comparison to the other groups, for the groups P3 and LP1 this constant value was relatively high at low competition, while it was relatively low at the higher competition index. The groups LP3 and C1 had a constant value that is comparatively low over the whole range of competition index. For groups LP1 and C1 that complete their whole life-cycle in the forest understorey this constant mortality is not surprising as they are assumed to be adapted to low light conditions. The constant mortality probability for the two emergent groups P3 and LP3 on the other hand is rather an effect of limited data availability than a reflection of the ecology of these species.

Table 6 For each functional group, the estimated parameter values m_0 and m_1 for the natural mortality function (Eq. 10) with their corresponding Wald statistics (squared ratio of the estimated coefficient to its standard error) and sample size (n). If the Wald statistic of a parameter is significant (*: $P<0.05$ or **: $P<0.001$), then it adds significantly to the model. If it is not significant (NS) then the parameter was set to 0. For the functional groups with a significant effect of C_d ($m_0 \neq 0$) the Nagelkerke pseudo coefficient of determination (R^2) is presented. D_{95} and D_{max} show the 95 percentile dbh and maximum dbh of trees used for calculation of additional natural mortality of trees > D_{95}.

FG	m_0	m_1	Wald m_0	Wald m_1	R^2	n	D_{95}	$D_{\max}$
P1[1]	-0.061	3.087	4.25^{*}	21.86^{**}	0.10	85	28	29
P2[1]							45	47
P3	0	2.639	NS	26.00^{**}	-	60	67	87
LP1	0	2.835	NS	273.26^{**}	-	649	28	41
LP2	-0.023	3.241	9.75^{*}	485.20^{**}	0.13	2099	70	71
LP3	0	3.326	NS	117.42^{**}	-	317	95	129
C1	0	3.390	NS	1124.21^{**}	-	3103	23	43
C2	-0.013	3.701	5.00^{*}	1237.66^{**}	0.03	6677	56	103
C3	-0.045	4.019	5.97^{*}	169.99^{**}	0.03	846	69	111

[1]) Parameter values for the natural mortality function of functional groups P1 and P2 were estimated based on their combined data.

3.7 Damage mortality

The data on mortality showed that 30% of the trees that died from natural causes had fallen (M_F=0.3). On average the annual probability that a tree was killed due to damage by falling trees and branches was 0.2%, ranging from 0.4 % for trees less than 10 cm DBH to 0% for trees greater than 50 cm DBH. We do not know, however, how many trees were damaged by falling neighbours but not killed. Therefore it was not possible to determine the probability (M_D) that a tree is being killed when it is within the damage area of a falling neighbour. As an alternative we evaluated different values for M_D in model simulations. The value that was used in the previous SYMFOR version for Guyana (Phillips *et al.* 2002b) gave good results as in test simulations the annual probability that a tree would be killed matched that of the data. Subsequently the M_D was set to this value, which was 8% (M_D =0.08).

3.8 Recruitment model

We parameterised the probability of recruitment (equation 11) for each functional group based on the recorded appearance of new saplings in the subplots in which saplings were inventoried (see table 2) and measured in the 1997 and 2000 censuses. For each subplot we determined the number of in-growths per year and we predicted the growth rate (equation 9) of a hypothetical tree of 2 cm DBH positioned at the centre of each subplot based on its calculated competition index. Using the competition index of the hypothetical tree we subsequently classified each subplot into one of seven classes. For each class we then determined the average growth rate of the hypothetical trees using the parameterised growth equation and calculated the probability of in-growth using:

$$F = \frac{\sum_{i=1}^{N_s} \left(\frac{N_i}{t} \right)}{N_s} \tag{14}$$

where N_s is the total number of subplots within the particular competition index class, N_i is the number of recorded ingrowths in the ith subplot in the same class and t is the period of time of the census interval in which N_i has been recorded. Subsequently for each functional group we parameterised the recruitment function (equation 11) using regression analyses on the combinations of growth rates of hypothetical trees with the calculated probabilities of in-growth of the 7 classes of competition index. The data points used for this regression were weighted by the total number of subplots in each class (N_s).

The estimated parameter values for the recruitment function of each functional group are shown in table 7. The model was not significant for three functional groups. Therefore we calculated for these groups the average in-growth probability for all competition index classes together. Subsequently we took the natural logarithms of these constant values as parameter r_1 in equation 11, while the value of parameter r_0 was set to 0.

Table 7 For each functional group, the estimated parameter values r_0 and r_1 for the recruitment function (equation 11) with the associated goodness of fit (R^2), *F* statistic (*: P<0.05) and degrees of freedom (*d.f.*). t_μ and t_σ give the average and standard deviation of years needed to recruit to a size of 2 cm dbh as used in the in-growth time function (equation. 12) of the recruitment model.

FG	r_0	r_1	R^2	*F*	*d.f.*	t_μ	t_σ
P1	32.05	-11.99	0.97	222.02^*	5	7	2.2
P2	0	-6.85	-	NS	-	8	2.4
P3	28.86	-13.16	0.96	144.2^*	5	10	2.5
LP1	11.27	-4.35	0.69	11.05^*	5	58	13.5
LP2	3.91	-3.89	0.87	39.88^*	5	37	7.1
LP3	0	-6.00	-	NS	-	28	7.0
C1	7.13	-4.00	0.59	7.30^*	5	68	14.9
C2	4.90	-3.55	0.57	6.57^*	5	59	12.8
C3	0	-5.17	-	NS	-	59	12.4

We found that the recruitment probability for the pioneer groups P1 and P3 was very low at high competition index (low light) while it increased very fast at the lowest competition index classes. This is in accordance with the general notion about pioneer species that they need high light conditions for regeneration (*e.g.* Brokaw 1987, Alvarez-Buylla & Martínez-Ramos 1992, Ellison *et al.* 1993, Peña-Claros 2003, chapter 2). The total recruitment of pioneer group P2 was limited to 3 occurrences during the 2 census intervals. On average this was only 0.8 individuals per year. Although these 3 recruits only happened at low competition index, they were not sufficient to give a significant relationship. Therefore the recruitment probability of this pioneer group was set to the overall probability, which was still very low. For the other two life history strategies there is no relationship between recruitment probability and competition index for the tall stature (emergent) groups (LP6 and C9), while for the remaining long-lived pioneers and climax groups the recruitment probability increased gradually with decreasing competition index.

3.9 Small tree generation

The DBH for trees between 2 and 20 cm DBH that were created during model initialisation at the start of each run was generated using equation 13. We parameterised this function using a cumulative frequency distribution of DBH for each functional group for the sub-sample containing measurements for these trees. We generated each distribution using size classes of 1 cm to create 18 bins between 2 and 20 cm DBH. Subsequently we calculated for each bin the cumulative fraction of poles in this size class using the data from the 1993 census of the plots and fitted the function through this distribution (table 8).

The total number of trees of each functional group that should be created during model initialisation per hectare (N_t) was calculated using the data of all plots in 1993, before harvesting took place as these data represent primary forest. Because the trees between 2 and 20 cm DBH were only inventoried in sub-samples of the total area (see table 2), we linearly

Table 8 For each functional group the number (N_t) of small trees ha^{-1} (2-20 cm DBH), that have to be generated at the start of each model run and the estimated parameter values g_0, g_1, g_2 and g_3 for the size distribution function (Eq 13) of generated trees, with their associated goodness of fit (R^2), F statistic (*: significant at P<0.001) and degrees of freedom (*d.f.*).

FG	g_0	g_1	g_2	g_3	R^2	F	*d.f.*	C_d^+	N_t
P1	1.00	0.2554	-	-	0.98*	875.5	1, 17	40	13
P2	1.00	0.1349	-	-	0.87*	118.94	1, 17	40	2
P3	1.00	0.3031	-	-	0.97*	559.37	1, 17	40	8
LP1	0.84	0.7711	0.16	0.2096	1.0*	20597.7	3, 15	65	265
LP2	0.22	1.4105	0.78	0.2170	1.0*	8440.36	3, 15	58	324
LP3	0.20	1.4903	0.80	0.1738	0.99*	576.57	3, 15	48	29
C1	0.28	0.8589	0.72	0.2838	1.0*	25803.9	3, 15	60	926
C2	0.49	0.8519	0.51	0.1707	1.0*	2920.13	3, 15	56	942
C3	0.29	0.8963	0.71	0.1941	1.0*	1503.24	3, 15	48	100

extrapolated for each plot the numbers of trees per sub-sample to numbers per hectare. Subsequently we averaged the number of trees per hectare for the 15 plots (table 8).

4 Model evaluation and conclusion

Model evaluation is an important element of model development (Vanclay 1994, Jørgensen & Bendoricchio 2001). Vanclay & Skovsgaard (1997) reviewed and discussed issues and procedures for evaluating forest growth models. During model development we continuously evaluated the parameterised functions and model behaviour. Subsequent adjustments to the functions and parameterisation finally resulted in the equations and sub-models as presented in the model description and the model parameterisation sections.

The model makes predictions on growth, mortality and recruitment of individual trees. For interpretation of different model simulations (*e.g.* different management scenarios), however, emerging properties (*e.g.* total stem density, total basal area or total volume) are often more interesting than the results for individual trees. These emerging properties are also important in view of our objective to develop a model with which it is possible to make sensible projections of the effect of various forest management regimes on extracted timber yields and species composition. Therefore we focused the evaluation of the model on these properties. This meant that we needed information on total numbers of stems (abundance), the sum of their basal area and volumes. We subsequently evaluated model performance and model sensitivity based on these aggregated result variables. Finally we also evaluated how the simulated forest will respond to logging.

4.1 Model performance and verification

In this section we evaluate the behaviour of the model. We compared for each functional group average number of trees (stem density) and total basal area (BA in m^2) of simulated data after 1000 years without management with field data for unharvested stands. To take into account the large variation in numbers of trees and basal area between plots in Pibiri, we used the data of the three control plots as input for the trees ≥ 20 cm DBH. Because the model contains stochastic components, each plot simulation was repeated 5 times, resulting in 15 repetitions. Data were output for all live trees only every fifth year to keep the size of output files manageable. Finally we compared the values of the result variables at stable state, with those found for the 1993 plot census.

Although in the simulations the abundance of some of the functional groups changed over time (figure 4a), all groups reached a stable state after approximately 250 years. The stem density of the small and tall stature long-lived pioneers (LP1 and LP3) increased strongly by

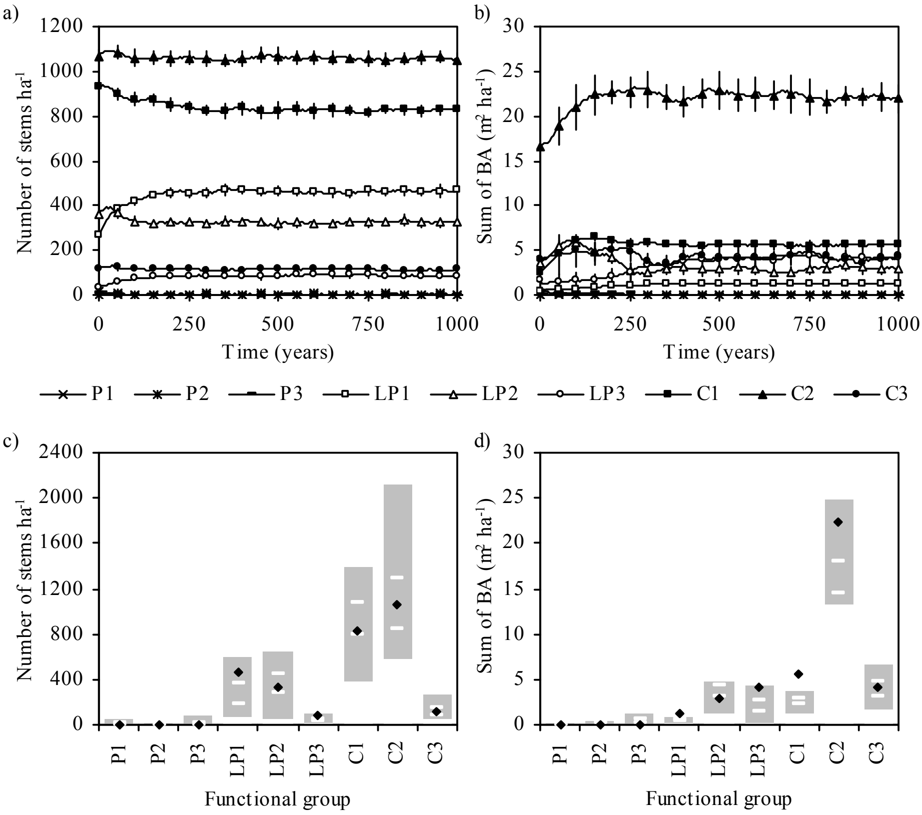

Figure 4 Modelled stem density and total basal area (BA) based on runs of 1000 years for 3 plots that are each repeated 5 times without forest management. a) the mean ± 1SD stem density, and b) the mean ± 1SD total basal area (m^2 ha^{-1}) for each functional group (P1-C3, see legend). In graphs c) and d) the stable state results (black diamonds) are compared with field. Stable state is the averages of the final 500 years of each model run. The shaded grey areas are the range of values in the field data (based on 15 plots) and the white lines are the accompanying 95% confidence limits.

a factor 1.7 and 2.5, respectively. The small and tall stature pioneer groups (P1 and P3) on the other hand declined very strongly in relative terms but in absolute terms their abundance was low throughout the simulations. The abundances of the other groups remained comparable to the initial condition, with factors of change ranging from 0.9 to 1.3. For all functional groups abundance at stable state was, within the range of abundances as found in the field data (figure 4c). Hence the simulated abundances remain within realistic values observed for natural primary forests from which the data were derived.

Total basal areas changed for some of the functional groups in the simulations (figure 4b). In particular the basal area of the small and tall stature long-lived pioneer groups (LP1 and LP3) and the small stature climax group (C1) increased relatively strongly by a factor of approximately 2.5. In absolute terms the change for the medium stature climax group (C2) was largest. Since the total abundance for this group remained almost unchanged over simulated time, this means that on average the trees became thicker. Mean basal area per stem increased strongest for the small climax (C1) group (factor 2.5) followed by the small long-lived pioneer (LP1) group. Only the total basal area of these groups exceeded the maximum limit of sum of basal areas as found for the sample plot data.

In most modelling studies it is assumed that that the forest is in dynamic equilibrium, *i.e.* that on average the forest composition, stem densities and basal area remain constant. Models are then parameterised and tuned to match this assumption. The current model did not show a dynamic equilibrium, but although the result variables changed over time, they generally stayed within the range of values found for the sample plots that were used for parameterisation. There are two main reasons why we did not adjust or tune the current model to fit the assumption of dynamic equilibrium. Firstly, recent research has shown that forests are very dynamic and composition and dynamics are not stable. Secondly, present day forest structure is not necessarily the result of present day demographic rates. We will further elucidate these two points below.

Recent studies in various undisturbed Amazonian forests show, however, that these forests are not stable and have become more dynamic during the past decades, while biomass is increasing (*e.g.* Baker *et al.* 2004, Malhi & Phillips 2004, Laurance *et al.* 2004a, Lewis *et al.* 2004a, Phillips *et al.* 2004a, Lewis *et al.* 2004b). Phillips *et al.* (2004a) found that both mortality and recruitment rates have increased across the Amazon during the past 25 years and that recruitment rates have consistently exceeded those of mortality. These increases were lowest, however, on the nutrient poor soils in the eastern Amazon, to which our research site in central-Guyana is adjacent. Laurance *et al.* (2004a) showed that during the past two decades Amazonian forests have experienced large changes in dynamics and composition. Mainly genera of faster growing species, but not pioneers, were found to increase in abundance, which is in agreement with the increase in abundance of long-lived pioneers as predicted by our model. At the same time they found that basal area of many genera increased significantly, indicating increased growth and carbon storage. As a likely main cause for the changes these studies point to increased plant fertilisation caused by rising atmospheric CO_2 concentrations (Laurance *et al.* 2004a, Phillips *et al.* 2004a).

The changes in stem density and total basal area over time in the model simulations could be similarly explained by recent variability in demographic rates. We measured the demographic rates used for model parameterisation over a relatively short period of time. Due to the high longevity of trees and the low rates of the processes, notable changes in forest composition may only be expected after a longer period of time. Hence, present day forest structure and composition would be related to demographic rates of the past while changes in current demographic rates would lead to changed forest structure and composition in the future. Likewise this implies that if environmental conditions keep on changing the demographic processes in the forest, a stable state will never be reached. For now we can only parameterise the model with the data at hand, which will give projections on the future of the forest under the assumption that the demographic rates in undisturbed forest will not change significantly in the near future. These observed changes of the result variables occurred gradually during the first 250 years of the simulations which is in accordance with the slow pace in which changing demographic rates affect forest structure

4.2 Sensitivity analysis

4.2.1 Sensitivity analysis methods

With sensitivity analyses it is possible to reveal which parameters or model components are most sensitive for the model output (Vanclay 1994, Jørgensen & Bendoricchio 2001). Generally parameter values or the outcome of forcing functions or sub-models are changes and then the corresponding changes in important result variables are recorded. Small changes in highly sensitive model components will result in relatively large changes in the model results. Hence, sensitivity analysis reveals which are the key input parameters in the model. This is important information for model users as it provides insight in the model. Besides that, future research and efforts to improve the model can then be directed towards these most sensitive components or parameters. In addition to the sensitivity, uncertainty in data and the confidence of parameter estimation are important. A highly sensitive component that can be estimated with high confidence is less of a problem than an equally sensitive component for which the estimation is less reliable.

The large number of parameters in the described model prohibits a comprehensive sensitivity analysis for all parameters separately. Moreover, meaningful interpretation of the results of such analysis would probably become very difficult. Therefore we evaluated the sensitivity of processes and variables that we consider important or likely to be most sensitive. These encompass the three key demographic processes, growth (I), natural mortality (M) and recruitment (F) and the variables that strongly influence these processes: damage probability (M_D), fall probability (M_F) and average in-growth time (T_i). Changes in damage probability and fall probability will affect mortality associated with damage and competition index, which in turn affects the demographic rates. The in-growth time parameter is important for timing of recruitment after disturbance and changes to it may be seen as changes to growth rates of juvenile trees < 2 cm DBH that are not explicitly included in the current model.

To enable comparisons between sensitivities of the different model components the same relative changes were used for all components. We determine the 95% confidence interval (*CI*) of each model component relative to the mean for all data of each functional group to evaluate the sensitivity of each component in relation to the precision of its prediction. We could determine these relative confidence limits, however, only for the three demographic components. For growth we determined the 95% confidence limits (upper limit L^+ and lower limit L^-) by conventional methods using the mean and the standard error on the mean (see Zar 1999). Because mortality is a binomial process, we estimated for this component binomial 95% confidence intervals (see Zar 1999). Recruitment on the other hand, can be regarded as a count of in-growths. Therefore we estimated for this component the 95% CI using an approach that exploits the Poisson distribution (see Motulsky 1995). The underlying distributions of the 95% CI of the latter two components are not symmetrical and that therefore the absolute values of L^+ and L^- are not the same. Subsequently we determined the relative confidence limits (L^+_{rel} and L^-_{rel}) using:

$$L^+_{rel} = \frac{L^+ - \mu}{\mu} \quad \text{and} \quad L^-_{rel} = \frac{\mu - L^-}{\mu} \tag{15}$$

where μ is the sample mean, L^+ is the upper limit of the 95% *CI* and L^- is the lower limit of the 95% *CI*. The relative confidence limits thus give the difference of the confidence limits as a proportion of the mean and as such are comparable with the relative changes that are applied to model components during sensitivity analysis. High values of the relative confidence limits imply high uncertainty in the data used for parameterisation.

Table 9 The relative confidence limits (L^-_{rel} and L^+_{rel}, see equation 15) for growth, mortality and recruitment for each functional group (FG).

FG	Growth		Mortality		Recruitment	
	L^-_{rel}	L^+_{rel}	L^-_{rel}	L^+_{rel}	L^-_{rel}	L^+_{rel}
P1	-0.37	0.37	-0.63	1.13	-0.52	0.83
P2	-0.21	0.21	-0.79	1.85	-1.00	4.89
P3	-0.20	0.20	-0.73	1.52	-0.94	2.43
LP1	-0.11	0.11	-0.30	0.38	-0.37	0.51
LP2	-0.04	0.04	-0.18	0.21	-0.36	0.44
LP3	-0.10	0.10	-0.50	0.78	-0.94	2.47
C1	-0.04	0.04	-0.18	0.21	-0.34	0.43
C2	-0.02	0.02	-0.14	0.15	-0.29	0.35
C3	-0.05	0.05	-0.37	0.50	-0.74	1.41

The uncertainties (table 9) appeared to be highest for the recruitment and mortality components. The pioneer groups (P1-P3) showed particularly high uncertainties. These high uncertainties for recruitment and mortality in pioneers reflect the small sample sizes for these components and functional groups.

We evaluated the sensitivities to changes in the six selected model components for twenty important result variables: (1) total density (stems ha^{-1}) of all trees in the whole stand, (2-10) stem density of trees for each of the nine functional groups, (11) sum of the basal area of all trees in the whole stand, and (12-20) total basal area per functional group. We applied four different relative changes to each of the model components separately. The first were relatively small relative changes of model components by +10% and -10%. The second were changes of +/-50% corresponding with the observed uncertainty in the underlying data (table 9). Subsequently we determined the sensitivity, $S_{(\beta,\ v)}$, of component β, for result variable v, using the conventional method (Vanclay 1994, Jørgensen & Bendoricchio 2001):

$$S_{(\beta,v)} = \frac{\partial v / v}{\partial \beta / \beta} \tag{16}$$

where $\partial v/v$ is the relative change in result variable v and $\partial\beta/\beta$ is the relative change of model component β. For the 10% changes, $\partial\beta/\beta$ is 0.1 and for the 50% changes, $\partial\beta/\beta$ is 0.5. If a 10% change in a component, for example, results in a 50% change in the result variable, the sensitivity $S_{(\beta,\ v)}$ will be 5, while the same 50% change in the result variable obtained for a 50% change in a component results in a sensitivity value of only 1. Likewise, if the sensitivity is 1, the relative change in the result variable is equivalent to the relative change in the model component β.

Each of the relative changes to model components was applied simultaneously for all functional groups. We used the mean of 15 repeated model simulations (3 different plots for input with 5 repetitions each) for each relative change to the model components and for a control with no changes. Because sensitivity is likely to increase with increasing time we determined sensitivities after four different simulation times: 25, 50, 100 and 200 years leading to 96 sensitivity values (6 components x 4 changes x 4 simulation periods) for each of the twenty result variables. We subsequently tested for each of the result variables for differences in ranking of sensitivities between the six components using Kruskal-Wallis tests (each component enters the test with 16 values for the 4 changes and 4 simulation periods). A second test was made within each combination of result variable and component for differences in sensitivities between the relative changes that were applied and for differences in sensitivities after different simulation times. A third test identified differences in sensitivities between the functional groups. We separately evaluated the sensitivities in relation to abundances and in relation to basal areas and then applied Dunn-Šidák corrections to all 143 tests within each of these properties.

Table 10 For the whole stand (All) and each functional group (P1 to C3) the 10 most sensitive model components for tree abundance (part A) and sum of basal area (part B), with accompanying sensitivities (S). The components that are among the 100 most sensitive in the overall ranking are marked in bold. All rankings were based on absolute values of S. The first letter of the codes in the table refer to the model component (growth (I), mortality (M), recruitment (F), probability of a dead tree to fall (M_F), damage probability (M_D) and in-growth time (T_i)) followed by the relative change that was applied (+10%, -10%, +50 % and -50%), and the time in the simulations (numbers in between brackets for 25, 50, 100 or 200 years).

(A)	Component	S	Component	S	Component	S	Component	S	Component	S
FG	All		P1		P2		P3		LP1	
	M-50(200)	0.81	M-10(200)	**-6.67**	F+10(25)	**3.79**	M+10(100)	**-6.04**	F-10(200)	-1.01
	F-10(200)	-0.75	I-10(200)	**-5.56**	I+10(25)	**3.18**	I+50(200)	**4.67**	F+10(100)	1.00
	F-50(200)	-0.72	M+10(200)	**4.44**	M_D+10(25)	**3.03**	I-10(200)	**-4.33**	F+10(50)	0.86
	M-50(100)	0.66	M+10(50)	**4.21**	T_i-10(25)	**3.03**	T_i+10(200)	**-4.00**	F-50(200)	-0.84
	F-50(100)	-0.65	M-10(25)	**3.38**	M+10(50)	**-2.92**	M_F-10(100)	**-3.75**	M-50(200)	0.82
	F+10(100)	0.65	M_D+10(200)	**3.33**	T_i-10(200)	**-2.38**	M_D-10(200)	**-3.33**	F+50(100)	0.80
	F+50(200)	0.64	F-10(200)	**3.33**	T_i-10(100)	**-2.36**	F-10(100)	**-3.13**	F-50(100)	-0.75
	F-10(100)	-0.63	M+10(100)	**-3.33**	F+10(100)	**2.36**	M+10(50)	**-2.73**	M+10(200)	-0.74
	F+50(100)	0.60	M-10(100)	**-3.33**	F-10(200)	**-2.22**	M-10(100)	**-2.71**	M-10(100)	0.73
	F+10(200)	0.49	M_F+10(100)	**-3.33**	M_F-10(25)	2.12	F+10(200)	**-2.67**	I-10(200)	-0.71
FG	LP2		LP3		C1		C2		C3	
	F-10(100)	-1.06	F-10(100)	-1.04	M-50(200)	0.88	F-10(200)	-0.79	F-10(200)	-0.94
	M-50(100)	0.91	F-50(200)	-0.99	F+10(100)	0.75	M-50(200)	0.78	F-10(50)	-0.81
	M-50(200)	0.81	F-10(200)	-0.92	F+50(200)	0.73	F-10(100)	-0.72	F-50(200)	-0.77
	F-50(100)	-0.72	M-50(200)	0.91	F-50(200)	-0.72	F-50(200)	-0.68	F-50(100)	-0.67
	M-50(50)	0.69	F-50(100)	-0.90	F+10(200)	0.68	M-50(100)	0.63	F+50(200)	0.62
	F+10(100)	0.69	T_i+10(200)	-0.89	F-10(200)	-0.62	F+50(200)	0.63	M-50(100)	0.61
	F+10(50)	0.61	F+10(25)	0.85	M-50(100)	0.61	F-50(100)	-0.62	F-10(100)	-0.59
	F-50(50)	-0.61	F+50(100)	0.84	F+50(100)	0.59	F+50(100)	0.55	M-50(200)	0.58
	M-10(50)	0.57	F+50(200)	0.81	F-50(100)	-0.58	M+10(100)	-0.52	F+50(100)	0.56
	F-50(200)	-0.56	F-50(50)	-0.75	M-10(200)	0.58	F+10(200)	0.51	F-50(50)	-0.50

Table 10 Continued. Part (B).

(B)	Component	S	Component	S	Component	S	Component	S	Component	S
FG	All		P1		P2		P3		LP1	
	M-50(200)	1.25	M-10(100)	**108.11**	M_F+10(200)	**25.52**	F+10(200)	**15.10**	I+50(200)	1.88
	I+10(100)	0.87	M_D+10(100)	**81.17**	F+10(200)	**12.81**	M_F+10(200)	**9.14**	I-10(200)	-1.50
	M-50(100)	0.86	F-10(100)	**80.57**	T_i+10(200)	**10.81**	I+50(200)	**7.12**	I+10(200)	1.11
	I-50(200)	0.85	T_i-10(100)	**56.09**	I-10(200)	**8.82**	M_D+10(200)	**6.49**	F+10(50)	1.09
	I+10(50)	0.85	I-10(100)	**51.14**	M_F-50(200)	**8.05**	M+10(100)	**-6.16**	F+10(25)	1.07
	M+10(200)	0.83	T_i+10(100)	**45.74**	M_F+10(100)	**-6.76**	M_F-10(100)	**-5.25**	M-10(100)	1.06
	M-10(100)	0.78	M_D-10(100)	**30.98**	I+50(200)	**6.47**	M_F-10(200)	**5.25**	M-50(200)	1.06
	I-50(100)	0.77	I+50(200)	**24.65**	M-10(100)	**-6.27**	I+10(200)	**-4.91**	I-50(200)	-1.01
	I-10(100)	0.76	M+10(100)	**22.41**	M-10(200)	**6.24**	M-50(200)	**4.75**	M-10(200)	0.94
	I+50(100)	0.71	I-50(100)	**21.09**	M_F-10(100)	**-5.29**	I-10(100)	**-4.54**	I+50(100)	0.91
FG	LP2		LP3		C1		C2		C3	
	M-50(200)	2.10	I+10(25)	**3.59**	M-50(200)	0.88	M-50(200)	1.11	I+10(100)	1.88
	M+10(100)	-1.42	T_i+10(200)	-2.32	I-50(100)	-0.82	M-10(100)	0.93	M-10(100)	1.78
	I-10(200)	-1.20	T_i-10(100)	-2.14	I+10(50)	0.80	I+10(100)	0.89	M-50(200)	1.46
	I-10(100)	-1.18	I-10(200)	-2.00	I+10(200)	0.73	M-50(100)	0.82	I-10(200)	-1.42
	I+50(200)	-1.14	M_F+10(200)	1.90	I-50(200)	-0.71	I-50(200)	-0.81	M-10(200)	1.27
	M-10(200)	1.14	M_F-10(50)	1.74	I-50(50)	-0.69	M-10(200)	0.77	M_D+10(100)	1.23
	I+10(50)	1.10	M_F-10(25)	1.67	I-10(100)	-0.68	I+10(50)	0.76	M-50(100)	1.18
	M-50(100)	1.07	I+10(50)	1.58	I+50(50)	0.67	I+50(100)	0.76	I-50(200)	-1.15
	M+10(50)	-0.97	M+10(25)	1.49	I+10(100)	0.67	I-50(100)	-0.73	I+10(50)	1.09
	I-50(100)	-0.87	M-50(200)	1.47	I-10(50)	-0.65	I-10(100)	-0.67	M_F+10(100)	1.08

4.2.2 Sensitivity analysis results

The results of the sensitivity analysis revealed that changes in recruitment en mortality are most important in determining tree abundance, whereas tree basal area is most affected by growth and mortality. This is illustrated in table 10, which contains the highest positive and negative sensitivity values for each of the 20 result variables. When considering all functional groups together, sensitivity values for tree abundance or basal area are rather low, indicating that the model is rather robust to (large) changes in the components we changed. Most values are between -1 and 1, meaning that a 10% change results in a change smaller than 10% in model output. Sensitivity values for the long-lived pioneer and climax tree groups (LP and C) are also within this range. The three pioneer groups are the exception to this general pattern: in these groups is it common to find that 10% changes result a shift of more than 30% and up to 1000% (absolute sensitivity values of 3-100). This is likely an effect of the small abundances of these groups. If the number of trees is low, small absolute changes to abundance or basal area will inevitably result in large relative changes and thus high sensitivities.

Using the results of the Kruskal-Wallis tests (table 11), we can evaluate whether there are differences in sensitivities between model components. Indeed, significant differences in ranks of sensitivities between the different components were found for both abundance and basal area. Only the differences within the three pioneer groups were not significant. Tree abundance of the entire community and of the non-pioneer groups was most sensitive to changes in recruitment and second most sensitive to changes in mortality (table 11-A). This can be explained as these two demographic rates directly affect the number of trees. For basal area the pattern was slightly different: this parameter was most sensitive to changes in growth in seven out of ten cases, followed by mortality with the second highest mean ranks (table 11-B). In the other three cases highest sensitivities were found to changes in mortality, while growth became second in mean rank order.

Comparing the output for the different simulation periods, it becomes clear that sensitivities of result variables generally increased with increasing simulation time. However, there were no significant differences in sensitivity between the periods. Contrary to what we expected, the result variables showed a consistent but not significant trend of highest sensitivities for the smallest relative changes that were applied. Sensitivity is a term relative to the applied changes (equation 16), however. Hence, while absolute changes in result variables may be higher for the larger changes of the component, in relative terms this may be not the case. This may be explained by feedbacks in the model. The relative changes to the different model components will also affect forest structure and will therefore indirectly affect competition index. Changes in competition index in turn will affect the demographic rates, which results in most cases in a reduction of the effect of the applied 10% or 50% change. For instance, if mortality probabilities are increased with 10% every time, the result will be that more trees will die and fall. Inevitably this will lead to decreased competition in the simulated forest which will result again in lower mortality rates, which reduces the effect of

Table 11 Mean ranks of the sensitivities of the components for the abundances (A) and basal areas (B) for the whole stand and each of the functional groups. Ranks were based on 96 values for sensitivity, *i.e.* all combinations of component * relative change * simulated time. If there were significant differences (Kruskal-Wallis tests) between the components within a result variable, the highest rank is printed in bold.

Component	All	P1	P2	P3	LP1	LP2	LP3	C1	C2	C3
(A)										
I	52.9	41.7	49.8	62.1	47.1	51.2	33.9	29.9	42.7	45.7
M	83.6	65.8	62.0	48.4	70.4	73.5	61.6	77.8	77.1	64.5
F	**89.4**	59	60.1	42.7	**84.4**	**82.7**	**82.3**	**81.7**	**83.3**	**77.7**
T_i	37.4	30.9	41.5	48.6	29.5	30.4	38.8	28.4	*19.4*	*33.9*
M_D	48.5	42.3	33.9	43.8	27.6	27.0	37.5	30.3	33.3	31.9
M_F	51.3	51.3	43.8	45.4	31.9	26.2	36.8	42.8	35.3	37.3
(B)										
I	86.1	53.2	48.7	57.5	**75.0**	76.0	**69.4**	**81.6**	**79.9**	**68.9**
M	**86.8**	55.4	57.3	53.9	64.7	**77.6**	57.0	70.4	74.9	66.9
F	52.3	50.7	47.8	43.4	56.4	34.9	40.9	41.0	34.3	37.6
T_i	37.8	41.2	45.8	45.3	25.3	37.0	46.3	27.6	32.0	35.3
M_D	49.2	46.2	39.9	41.1	36.2	30.3	34.8	31.9	31.2	40.3
M_F	50.8	44.4	51.5	49.9	33.5	35.1	42.6	38.4	38.7	42.0

the applied increase of mortality. Similar reasoning can be applied to negative changes to mortality and to recruitment and growth. The negative feedback will be stronger for the higher applied changes resulting in the observed pattern of lower sensitivities at higher relative changes applied to the components. The overall effect of this feedback will be stronger for the functional groups with the strongest response to competition index, which are primarily the pioneer species. This negative feedback, thus, provides model stability that directly reflects stability inherent in the forest ecosystem, via the processes of growth, recruitment and mortality and a range of functional groups.

Overall the sensitivity analysis shows that the model is rather robust for changes in tested model components. Exceptions are the pioneer groups, which show very large changes in abundance and especially basal area when model components are changed. Further, we can conclude that the model results are most sensitive to mortality and recruitment, which are also the components that had the highest uncertainty. This result is consistent with findings of other studies (Kammesheidt *et al.* 2001, Phillips *et al.* 2003). Since the high uncertainties for mortality and recruitment mainly reflect small sample sizes, this indicates that future research should concentrate more on mortality and recruitment, especially for pioneer species. This means that data on mortality and recruitment have to be collected either on larger sample areas or over longer periods of time since their recordings are rare and infrequent.

4.3 Logging simulations

Finally we evaluated model behaviour with simulated management actions. We were not able to validate the model against long-term data of logged forests, as these were not available. Therefore we only evaluated whether model predictions of responses to management actions were sensible. Simulated logging creates additional damage in the simulated forest. Felled trees create damage areas in which all trees smaller than 40 cm DBH are killed. Additionally, spatially explicitly simulated skidder damage also kills all trees smaller than 40 cm DBH within the skid-trails. This additional mortality caused by simulated logging will heterogeneously decrease the competition index for the trees that remain in the forest. Consequently this will affect the growth, mortality and recruitment models. Responses to decreased competition index are especially strong for the small stature pioneers (P1). Of all functional groups they showed both the strongest increase in recruitment (parameter r_0, table 7) and decrease in mortality (parameter m_0, table 6) in relation to competition index. The responses of the climax species are much slower, while the long-lived pioneers have an intermediate response. Therefore it can be expected that especially the pioneer groups will benefit from the disturbance caused by logging.

We performed simulations of two different logging scenarios for 1 ha of forest. For the first scenario we simulated one hectare of forest for 1000 years with heavy logging (12 trees ha^{-1}) simulated only once in year 10 after the start of the simulation. We did this to test whether the simulated forest would be able to recover from disturbance at all and whether after some time again a stable state would be reached.

After logging the abundances of all functional groups were drastically lowered (figure 5a). A total of 1270 trees, with mainly small DBH, were smashed by logging activities. Within the first 20 years following logging, the small pioneers (P1) increased in abundance from almost zero to 70 trees ha^{-1}. Thereafter the abundances gradually decreased again to pre-logging values in year 100. The response of the other two pioneer groups (P2-P3) was much lower, which may be explained by their low recruitment. All other groups increased in abundance more slowly, but also reached pre-logging abundances again after approximately 100 years. After approximately 250 years, the simulated forest reached again a stable state. The stable abundances of all groups were similar to those reached in the model simulations without interventions. Hence, no anomalous effects were observed with simulated.

In the second scenario we simulated one hectare of forest for 100 years with simulated logging according to current legal limits in Guyana, with a moderate number of trees felled per hectare. This comprised a cutting cycle of 25 years with a minimum cutting diameter of 35 cm and a maximum of 8 trees felled per hectare at each logging event.

The results showed that the climax groups (C1-C3) gradually decreased in abundance (figures 5b and 5c). The period of time between two subsequent harvesting events was too short for these groups to replace the trees that have been harvested or smashed during the

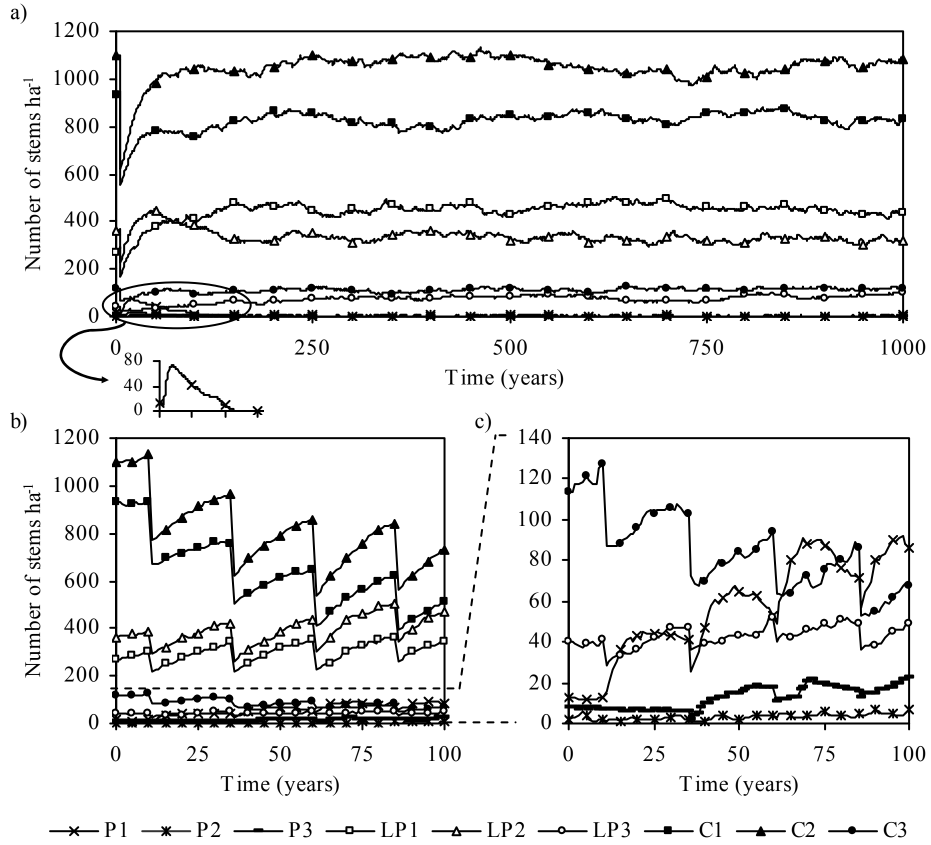

Figure 5 Number of stems per functional group (see legend) for a) one 1000 year simulation run for one hectare of forest with rather heavy logging (52 m^3) simulated in year 10 of the simulation. The inset shows a magnification of the first 150 years for the small pioneers (P1). In graphs b) and c), the number of stems per functional group (see legend) are shown for one 100 year simulation run for one hectare of forest that is logged according a harvesting regime similar to current legal limits for logging in Guyana (25 years cutting cycle, each cycle 8 trees were felled per ha and dbh of felled trees ≥ 35 cm). First logging took place in year 10. Graph b) shows the results for all functional groups and c) shows a magnification of the results for functional groups < 140 stems.

simulated logging operation. As expected, especially the small pioneers benefited very much from the repeated disturbances caused by logging. This group showed the fastest and strongest response to logging in the simulated forest. The tall pioneers (P3) did respond slower, but still increased in abundance, but the intermediate sized pioneers (P2) appeared to be rather unresponsive to the logging. This indifference of group P2, however, was also found in the field as the total recruitment of this group was very low and did not appear to respond to decreased competition. It appears that the limited recruitment of species in this functional group is limited by the low abundance of mature trees in the plots, in other words, it may be an artefact of rare occurrence leading to inaccurate parameterisation. The intermediate group of long-lived pioneers had also an intermediate response to logging as they were able to recruit sufficiently to replace smashed trees. These results are consistent with general notions about forest succession after disturbance and gap dynamics (*e.g.* Horn 1974, Brokaw 1985, Finegan 1996, Peña-Claros 2003). Overall the results of this scenario appear to be sensible in relation to the ecology of the different functional groups. These results also indicate that the current legal limits for logging are not ecologically sustainable. An extensive evaluation of alternative logging scenarios will follow and will be done in chapter 4.

4.4 Conclusion

The evaluation of the model without logging indicates changes in abundance and basal area for various functional groups but these were all well within the natural range of variation observed in the sample plots. The directions of the changes found in abundance and basal area were in accordance with recently demonstrated changes of forest structure and dynamics across Amazonia. Responses to simulated logging appeared to be sensible. Furthermore, model evaluation did not reveal any strange errors. Hence, we are confident that the model is able to give reasonable projections of forest structure, composition and future timber yields in relation to forest utilisation. Rigorous validation of the model, however, could unfortunately not be done. More data, especially on mortality and recruitment would be needed to further refine the current model.

Finally, one should bear in mind that simulation models cannot be proven true (Vanclay 1994) without waiting many decades, and that they should be considered as reflecting extrapolations of current knowledge and assumptions rather than giving “true” predictions. When more independent data become available, more rigorous benchmark tests and validation of the model can be done. Until then scenario studies using the current model provide the best educated guesses regarding the future of managed forests in central Guyana. Careful interpretations of model results, however, can guide discussions on sustainable forest management and are valuable for strategic management planning. When in the future models can be improved due to additional data availability and increased understanding of forest dynamics, management planning can be adjusted accordingly.

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Appendix I List of variables and parameters used in the described model. For all variables and parameters we give a summary of their usage and we indicate whether parameter values differ between functional groups (FG) or allometry groups (AG). In the last column we give the number of the equation(s) in which it is used.

Variable / parameter	Usage	Equation
D	Diameter (cm) at breast height (at 1.3 m height). It is the basic tree attribute to which most other allometric properties are related.	Various
H	Tree height (m).	(1)
h_0, h_1, h_2	Parameters used in DBH-height function. (AG)	(1)
C_R	Crown radius (m).	(2)
c_0, c_1, c_2	Parameters used in the function between crown radius and DBH. (AG).	(2)
C_p	Crown-point (m). Height at which the tree has maximum crown width.	(3)
f_c	Parameter used in the function between crown-point and total tree height (H).	(3)
C_d	Competition index.	(4), (7) & (8)
G	Part of the competition index describing competition effect caused by neighbouring trees > 20 cm dbh.	(4) & (5)
O	Part of the competition index describing competition effect caused by neighbouring trees 2-20 cm dbh.	(4) & (6)
a_p	Area of simulated grid-squares.	(6) & (11)
b_0, b_1, b_2	Parameters used in the size independent competition model.	(7)
C	Size independent competition index.	(8)
I	Annual diameter increment (cm).	(9)
a_0, a_1, a_2, a_3, a_4	Parameters used in the growth function. (FG)	(9)
M	Annual natural mortality probability.	(10)
m_0, m_1, m_2	Parameters used in the natural mortality function. (FG)	(10)
D_{95}, D_{max}	95 Percentile of dbh and maximum dbh that trees of a certain functional group can attain. Used to calculated an additional mortality probability for the largest trees, representing senescence of these trees. (FG)	-
M_F	Probability that a tree that died from natural causes, falls in a random direction.	-
M_D	Probability that a tree, standing in the damage area of a bigger fallen tree, is killed.	-
F	Annual recruitment probability.	(11)

Variable / parameter	Usage	Equation
r_0, r_1	Parameters used in the recruitment function. (FG)	(11)
I'	Predicted growth rate of a virtual tree of 2 cm dbh positioned in the centre of the grid-square, used to determine recruitment probability.	(11)
T_i	In-growth time variable. Determines the time needed for seedlings to recruit to 2 cm dbh.	(12)
t_μ, t_σ	Average and standard deviation of time (years) needed for seedlings to recruit from seed to 2 cm dbh. These parameters determine the properties of the normal distribution from which the in-growth time parameter T_i is randomly drawn. (FG)	(12)
Q	Cumulative probability distribution of tree sizes for trees between 2 and 20 cm dbh. This is used for determining the size of trees that have to be generated at the start of each run.	(13)
g_0, g_1, g_2, g_3	Parameters used in the function for cumulative probability distribution of tree sizes of trees between 2 and 20 cm dbh.	(13)
N_t	Number of trees between 2 and 20 cm dbh that have to be generated at the start of each run.	-

Chapter 4

Logging scenarios for sustainable timber harvesting in the tropical rain forests of central Guyana

With Roderick J. Zagt, Peter van der Hout, Paul D. Phillips & Paul R. van Gardingen

Abstract

For sustainable forest management, information is required on the long-term consequences of current logging practises for tree species composition and future timber yields. Yet, little is known about these long-term effects of logging on species composition and forest recovery. We used a simulation model of forest dynamics to study the effects of logging with different harvest intensities on stem densities of different functional groups and on remaining commercial volumes for forests in central Guyana. We also assessed the time needed for these stem densities and volumes to return to base-line values obtained from simulations without logging. In addition we compared 18 alternative logging scenarios for sustainable timber harvesting. These scenarios consisted of 18 combinations of maximum allowable harvest intensity (4, 8 or 12 trees ha^{-1}), minimum felling diameter (35 or 60 cm) and felling cycles (25, 40 or 60 years).

After logging once, the commercial volumes at all harvest intensities returned to base-line values. At the highest harvest intensities, however, the two classes of commercially most valuable species needed approximately 100 years to recover their commercial volumes. This is substantially longer than the currently advised felling cycle of 60 years. As a consequence, for all evaluated poly-cyclic scenarios the commercial volume declined over simulation time. The highest average annual yields were obtained with felling cycles of 25 years, but at high harvest intensities these felling cycles led to rapid depletion of the commercial volume.

After logging once the abundances of all functional groups returned at all harvest intensities to values similar to that of the base-line simulations without logging. Generally, return times increased with increasing harvest intensities. The longest return times were found for the small pioneers, small climax species and medium sized climax species that at highest harvest intensities need between 113 and 161 years to return to base-line values. After simulated logging the stem density of small pioneer increased rapidly. Over simulation time these pioneers thus need a long time to decrease again to base-line abundances. The climax groups on the other hand needed a long time to recover from the loss of stems that were killed or harvested during logging. The effects of logging on functional group composition were, however, found to be rather small.

The results of this study show that it is possible manage the forests in central Guyana in a way that results in relatively small changes in functional composition and still achieves more or less sustained yields. The results of this study can be used to rank the scenarios based on criteria for productivity and sustainability. Forest managers and decision makers can use these results as input for multiple criteria analysis to objectively decide on what would be the most desirable logging practices.

1 Introduction

Like in many tropical countries, also in Guyana timber harvesting has become an important source of income (van der Hout 1999). The country, situated in the northeast of South America, is covered with 17 million hectares of forest, which is about 80% of its land area. Although the majority of these forests are still untouched, 8.9 million hectares are designated state forest lands of which in 1997 roughly 75% had been allocated for timber harvesting (van der Hout 1999). Currently annually an estimated 160,000 ha is selectively harvested (FAO 2000).

In contrast, just over 1% of the total land area is part of a National Protected Area System (ter Steege 2000), but the Government of Guyana is in the process of extending this area. Nevertheless, even by protecting 10% of its land area an estimated 4500 species would not be protected (ter Steege 2000). Although diversity may not be as high as in primary forest or species composition may have changed, in recent years the conservation value of secondary forests and logged forests is getting increasingly recognised (*e.g.* Putz & Viana 1996, Chazdon 1998, Cannon *et al.* 1998a). Hence, logged forests and forests that will be logged in the future may play an important role in conserving Guyana's biodiversity. Sustainable forest management, consequently, should result in sustained timber yields over long periods of time to provide lasting revenues for the country and to secure the livelihoods of many peoples that depend on employment in the forestry industry, but on the other hand it should also conserve as much of the forest's diversity as possible.

Although generally the intensities of selective logging are rather low, damage to the residual forest may be considerable (Johns 1988, ter Steege & Hammond 1996, Zagt 1997, van der Hout 1999). For sustainable forest management, information is required on the long-term consequences of current logging practises for future timber yields, species composition and recovery of exploited forests. Presently quite some information is available on the sustainability of different management regimes for a limited number of important timber species (*e.g.* Zagt 1997, Zagt *et al.* 2000). Yet, little is known about the long-term effects of logging on future timber yields, species composition and forest recovery.

An important difficulty in obtaining this information is that tropical trees are slow-growing and long-lived organisms that may reach ages of several hundred years (*e.g.* Lieberman & Lieberman 1987, Korning & Balslev 1994, Fichtler *et al.* 2003, Laurance *et al.* 2004). In this study we will therefore evaluate the long-term effects of different logging intensities on future timber yields, species composition and on the recovery of the whole tree community using a simulation model. Subsequently we compare the silvicultural and ecological sustainability between different alternative logging scenarios.

Currently in Guyana the length of felling cycles (FC) and minimum felling diameters (MFD) are important issues in forest management and yield regulation. So far the minimum allowed felling cycle is 25 years and MFD is 35 cm, but recent post harvest surveys (Bird 2000) and previous research (*e.g.* Zagt 1997) indicated that such a short logging cycle and low MFD will not sustain future yields. Therefore felling cycles of 60 years and MFD of 60 cm are advised in a recent edition of the Code of Practice (CoP) for timber harvesting (GFC 2002). In this study we will include management scenarios with different felling cycles, MFD and harvest intensities. In this way our investigations can also contribute to the ongoing discussion on yield regulation in Guyana.

We will address the following questions: What are the long term effects of different intensities of timber harvesting on species composition? Will species composition recover from logging? How long will it take before the forest returns to a state that is comparable with non-logged forest? Will commercial volumes recover after harvesting and how long will that take? What is the effect of different poly-cyclic management regimes on timber yields and on species composition? Is it possible to have sustained yields with poly-cyclic harvesting?

2 Methods

2.1 Study area

This study was based on data from 15 experimental sample plots (ESP) in the West-Pibiri compartment of Demerara Timbers Ltd.'s logging concession in Central Guyana (5°02' N, 58°37' W), approximately 250 kilometres south of Georgetown, Guyana's capital (van der Hout 1999). Each ESP measured 140 x 140 m (1.96 ha). The plots were set up in 1993, and covered four different intensities of experimental reduced impact logging (RIL) and control plots without intervention. The plots are in mixed Greenheart (*Chlorocardium rodiei*) forest (Ek 1997, van der Hout 1999), that is dominated by 8 tree species that account for nearly 45% of the trees with diameter at breast height (DBH, *i.e.* diameter at 1.3 m height) larger than 5 cm (chapter 2). The soils in this area belong to the well-drained brown sand series with a moderate to high percentage of clay (Ferralsols) (van der Hout 1999, van Kekem *et al.* 1995). The average annual rainfall in the period 1996-2000 was 2772 mm (van Dam 2001).

2.2 Model framework

We made projections on the future of the forest after harvesting using the SYMFOR modelling framework (Phillips & van Gardingen 2001a, 2001b, Phillips *et al.* 2002, 2003, 2004, Chapter 3). The framework contains spatially explicit individual-based ecological models that can be linked to forest management models (Phillips & van Gardingen 2001b, van Gardingen *et al.* 2003), which allows users to simulate a range of alternative management scenarios. The ecological model in SYMFOR that we used in this study for forests in central Guyana is described in detail in chapter 3. Here we will only give a brief overview of this model. For a full description of the used functions, their parameterisation and the evaluation of its performance we refer to chapter 3. Further on we will outline the choice of functions of the management model and the parameter settings that we used. More details on the management model are provided in Phillips & van Gardingen (2001a) and van Gardingen *et al.* (2001)

2.3 Ecological model

The ecological model was developed based on the permanent sample plot data from the reduced impact logging (RIL) experiment in Pibiri. It represents the three main demographic processes in populations of forest trees, namely, *growth*, *mortality* and *recruitment*. The rates of these processes for individual trees depend on their own size and competition with other trees, mainly for light, and were parameterised from data. Competition among individuals is represented as a distance and size dependent competition index that is explicitly derived from the data. The model is individual-based and spatially explicit, meaning that all trees are individually represented and occupy a unique spatial position in the simulated forest stand. Trees have a diameter at breast height (DBH) that is updated each time-step using the diameter-growth function. Other allometric properties, like height and crown width of the trees are determined using functions with DBH. Trees that die from natural causes as determined by a semi-stochastic mortality function, have a certain probability to fall in a random direction and damage smaller neighbour trees that are within its damage area. The recruitment function describes the appearance of new trees at the minimum DBH threshold, which was 2 cm. The probability of recruitment of a new tree in a grid-square of 25 m^2 depends on the light availability in that grid-square. The model runs with annual time-steps.

High tree species diversity in tropical forests often causes problems for testing hypothesis in ecology, because it implies that many species are rare. Consequently little ecological information is available about most species and species abundances of many species are too low for rigorous parameterisation of functions describing demographic processes like growth, mortality and recruitment. Therefore we objectively classified species into functional groups with similar ecological characteristics and used these to parameterise the model. Tropical trees are often classified depending on the stage of succession in which they appear in the forest (*e.g.* Swaine & Whitmore 1988, Finegan 1996). This is often related to the light demand of the species. The basis of many classifications is the dichotomy between pioneer and climax species (Swaine & Whitmore 1988). Pioneers are fast growing and light demanding species that dominate early in succession while climax species grow slower and are more shade-tolerant that become dominant late in the succession. Individuals of an intermediate group of long-lived pioneers dominate later than the pioneers and live for a prolonged period of time (Finegan 1996). Our classification (table 1) was objectively based on differences in three morphological characteristics: wood density, seed mass and adult stature, which are predictors of species' responses to disturbance in terms of growth, recruitment and survival (see Favrichon 1994, Finegan 1996, ter Steege & Hammond 1996, ter Steege & Hammond 2001). This classification is further elaborated on in chapter 3.

Table 1 Classification of the 9 functional groups. WD: Wood density (Low: < 0.8 g cm-3, High: ≥ 0.8 g cm-3), SM: Seed Mass (Low < 0.1 g, High: ≥ 0.1 g), TH: maximum Tree Height (small (understorey): < 25 m, medium (canopy): 25 – 35 m, tall (emergent): ≥ 35 m). Nspecies: number of species occurring in the Pibiri sample plots for each functional group, see appendix A for an overview of species per functional group.

Functional group		WD	SM	TH	$N_{species}$	Coding
Pioneers	small	Low	Low	< 25	13	P1
	medium	Low	Low	25 - 35	5	P2
	tall	Low	Low	≥ 35	5	P3
Long-lived pioneers	small	Low	High	< 25	14	LP1
	medium	Low	High	25 - 35	31	LP2
	tall	Low	High	≥ 35	21	LP3
Climax	small	High	All	< 25	29	C1
	medium	High	All	25 - 35	49	C2
	tall	High	All	≥ 35	18	C3

2.4 Management model

The management model was the same as the one used for other management evaluations with SYMFOR (van Gardingen *et al.* 2003, Phillips *et al.* 2004). The management model simulates the harvesting and management of the forest according to a set of criteria that can be set by model users. For several management practices there is choice from alternative modules, and parameters can be set to match the specific needs of the users. We choose the modules and the values of parameters of the selected components to match the Code of Practice (CoP) for timber harvesting in Guyana (GFC 2002) and general logging practices in Guyana.

The management model uses a number of utility groups to distinguish trees that can be subject to different management decisions, *e.g.* related to their commercial attractiveness and legal management. The classification that we made was based on a classification of established commercial species as used by the Guyana Forestry Commission and additional data from van der Hout (1999) and is shown in table 2. Species from the same functional group (with similar ecological characteristics) may belong to different utility groups and *vice versa*. The first three utility groups identify single species. We only used the different utility groups to be able to distinguish them in the total harvested volumes. Therefore we used for each utility group the same management criteria, *i.e.* felling cycles and minimum felling diameters.

New trees of a functional group that are recruited at the minimum size limit of 2 cm DBH in the ecological model, will get a utility group value that is assigned stochastically according to fixed proportions of utility groups within a specific functional group. These fixed proportions were parameterised based on the proportions as found for trees smaller than 20

Table 2 Classification of utility groups that were identified for this study. The classes (Special category (S), 1 and 2) refer to a classification of established commercial species as currently used in Guyana. They reflect the economic marketability and variation in taxation of the species. Species in the special category are of high economic value, species in class 1 are mainly hard wooded species used for production of sawnwood, while those in class 2 are mainly species with softer wood used for production of for instance plywood and veneer.

Utility group	Class	Description
1	S	Greenheart (*Chlorocardium rodiei*)[1]
2	S	Purpleheart (*Peltogyne venosa*)[1]
3	S	Brown Silverballi (*Licaria cannella*)
4	1	Crabwood (*Carapa guianensis*), Kabukalli (*Goupia glabra*), Locust (*Hymenaea courbaril* var. *courbaril*), Mora (*Mora excelsa*) & Suya (*Pouteria speciosa*)[2].
5	1	Currently marketable species[3] – class 1, *e.g.* Morabukea (*Mora gongrijpii*), Simarupa (*Simarouba amara*) and Soft Wallaba (*Eperua falcata*).
6	2	Currently marketable species[3] – class 2, *e.g.* Baromalli (*Catostemma* 2 spp.), Kereti Silverballi (*Ocotea puberula*) and Maporokon (*Inga alba*).
7	-	Currently marketable species[3] – rest (*e.g.* Barataballi (*Chrysophyllum sanguinolentum*), Futui (*Jacaranda copaia*) and Wadara (*Couratari guianensis*).
8	-	Potentially marketable species[3], *e.g.* Black Kakaralli (*Eschweilera sagotiana*)[4], Huruasa (*Aberema jupunba*)[4] and Sarebebeballi (*Vouacapoua macropetala*)[4].
9	-	Currently non- marketable species[3]

[1]) These 2 species covered 62% of the total annual log production over the period 1996-1998 in the concession in which the study area was situated (Greenheart 51% and Purpleheart 11%). Greenheart is the most important timber species in Guyana.

[2]) These species were the most frequently logged class 1 species in the concessions, covering 16% of the total annual log production over the period 1996-1998. Since April 2000 the Guyana Forestry Commission (GFC) has put restrictions on export of Crabwood and Locust due to shortage of wood of these species for utilisation in the local furniture industry.

[3]) Based on Appendix A in van der Hout (1999).

[4]) Marketability of these example species is currently explored by the GFC (ITTO 2003).

cm DBH in the experimental sample plot data that were used to parameterise the ecological model (table 3).

The management model can be used to simulate various different logging scenarios. Different options exist for regulating yield, like maximum and minimum timber volumes to extract and the maximum number of trees to be extracted. Also parameters exist to define felling cycles (FC) and minimum felling diameters (MFD). In table 4 we present the various silvicultural parameters used in the management model, give a description of their use and give the values that we used for this study.

The selection of trees for logging is made in two steps. First all trees that pass the logging requirements (minquality and MFD) are selected, after which a random selection of these qualifying trees is made until the maximum allowed harvest intensity is reached. Because the selection of trees that will be felled is random, on average the ratio of harvested trees among

Table 3 Fraction of trees < 20 cm DBH of each functional group (FG) that is in a specific utility group. For instance 7% of the trees in FG C2 are in utility group 1, but on the other hand, utility group 1 is made up only from trees of FG C2. If a new C2 tree recruits it has a probability of 0.07, 0.19, 0.24 and 0.5 that it will be of utility group 1, 5, 8 or 9 respectively. Note that all individuals of functional groups P1 and C1 are in the non-commercial utility group.

FG	Utility group								
	1	2	3	4	5	6	7	8	9
P1	0	0	0	0	0	0	0	0	1
P2	0	0	0	0	0	0	0.75	0	0.25
P3	0	0	0	0.61	0	0	0	0	0.39
LP1	0	0	0	0	0	0	0.02	0	0.98
LP2	0	0	0	0.11	0.01	0.55	0	0.01	0.32
LP3	0	0	0	0.06	0.13	0.51	0.08	0.11	0.11
C1	0	0	0	0	0	0	0	0	1
C2	0.07	0	0	0	0.19	0	0	0.24	0.5
C3	0	0.07	0.02	0.01	0.25	0.2	0.31	0.04	0.1
Total	0.02	0	0	0.02	0.08	0.08	0.02	0.09	0.69

the utility groups is proportional to the percentage of harvestable trees of each utility group in the simulated forest.

For all our simulations we selected the felling sub-model that simulates directional felling. This lets felled trees fall in the specified direction relative to a simulated skid-trail. Damage to surrounding trees is simulated in the same way as the damage caused by falling trees that died naturally. Trees smaller than the felled tree and within the damage area, which is a kite-shaped area defined by the height and crown-width of the falling trees, have a probability of 8% to get killed (see chapter 3).

The management model offers two options for the simulation of the skid-trails. The first option will simulate a straight skid-trail from the entry point in the plot for each felled tree. The second option will minimise the total length of the simulated skid-trail by simulating branched skid-trails. This second option reflects a certain degree of planning of the skid-trails and was the option that we choose for this study. The simulated skid-trails have a certain width within which all trees smaller than a certain diameter will be killed. Also damage is simulated to trees next to the skid-trail that is caused by skidding felled trees around corners. Yet another damage area is simulated around the base of a felled tree to represent damage caused by manoeuvring of the skidder to attach to the bole. Effectively all these damage areas that are related to skidding are stripped of trees smaller than the defined DBH limit.

The modules that we selected and their parameter values were associated with at least some degree of reduced impact logging (RIL). The selection of branched skid-trails, for instance, minimises the length of the simulated trails and thus reflects a certain degree of planning of the skid-trails. Also directional felling (*i.e.* felling angle relative to the skid-trail) is

Table 4 Silvicultural parameters as used in the management model. The felling cycle (FC), minimum felling DBH (MFD) and harvest intensity (HI) were varied depending on the simulated logging scenario. To set the parameters to values that match the situation in Guyana we used the recommendations from the Code of Practice (CoP) for timber harvesting in Guyana (GFC 2002) or data from van der Hout (1999). If no information on parameters was at hand, we used the default value from SYMFOR.

Parameter	Value	Description
firstlogging	10	The year when to do the first harvest.
FC	25, 40 or 60	Felling Cycle (yrs), the period of time in between two subsequent harvests. The actual value depends on the logging scenario.
MFD	35 or 60	Minimum Felling DBH (cm), the minimum diameter to qualify for felling. This MFD can be different for different utility groups. In this study, however, it was set to the same value for the utility groups 1 through 7. The actual value depends on the logging scenario. The MFD for the non-logged utility groups (8 and 9) was set to 500, which will never be reached by any of the trees.
HI	4, 8 or 12	Harvest Intensity (ha^{-1}), the maximum number of trees per hectare allowed to be harvested at each event. The value depends on the logging scenario.
maxextract minextract	500 0	Maximum and minimum timber volume to extract (m^3 ha^{-1}). Because we wanted the harvest intensity to be only limited by numbers of extracted trees, the maximum was set to a value that never will be reached within the limits set by HI, and the minimum was set to 0.
minquality	0.3	Minimum stem quality for harvesting. When a new tree recruits at 2 cm DBH the quality is randomly set to a value between 0 and 1. Simulated trees with a quality <= minquality will not be harvested. Often a certain fraction of the trees has defects that will disqualify it for harvesting. Generally these trees are hollow, show signs of decay or have malformed stems. In the experimental plots 30% of the trees belonging to commercial species had serious defects and were rejected for harvesting (see van der Hout 1999).
cutdirection	35	Felling angle (°) relative to skid-trail. Simulates directional felling. The CoP recommends felling angles between 30° and 40°.
accesspoint	(50, 0)	The x and y position of the point where the simulated skid-trail enters and leaves the plot.
skidprepradius	5	The radius (m) of the area around the base of a felled tree that is damaged by the skidder manoeuvring to attach to the bole.
joinangle	60	The angles (°) at which branched skid-trails join. The CoP recommends joining angles of 60°.
skidwidth	3.5	The width (m) of skid-trails. The CoP recommends skid-trails not to exceed a width of 4 m. The widths of, for instance, wheel skidders of Caterpillar are approximately 3.4 m.
maxdbhdamage	40	The maximum DBH (cm) of trees that can be fatally damaged during skidding. Value is SYMFOR's default.
damageprob	1	The probability that a tree smaller than maxdbhdamage will be killed due to skidding (in skid-trails and in the area defined by skidprepradius). Value is SYMFOR's default.
skidpersist	40	The time (yrs) that skid-trails remain re-usable for. If possible these old ones are used at subsequent harvests to reduce damage. Value is SYMFOR's default.

commonly recommended to reduce the impact of the harvesting operation (van der Hout 1999). We did not apply the complete range of possible measures for RIL, because it is currently not widely applied in forest management in Guyana. No post-harvest silvicultural treatments such as thinning or planting were simulated.

Because tree volume differs between the utility groups we implemented three new functions for tree volume in the ecological model. The volumes (bole volume over bark, V, in m^3) of trees were modelled as a function of their DBH (D in m). These functions were taken from van der Hout (1999), and were based on data of trees that were felled in and around the permanent experimental plots that were used for parameterisation of the ecological model:

$V = 9.342D^2 + 0.0274$ for utility group 1 (*Chlorocardium rodiei*) (1)
$\log V = 2.031 \cdot \log D + 1.057$ for utility group 2 (*Peltogyne venosa*) (2)
$\log V = 2.0 \cdot \log D + 0.965$ for all other utility groups (3)

2.5 Simulated management scenarios

We simulated two types of logging scenarios: scenarios with logging once and poly-cyclic scenarios. For comparisons with the logging scenarios we also simulated forest without logging, which we used as base-line simulation. To minimise the effect of systematic errors in the model, whenever possible, we either compared the results from simulations among each other, or with the base-line simulations instead of with the initial situation. All scenarios were simulated for 200 yrs with first logging simulated at year 10. Output on all living trees was generated every 5 years and output for felled trees after each logging event. To take into account the variation in structure and composition that existed among the permanent experimental plots, for each scenario, simulations were applied to the central hectares of the three control plots. For each of these plots 10 replicate simulations were performed, resulting in a total of 30 replicated simulations for each scenario.

We simulated six different scenarios with logging once, based on combinations of two minimum felling diameters (MFD) and three maximum allowed harvest intensities (HI), and 18 poly-cyclic scenarios based on all combinations including felling cycle (FC). The used options for MFD were: 35 cm (current statutory limit) and 60 cm (proposed by GFC (2000)). The used maximum harvest intensities were 4 (low), 8 (medium) and 12 (high) trees ha^{-1}. The poly-cyclic logging scenarios were simulated with felling cycles of 25 (current statutory limit), 40 and 60 (advised limit, GFC (2000)) years. The timing of each logging event for the different felling cycles is shown in table 5.

Table 5 Timing (yr) of the simulated logging events for the scenarios with different felling cycles.

	Felling cycle			
Event	25	40	60	Once
1	10	10	10	10
2	35	50	70	
3	60	90	130	
4	85	130	190	
5	110	170		
6	135			
7	160			
8	185			

From this point forward we specify the different scenarios in the main text, tables and figures using the following coding: C_{FC}-D_{MFD}-I_{HI}. For example the scenario with a felling cycle of 25 years, minimum felling diameter of 35 cm DBH and a maximum harvest intensity of 8 trees ha^{-1}, will be notated as C25-D35-I8.

2.6 Analyses

2.6.1 Single logging event

We determined differences in actually realised HI and volume between the scenarios with different MFD and maximum allowed HI using the scenarios with logging once. To get an idea of the amount of disturbance the simulated logging caused, we calculated for each scenario just after logging the mean reduction in basal area (m^2 ha^{-1}) in the simulated plots.

The minimum time needed after logging for the commercial volumes (sum of the volume of trees that would qualify for harvesting) to return to similar volumes as in the base-line simulations (henceforth referred to as return time) were calculated from the logging once scenarios. Because of the large variation between the simulated plots we decided to calculate the return time values separately for each plot. For the base-line simulations we calculated at each year with output (every 5th year) a 95% CI of volume, based on the data of all repetitions of a plot. Subsequently we determined for each single repetition of a logged once scenario the minimum time after harvesting for which the volume returned within the 95% CI of the base-line simulations. In this way we got 30 values for minimum return time for which we calculated the mean. We determined these times for both the total commercial volume as well as for the commercial volumes of each utility class. Because utility groups 2 and 3 occurred very irregularly we decided to use the commercial classes (see table 2) instead of the groups. Only groups 7 and 8 remain identified by their group instead of class. Finally we determined in a similar way as was done for the return times of commercial volume the minimum return times of abundance and basal area for each functional group.

We applied the G-test to detect differences in the relative composition of functional groups at year 200 between the logging once scenarios and the base-line simulations. We did this for abundances of trees larger than 2 cm DBH and for basal area.

2.6.2 Multiple logging events

For analyses on yields from the scenarios we focused on the first three harvests, as these are probably the harvests that a forest manager would still be interested in and for which the model is still remotely accurate. In practise a period of time beyond the third harvest is too far away to be of interest for current day yield planning, especially when the felling cycles are as long as the 60 years proposed in the Code of Practice.

To summarize and compare the performance of the scenarios relative to each other we determined a set of indicators of productivity and sustainability. As indicators for productivity we used total yield and average annual yields over the first three logging cycles. The total yield over the first three harvests is the sum of the total yield of all utility groups irrespective of the length of the felling cycle. The average annual yield over the first three harvests was calculated by dividing the total yields by 3 times the felling cycle and thus correct for differences in felling cycle. Differences between the scenarios were tested using ANOVA and Tukey post-hoc tests.

As indicators for sustainability of the scenarios we determined the yields of the second and of the third harvests as percentage of the yield of the first harvest (henceforth referred to as: % first yield (%FY)) and we determined the level of changes in relative functional group composition just before the third and just before the last harvest of the 200 years simulated. The %FY of the second and of the third harvest was calculated for each repetition. For some scenarios the relative differences between the first and other two yields were very large for some of the repetitions. For each scenario we therefore calculated the median %FY. To test for differences between the scenarios we used Kruskall-Wallis ANOVA with %FY for both harvests combined (n=60 per scenario). Finally the rank order of scenarios for %FY was based on the mean ranks resulting from the Kruskall-Wallis ANOVA. We applied the G-test to detect differences in the relative composition of functional groups between the logging scenarios and the base-line scenarios. This was done for compositions just before the third harvest and just before the last harvest, which gives an indication for long-term sustainability. For each scenario the average composition was compared with that of the base-line simulations at the same simulation times.

To facilitate evaluation of the scenarios we tested each of these indicators for differences between the scenarios using ANOVA of Kruskall-Wallis ANOVA. Subsequently we ranked the scenarios in order of highest productivity or highest sustainability.

Additionally we determined for each result variable (*e.g.* return times, %FY, total yield, etc.), which factors (FC, MFD or HI) determined most of the variance in result variable between the logging scenarios, either using Kruskal-Wallis ANOVA or regular ANOVA.

3 Results

3.1 Single logging event

Using a minimum felling diameter of 35 cm, in all but 4 simulations the maximum allowable harvest intensity for the simulations of 4, 8 and 12 trees ha^{-1} could be reached (figure 1a). On average this resulted in total harvested volumes that ranged from 18.8 m^3 ha^{-1} for D35-I4 to 43.9 m^3 ha^{-1} for D35-I12 (figure 1b). For the simulations with minimum MFD of 60 cm the average actually achieved HI were 4, 6 and 6.9 trees ha^{-1}. This means that on average the maximum allowable HI could not be reached for HI 8 and 12 (figure 1a) due to a lack of suitably sized trees. The actually harvested number of trees, however, differed considerably between the three simulated plots. Consequently, simulated achieved yields for MFD 60 hardly varied even as allowable HI increased by a factor 3 (from 4 to 12 trees ha^{-1}) (figure

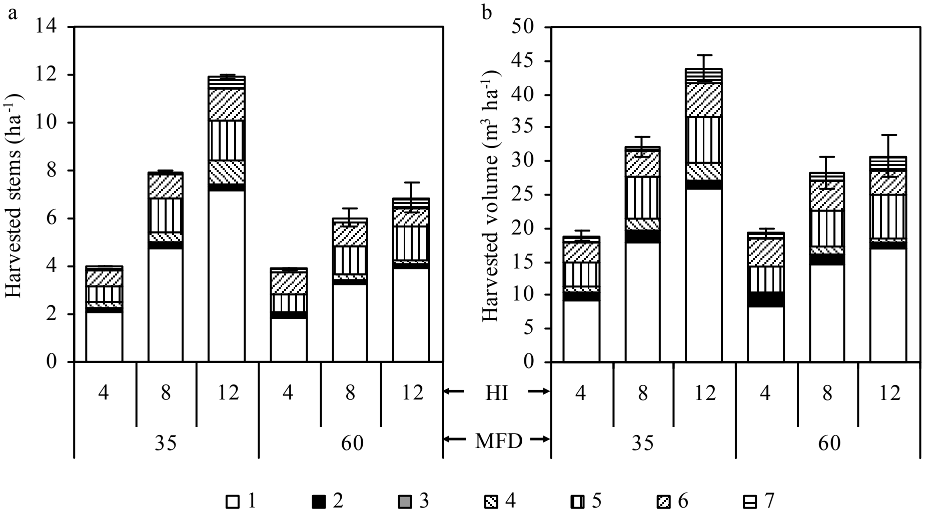

Figure 1 Mean of actually harvested number of stems (a) and mean of harvested volume (b) for each utility group (1-7, see legend and table 2) for 6 simulated scenarios of logging once at year 10. The means are based on 30 repeated runs of each scenario. HI refers to maximum harvest intensity (stems ha^{-1}) and MFD refers to minimum felling diameter (cm) as used in the different scenarios. The total height of each bar indicates the mean of the totally harvested number of stems (ha^{-1}) and volume (m^3 ha^{-1}) with 1 SE (error bars).

1b). In all cases utility group 1 (Greenheart), the most important timber species, made up about 50% of the total harvest.

Just after logging the mean reduction in total basal area of trees larger than 20 cm DBH (both felled and killed) ranged from 2.9 m^2 ha^{-1} (-14%) for HI 4 at both MFD, to 6.7 m^2 ha^{-1} (-31%) for D35-I12 (table 6). For all scenarios the total reduction is on average twice as high as the felled basal area.

Table 6 Mean reduction of the basal area (BA) of trees larger than 20 cm DBH just after simulated logging for the different scenarios of logging once, given in absolute numbers (ΔBA) and as percentage of total (ΔBA%). For comparison also the mean felled BA and the mean fraction of ΔBA to felled BA is shown. The means are based on 30 repetitions each. Significantly different reductions in BA are indicated with different letters (P<0.01).

Scenario	ΔBA (m^2 ha^{-1})	ΔBA%	Felled BA (m^2 ha^{-1})	ΔBA/Felled BA
D35-I4	3.0	14^{a}	1.6	2.0
D35-I8	5.1	23^{c}	2.7	2.0
D35-I12	6.7	31^{d}	3.7	1.9
D60-I4	2.9	13^{a}	1.6	1.9
D60-I8	4.3	19^{b}	2.4	2.0
D60-I12	4.6	21^{bc}	2.6	1.9

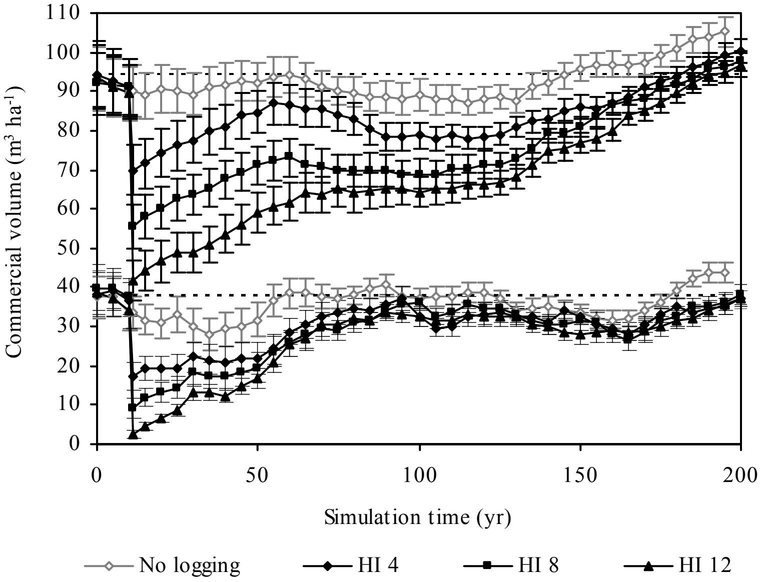

Figure 2 Mean ± 1 SE (error bars) of standing commercial volume over simulation time for 6 scenarios with logging simulated once at year 10 and one simulation without logging. The 4 lines at the top represent commercial volumes for simulations with MFD of 35 cm and the lower 4 lines are volumes for the simulations with MFD of 60 cm. The graphs for the different HI are indicated with different markers (see legend). The volumes for the two lines of simulations without logging were based on the same simulations. The dotted lines show the initial volumes for each MFD.

The reduction in commercial volume after harvesting is strongest for the scenarios with MFD 35 and increases with increasing HI as illustrated in figure 2. After the reduction of commercial volumes, return times for the commercial volumes vary widely (table 7a). For the total volume, these were longest for the scenarios D35-I8 and D35-I12 with mean values of 114 and 118 years, respectively. Both minimum felling diameter and harvest intensity contributed significantly to variation in return times ($F_{2,174}$=5.27, P<0.01, see table 7). At high HI (8 and 12), recovery took longer for more heavily harvested forest (MFD 35) than for lightly harvest forest (MFD 60). Scenario D35-I12 had also the longest return times for commercial timbers of classes S and 1. At the end (year 200) of the simulations, however, all volumes in all scenarios were again similar to the volumes of the base-line simulations.

The response to logging varied greatly between the different functional groups. Especially the small pioneers P1 responded strongly in abundance to logging. For all scenarios the average abundance of group P1 peaked approximately 15 years after logging. This peak abundance was highest for D35-I12 (the heaviest treatment) (figure 3). This was approximately nine times higher than in the base-line simulations.

Table 7 Minimum return times for each scenario with logging once, a) per commercial class (see table 2, if not belonging to a class, then the number of the utility group is used, All refers to the total commercial volume), the mean (± SE) of the minimum time needed after simulated logging to reach again similar commercial volumes as simulations without logging. b) Per functional group the mean (± SE) of the minimum time needed after simulated logging to reach again similar abundances as base-line simulations. Significantly different times between scenarios within each class or FG are indicated with different letters (P<0.05, ANOVA with Tukey post-hoc test). The means are based on 30 repeated runs. These minimum return times for each of these runs was defined as the first simulation year after logging took place for which the abundance or volume was within the 95% CI of 30 repeated simulations without logging. Note that class (UG) 8 are potentially marketable species, but were not harvested in the simulations and were not taken into account for the return times of the total volume. The column with factor shows the factor with the highest significant *F* statistic from two-way ANOVA on return time after harvest with MFD and HI as factors. This is followed by its *F* value. For MFD, DF= 1,174 and for HI and interaction term MFD*HI, DF=2,174. All P<0.01.

	Scenario						
	D$_{35}$I$_4$	D$_{35}$I$_8$	D$_{35}$I$_{12}$	D$_{60}$I$_4$	D$_{60}$I$_8$	D$_{60}$I$_{12}$	Factor
a)							
Class							
S	54 ± 11^{ab}	84 ± 10.1^{bc}	90 ± 9.4^{c}	34 ± 5.3^{a}	48 ± 5.7^{a}	48 ± 4.8^{a}	MFD, 24.3
1	34 ± 8.4^{a}	47 ± 9.6^{a}	107 ± 11.1^{b}	37 ± 5.6^{a}	36 ± 4.2^{a}	48 ± 4.7^{a}	MFD*HI, 8.6
2	39 ± 7.7^{ab}	50 ± 8.1^{ab}	64 ± 10.4^{b}	23 ± 4.2^{a}	29 ± 5.1^{a}	28 ± 4.9^{a}	MFD, 17.8
7	27 ± 6.3^{a}	29 ± 6.2^{ab}	51 ± 10.7^{b}	11 ± 0.5^{a}	11 ± 1.2^{a}	17 ± 2.4^{a}	MFD,23.4
8	56 ± 11.1	40 ± 9.9	41 ± 9.4	30 ± 7	30 ± 7.9	20 ± 4.6	MFD, 7.3
All	56 ± 8.6^{a}	114 ± 10.1^{b}	118 ± 8.3^{b}	45 ± 6.9^{a}	61 ± 5.1^{a}	62 ± 6^{a}	MFD*HI, 5.3
b)							
FG							
P1	100 ± 2.4^{b}	107 ± 2.5^{b}	113 ± 2.2^{b}	82 ± 7.1^{a}	101 ± 3.7^{b}	99 ± 4.8^{b}	MFD, 13.4
P2	18 ± 2.7	16 ± 2.9	19 ± 2.6	20 ± 2.4	17 ± 1.3	21 ± 3	-
P3	48 ± 8.6	68 ± 12.5	81 ± 9.5	40 ± 9.2	60 ± 9.8	69 ± 10.3	HI, 4.8
LP1	45 ± 5.2	38 ± 3.3	43 ± 4.4	33 ± 5.9	38 ± 5.3	36 ± 4.6	-
LP2	19 ± 2.5^{a}	26 ± 6.2^{a}	56 ± 11.7^{b}	21 ± 3.3^{a}	19 ± 2.4^{a}	44 ± 9.6^{ab}	HI, 11.8
LP3	42 ± 6.7	60 ± 7.5	76 ± 10.2	49 ± 7.4	56 ± 9.3	61 ± 10.1	HI, 3.5
C1	124 ± 7.7^{a}	145 ± 7.6^{ab}	161 ± 5.8^{b}	121 ± 9.4^{a}	111 ± 8.9^{a}	126 ± 9.7^{a}	MFD, 12.3
C2	88 ± 8.4^{a}	111 ± 7.2^{ab}	120 ± 7^{b}	83 ± 7.2^{a}	99 ± 8.3^{ab}	99 ± 9^{ab}	HI, 5.5
C3	42 ± 4.5^{a}	54 ± 5^{ab}	68 ± 6.9^{b}	38 ± 6.6^{a}	45 ± 5.1^{a}	43 ± 4.3^{a}	MFD, 7.8

The average return time for the abundance of P1 was significantly shorter for D60-I4 (the lightest treatment) than for the other scenarios (table 7b), while scenario D35-I12 tended to have the slowest return time. For the other scenarios the return times hardly differed significantly between the scenarios (table 7b). Yet, there were significant effects of HI and MDF. Two-way ANOVA showed that mainly maximum allowed HI explained differences in return times, with longer return times as HI increased. MFD mainly explained the within functional group variation in return times for P1 and C1, with longer times for the lowest MFD. Comparisons between functional groups (table 7b) showed that in particular the groups P1, C1 and C2 need much time to return to no-logging abundances. At the end of the simulations (year 200) for each scenario the abundances and basal areas of the functional groups were similar to the base-line simulations. Likewise, the relative composition of functional groups within each scenario did not differ after 200 years.

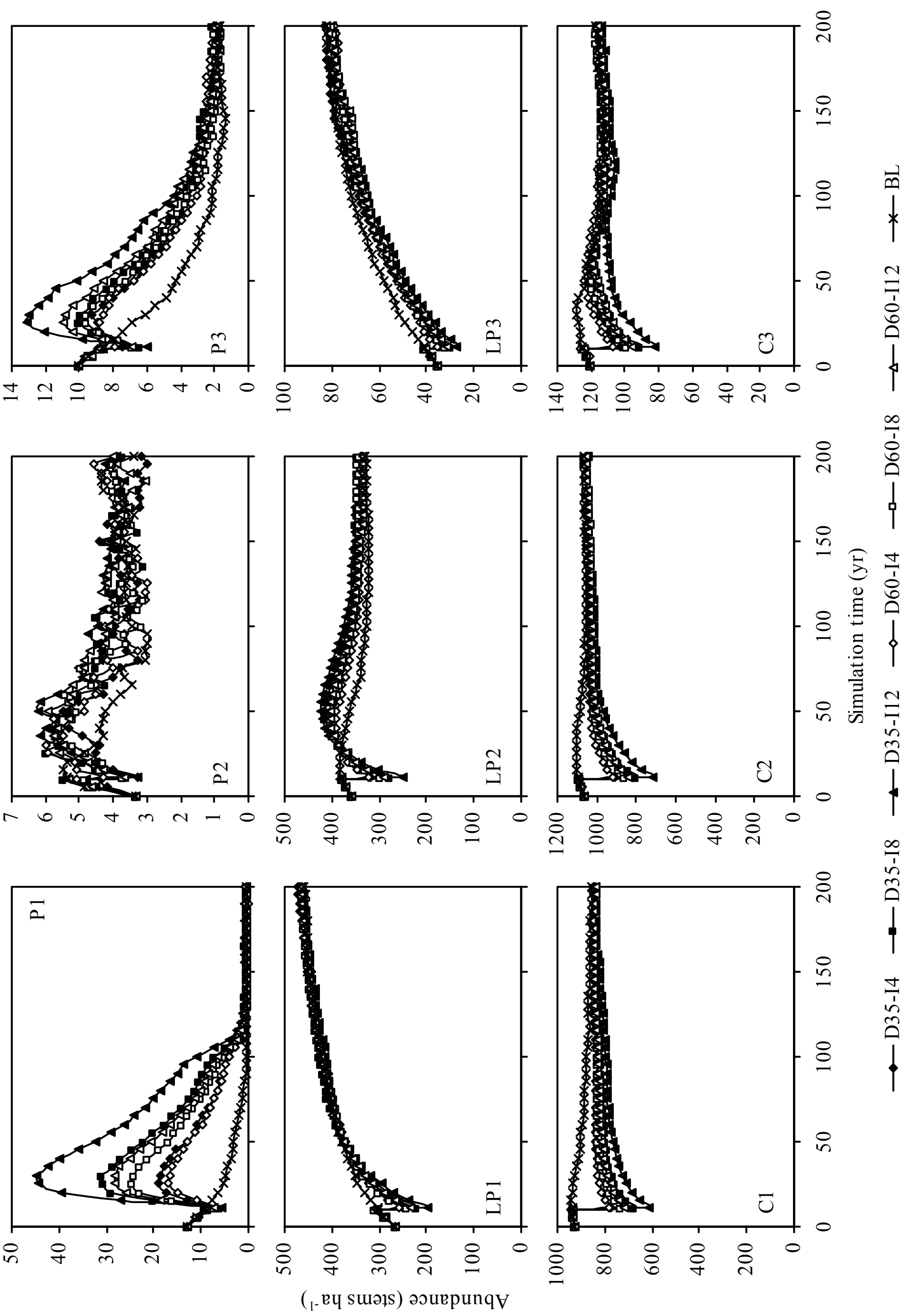

Figure 3 Responses to a single logging event and to no logging. For each functional group (see code in graphs) the mean abundances (stems ha^{-1}) over simulation time for 6 simulated scenarios of logging once at year 10 and simulations of no logging are given. Each mean results from 30 repeated runs. The D in the coding of the legend keys refers to the MFD and the I refers to harvest intensity, while BL refers to the base-line (no logging) simulations. Note that the scale varies between graphs.

3.2 Multiple logging events

Yields at the first harvest of the poly-cyclic logging scenarios were similar to the yields of the simulations of logging once with the same combination of MFD and maximum allowed HI (table 8). The total cumulative yield of the first three cycles was significantly higher for the scenarios with a low felling limit and high harvest intensity (MFD 35 and HI 12 (table 8)) and increased slightly, though not significantly with increasing felling cycles. Lowest yields were generally found for scenarios with the lowest harvest intensity of 4 trees ha^{-1}. Clearly, HI and MFD were the most important factors explaining the differences in total yields (table 8), although there was a significant interaction between the two factors.

Consequently the highest average annual yields were realised in the scenarios with high harvest intensity and small MFD (as for the total yields) in combination with short felling cycle, *i.e.* C25-D35-I12 and C25-D35-I8 (table 8). These two scenarios were also among the scenarios with the highest total cumulative yields.

%FY, on the other hand, was much higher for the scenarios with low harvest intensity and long felling cycle (table 8). Scenario C60-D35-I4 ranked highest for %FY for the second and third harvest, when ranking was based on the mean ranks given by Kruskal-Wallis ANOVA. Again felling cycle and harvest intensity were more important than MFD in explaining the differences in %FY between the scenarios. The actual %FY, however, was highest for scenario C60-D60-I8. A more thorough evaluation of this mean showed, however, that this high value was mainly based on a few outliers, again caused by the large variation between repetitions at MFD 60. This time the two scenarios with the shortest felling cycle and highest harvest intensity, (C25-D60-I12 and C25-D35-I12) had the lowest ranking of their %FY (table 8). The differences between the two scenarios with the highest %FY and those with the lowest %FY are illustrated in figure 4 and figure 5. Figure 4 shows the harvested volumes for each harvesting event. Figure 5 shows the development of total standing commercial volume over simulation time. The analysis summarised in table 8 only pertains to the first three harvests.

►

Table 8 See opposite page. Modelled yields and changes in functional group composition for the first three harvesting events for 18 logging scenarios. For the 18 simulated poly-cyclic logging scenarios an overview is given of the evaluated indicators of productivity and sustainability (see also main text). These were for productivity: mean total yield and mean annual yield of the first three cycles. The indicators for sustainability are: median of % first yield (yield as percentage of the yield of the first harvest) for second and third harvests, and changes in functional group composition (*G*) just before the third harvest and just before the last harvest. The yield of the first harvest is shown in m^3 ha^{-1}. The rank order of the scenarios for % first yield, was based on Kruskal-Wallis ANOVA using all the percentages from both 2nd and 3rd harvest of 30 repeated simulations (n=60 per scenarios). The scenario with the highest mean rank received rank order (1). High *G*-values were used as indicator for strong changes in functional group composition between a scenario and base-line simulations. The rank order of scenarios increased with increasing *G*-values (most affected). Most productive or most sustainable ranks (1) are shown in bold, while the lowest ranks (18) are underlined. Below each indicator the factors that significantly explained part of the differences between the scenarios are shown with accompanying values for *F* (if ANOVA was used) or χ^2 (if K-W ANOVA was used). The factors are ordered from most important to least important. Additionally significant interactions (if any) are shown.

	Volume	% first yield			Total yield		Average annual yield		FG composition			
Logevent:	1	2	3	2 & 3	∑ 3 events		∑ 3 events		3		Last	
Scenario	(m^3 h^{-1})	%	%	order	(m^3 h^{-1})	order	(m^3 h^{-1} yr^{-1})	order	*G*	order	*G*	order
C25-D35-I04	19.1	79	81	10	48.9 ± 1.99	17	0.65 ± 0.026	7	30.4	9	63.2	14
C25-D35-I08	32.5	76	71	12	79.8 ± 3.68	7	1.06 ± 0.049	2	81.5	16	99.4	18
C25-D35-I12	43.7	69	55	17	95 ± 6.26	3	**1.27 ± 0.083**	**1**	135.4	18	92.4	17
C25-D60-I04	18.5	67	78	14	43.8 ± 3.05	18	0.58 ± 0.041	10	19.6	5	43.9	11
C25-D60-I08	26.4	48	68	16	56.2 ± 5.42	12	0.75 ± 0.072	5	36.9	11	44.8	12
C25-D60-I12	31.3	38	48	18	58.1 ± 5.57	11	0.77 ± 0.074	4	40.9	13	40.2	9
C40-D35-I04	18.4	90	98	3	52.4 ± 2.1	15	0.44 ± 0.018	14	20.9	6	25.7	5
C40-D35-I08	33.1	87	79	9	86.8 ± 3.66	5	0.72 ± 0.031	6	58.0	15	68.9	15
C40-D35-I12	42.3	80	58	13	101.1 ± 5.54	2	0.84 ± 0.046	3	97.2	17	81.2	16
C40-D60-I04	18.9	74	93	7	49.2 ± 2.48	16	0.41 ± 0.021	16	17.6	3	26.3	6
C40-D60-I08	25.3	57	112	11	65.6 ± 5.31	10	0.55 ± 0.044	11	27.6	8	42.2	10
C40-D60-I12	32.6	42	94	15	73.5 ± 5.64	9	0.61 ± 0.047	9	38.2	12	37.4	8
C60-D35-I04	18.8	**95**	**101**	**1**	55.3 ± 1.58	13	0.31 ± 0.009	17	**9.9**	**1**	12.1	2
C60-D35-I08	32.3	98	89	4	91.9 ± 3.24	4	0.51 ± 0.018	12	31.4	10	37.0	7
C60-D35-I12	43.2	90	70	8	**112.4 ± 4.77**	**1**	0.62 ± 0.026	8	55.4	14	53.5	13
C60-D60-I04	18.8	92	104	2	54.7 ± 1.94	14	0.3 ± 0.011	18	10.6	2	**12.1**	**1**
C60-D60-I08	26.3	97	112	5	78.2 ± 4.83	8	0.43 ± 0.027	15	18.9	4	18.5	3
C60-D60-I12	32.8	87	81	6	83 ± 5.7	6	0.46 ± 0.032	13	24.0	7	22.2	4
			Factor	χ^2	Factor	F	Factor	F	Factor	χ^2	Factor	χ^2
Factor 1			FC	197.3	HI	112	FC	137	HI	9.3	FC	7.7
Factor 2			HI	88.6	MFD	77	HI	85				
Factor 3			MFD	9.1	FC	19	MFD	72				
Interaction			All		MFD*HI		MFD*HI					

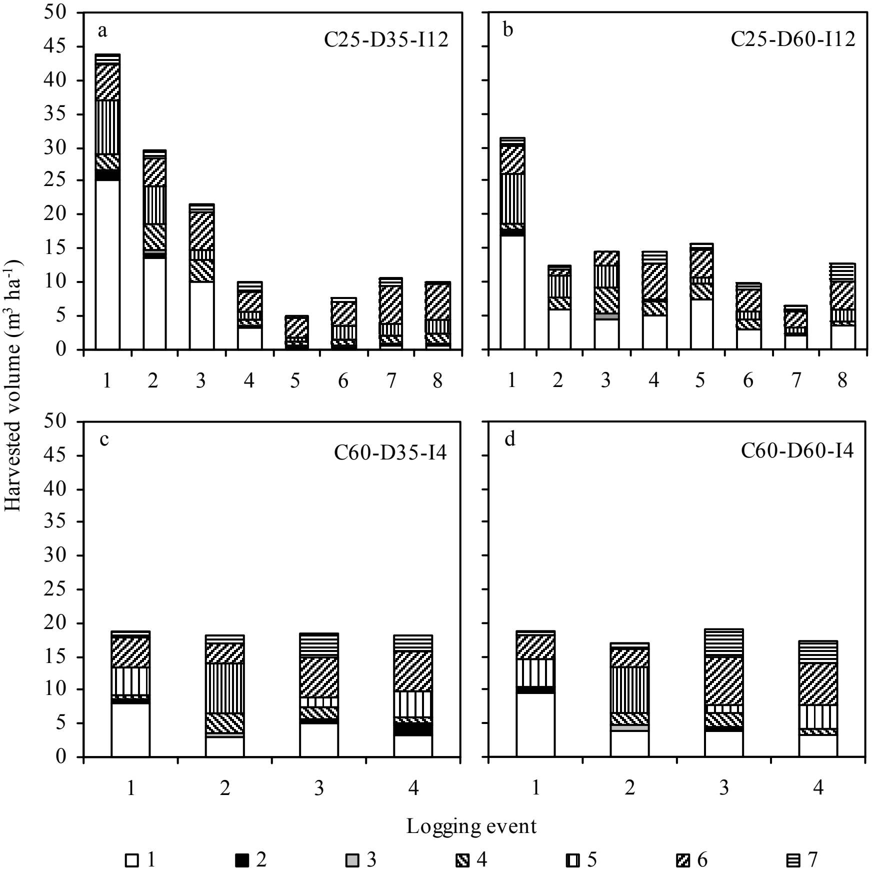

Figure 4 Mean of harvested volume for each utility group (1-7, see legend and table 2) at each logging event for a) and b) two scenarios with the lowest percentages sustained yield, and c) and d) the two scenarios with the highest percentages sustained yield (codes in graphs refer to scenario). The total height of each bar indicates the mean of the totally harvested volume (m^3 ha^{-1}).

All six scenarios with combinations of FC 40 or FC 60 and MFD 60 had a %FY that was just above 100% at the third harvest. Important difference here is that the scenarios with FC 60 also had a high %FY at the second harvest, while those percentages were as low as 39 to 61 % for the scenarios with FC 40, indicating that it is too short to sustain yields.

The effect of different felling cycles and MFD on functional group composition over time is illustrated in figure 6. All scenarios in that figure have the same maximum allowable harvest intensity. In all cases the abundances of the pioneer groups P1 and P3 rapidly increased within 5 to 10 years after the initial decrease following logging. With short felling cycles the pioneer abundance keeps on increasing with each subsequent harvest. After 4 harvests, however, the pioneer abundances decrease again, which is most likely an effect of lower harvesting intensities as yields cannot be sustained at these short cycles. A felling cycle of 60 years is sufficiently long for the pioneer abundance to decrease again to initial values, but not

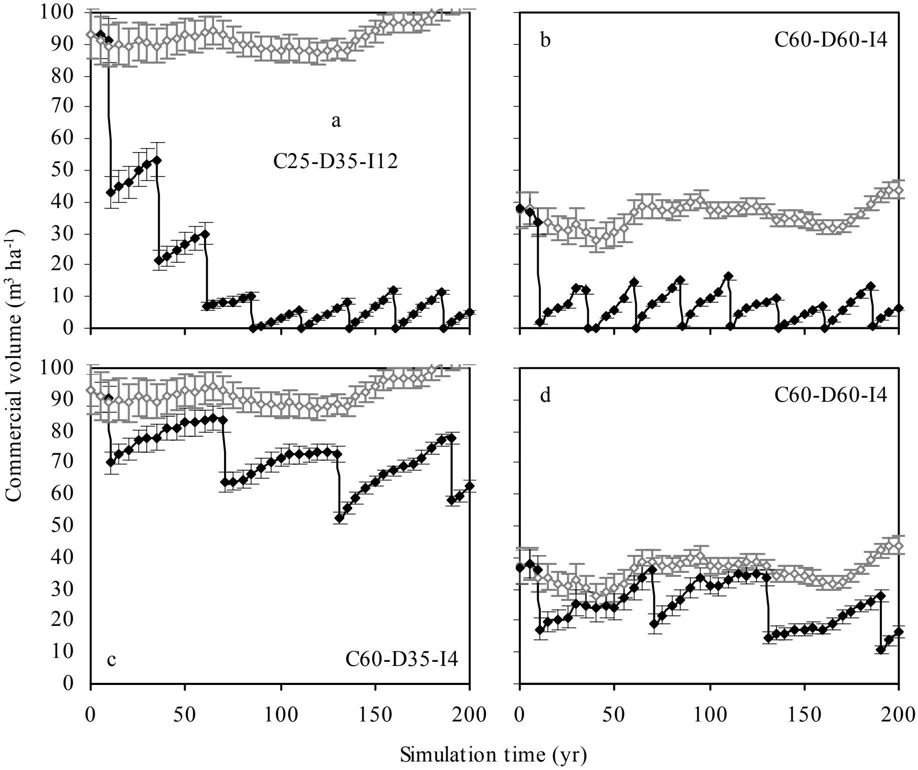

Figure 5 Mean ± 1 SE (error bars) of standing commercial volume (m^3 ha^{-1}) over simulation time for a) and b) the two scenarios with the lowest percentages sustained yield, and c) and d) the two scenarios with the highest percentages sustained yield (codes in graph refer to scenario). The light grey graphs show the standing commercial volume for scenarios without logging. The volumes for the two lines of simulations without logging were based on the same simulations but different limits were used for aggregation of the commercial volumes from the output.

as low as in the base-line simulations. Patterns for P2 are less clear, mainly due to low abundances in general. Long-lived pioneer group LP2 takes slightly longer to return to a base-line situation, but then also stays at increased abundances. The abundances of all other functional groups were negatively affected by logging. The effect was stronger for the scenarios with shorter felling cycle.

The effect of harvest on functional group composition just before the third harvest is shown in figure 7. Although composition was significantly different for most logging scenarios in comparison with base-line simulations (figure 7, table 8) the differences remain rather small. In the most affected scenario (C25-D35-I12) the total pioneer (P1-P3) abundance increased from 0.3% to 3.5%, while at the same time the total abundance of all climax groups decreased from 72 to 64 %. Just before the last harvest the relative abundance of the pioneers had decreased again to 1.8%. Harvest intensity and felling cycle, again, were more important factors explaining the differences than minimum felling diameter.

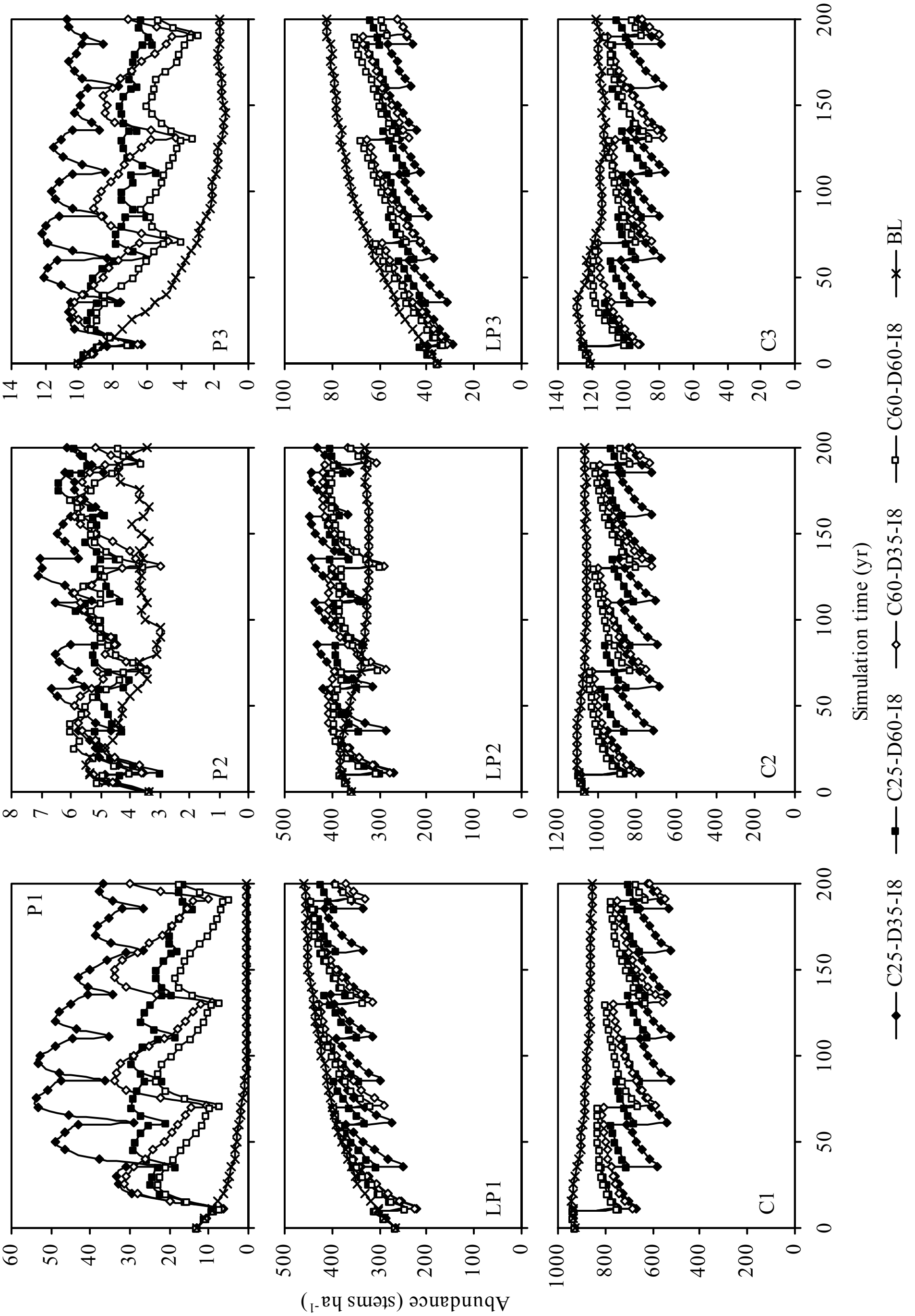

Figure 6 Response to multiple logging events. For each functional group (see code in graphs) the mean abundances (stems ha^{-1}) over simulation time for 4 simulated scenarios of poly-cyclic logging with HI of 8 trees ha^{-1} and two combinations of FC and MFD (C25-D35-I8, C25-D60-I8, C60-D35-I8 and C60-D35-I8, see legend). Graph NL (see legend key) shows the abundances for simulations without logging (base-line). Each mean results from 30 repeated runs with output every 5th year (markers). Note that the scale varies between graphs.

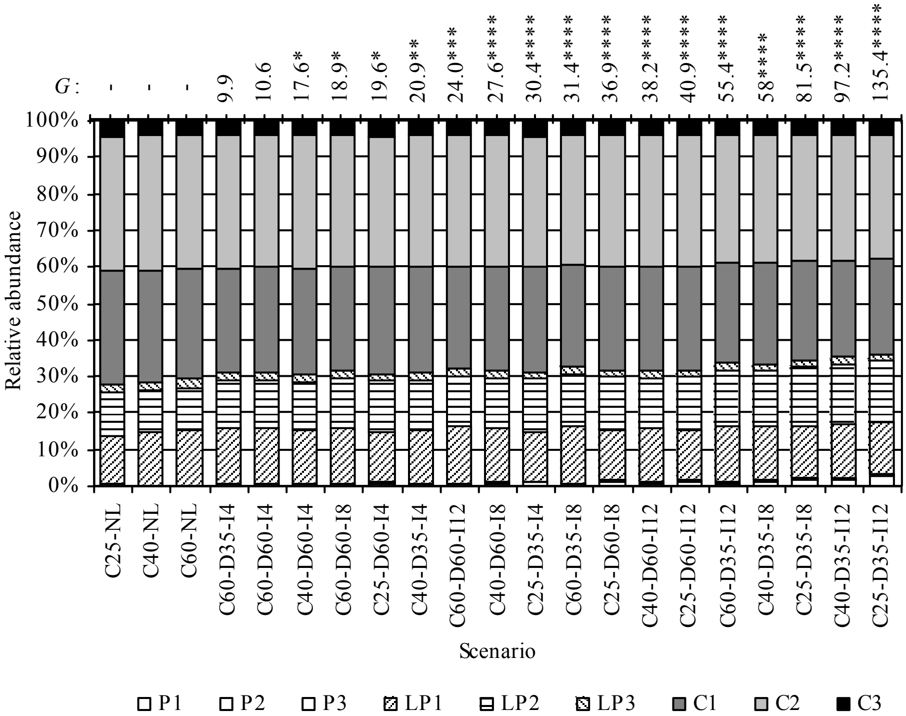

Figure 7 The relative composition of functional groups (see legend), for simulations without logging at three different timings (C25-NL, C40-NL and C60-NL) and the 18 logging scenarios just before their third logging event. The three different bars of the simulations without logging equal the three different timings of the third harvest of the three felling cycles (C25, C40 and C60). The relative composition just before the third logging event was always compared to the relative composition for simulations without logging at the same simulation time (corresponding C-values). Significant differences are indicated at the top of each bar (G-test, *: $P<0.05$, **: $P<0.01$, ***: $P<0.005$ and ****: $P<0.001$), with their accompanying *G* values. Larger *G* values imply larger differences to simulations without logging. The logging scenarios are ordered from left to right with increasing *G* values.

4 Discussion

4.1 Modelled and actual harvests compared

Comparison of the simulated logging using the statutory minimum felling limit of 35 cm with real logging in the same area showed that the harvested volumes (see van der Hout 1999) were slightly higher in the simulations than in reality. The averages of harvested volumes in the simulations were 18.8 and 32 m^3 ha^{-1} at harvest intensities of 4 and 8 trees ha^{-1} respectively, in comparison to volumes of 16.2 and 26.5 m^3 ha^{-1} for the actual harvests. The basal area reduction of trees >20 cm DBH was -14% and -23% for harvest intensities of 4 and 8 trees ha^{-1} respectively. This is almost twice as high as the same reductions observed in the real logging experiment that had reductions of 7% and 11% for HI 4 and 8 respectively. This suggests that the DBH of trees that were harvested in the simulations was bigger than of the trees harvested in reality and that simulated logging damage was higher than in reality. One should keep in mind, however, that the model rigidly applies the rules that were defined by the management model and cannot simulate ad hoc human decisions during felling if, for instance, a tree appears not to be suitable for one reason or another. Hence the absolute values of the projections of harvested volumes should be used with caution. Yet, the relative differences between simulated scenarios will probably be realistic as potential systematic model errors would affect the results from the two simulations in the same way.

4.2 Recovery of commercial volumes

After logging once, commercial volumes in all scenarios returned to similar values as in base-line simulations. This indicates that sustainable harvesting is in principle possible. The time needed to return, however, was long for the high harvest intensities. At a harvest intensity of 12 trees ha^{-1} the two most valuable utility classes S and 1 needed approximately 100 years to recover, which is much higher than the currently advised felling cycle of 60 years. Both classes consist mainly of slow growing species. The other classes contain also species that have faster growth and recruitment rates, which subsequently can explain the shorter return times for these groups.

The effect of the long volume recovery periods in relation to felling cycles is found back in the development of commercial volumes in the poly-cyclic scenario. Even for the management scenarios with the highest %FY and lowest average annual yields the total commercial volume decreased.

4.3 Functional group composition

After logging once the abundances of all functional groups returned in all scenarios to values similar to base-line values (table 7, figure 3). Functional groups P2, LP1, and LP3 appeared least affected by logging: although for P2 this is likely due to the very low abundances (< 6 stems ha^{-1}). From the calculated average return times in table 7 it appears that group LP 2 was also hardly affected, but figure 3 showed that after a first return after approximately 20 years, the abundances in the logged scenarios became higher than for the base-line simulations. The response of this group is thus similar as for the pioneers P1 and P3, but slower (figure 3). The pioneers P1 and P3 and the climax groups C1 and C2 had the longest return times, but the reasons were different. For the pioneers it takes long before they decrease to no-logging abundances, while for the climax groups it takes long before they increase to no-logging abundances.

Although at the end of all logging once simulations functional group composition was similar to the base-line situation, shifts in species composition within functional groups may have occurred. In a long-term large-scale survey ter Steege *et al.* (2002) found that neither the functional group composition nor diversity had changed significanlty over 75 years of harvesting with an average total harvest intensity of 7.9 trees ha^{-1}. The impact of harvesting in the past was likely to be less severe (logging until the late sixties took place using axe and oxen, instead of chainsaws and heavy extraction machinery) than present day harvesting as simulated with the model. Yet the effect on functional group composition was comparable to the effects found in the present study. Hence, it is likely that also long-term effect of the simulated logging scenarios on diversity may be limited. With the current model, species diversity cannot be evaluated, however.

As could be expected, repeated disturbance by logging is especially favourable for the small pioneers P1. This group showed the fastest and strongest responses to increased HI and shorter FC. The tall pioneers (P3) did respond slower, but still increased in abundance. The long-lived pioneers had an intermediate response to logging as they were generally able to recruit sufficiently to replace killed trees within one cycle. These results are consistent with general notions about forest succession after disturbance and gap dynamics (*e.g.* Horn 1974, Brokaw 1985,Swaine & Whitmore 1988, Finegan 1996, Peña-Claros 2003). The climax species on the other hand generally were not able to replace lost trees within one felling cycle. Although for most scenarios the functional group composition just before the third and last harvests was different from the base-line simulations these changes were generally rather small. These changes were, however, always determined at the end of a felling cycle, which for all functional groups is the moment within a felling cycle that the abundances are closest to the no-logging situation. Hence the differences in functional group composition will be much larger earlier in each felling cycle.

4.4 Determining factors

Return times for the commercial volume at single logging scenarios were often explained by an interaction between MFD maximum allowed HI. This can bee explained by the fact that the actually realised HI were much higher for the MFD of 35 cm than for the MFD of 60 cm (figure 1). For the scenarios with maximum allowed HI of 4 there were no differences among the two MFD, but at the higher maximum allowed HI, MFD 60 restricted the realised HI. Consequently these two factors were not independent from each other, which most likely led to the observed interactions. Usually FC and HI were the most important factors for determining the differences in (levels of sustained) yields and functional group composition among the simulated logging scenarios. Hence, it appears that the only effect of MFD is just a further restriction on maximum allowed HI that is determined by the quality of the forest. In practice MFD is more versatile for application in yield regulation and planning. However, if MFD is used as criterion for yield regulation the actually harvested yield depends largely on the quality of the forest and therefore is less predictable than with yield regulation that only uses HI.

It should be stressed, however, that MFD also has other important applications that were not further explored in this study. High MFD guarantees, for instance, that sufficient seed-trees remain standing in the forest after logging. These trees are important for the necessary input of seeds for regeneration (*e.g.* van Ulft 2004). Trees of commercial species found in our research area become reproductive from a minimum DBH of approximately 25 to 35 cm (van Ulft 2004). For Greenheart the minimum reproductive size was 35 cm DBH, while the DBH at which 50% of the trees would be reproductive, was 65 cm (van Ulft 2004). With a MFD of 35 and no other regulations for seed trees this means that potentially a significant part of the seed producing trees could be harvested. As a consequence management regimes with higher MFD allow these seed trees a longer period of time to produce and disperse seeds, which may be important on the long term regeneration (*e.g.* Peres *et al.* 2003). Because in the ecological model (see chapter 3) tree recruitment is not dependent on the abundance of seed trees a potential effect of changes in MFD may have been missed. On the other hand, for the slowest growing functional groups (to which the most valuable timber species generally belong), seedlings of climax species need on average 68 years to grow from a seed to 2 cm DBH (see chapters 3 and 5), although this may be considerable faster if they grow in gaps. Hence for these groups the effect of a reduction in seed input would only become apparent in the smallest modelled size classes after these 68 years. Then, based on a rough calculation using the 90-percentile growth rate (see chapter 2) it would take climax species again 72 years before they would reach a size of 20 cm DBH. Hence, within three felling cycles it is not likely that a reduction in number of seed trees will have large effects on commercial volumes, but it may have effects on the abundances and composition of the functional groups. Hence the effects on functional group composition as found in the projections with the current simulation model may be underestimated.

4.5 Conclusions

Forest managers and decision makers can use the results of the simulated logging scenarios to decide on what would be the most desirable logging practices. For instance, mean ranks of %FY, total yields, average annual yields, and values of the *G* statistics describing effects on functional group can be used as input for multiple criteria analyses. The most important deliberations that have to be made then are how to value each of these silvicultural and ecological effects. Obviously, maximisation of total yields on short periods of time and conservation of functional diversity or sustained yields are conflicting scenarios. In addition also socio-economic considerations should be taken into account, as we only focused on the ecological and silvicultural consequences.

The results of this study show that it is possible manage the forest in a way that results in relatively small changes in functional composition and still achieves more or less sustained yields. From scenarios with a felling cycle of 60 years, all would more or less qualify. From the rank orders of the scenarios with FC 60 all would more or less qualify for sustainable forest management. Yet within this set of scenarios there is still a trade-off between productivity and sustainability, *i.e.* scenarios with highest yields have the lowest %FY and strongest effects on functional group composition. To minimise the effects of logging on long-term regeneration of harvested species a minimum felling diameter of 60 cm should be used.

On the long-term functional group composition appeared to be not much affected by logging. Hence, we conclude that also logged forests in Guyana have still high conservation values. Nevertheless, the times after logging needed to return to commercial volumes and abundances of functional groups that would be similar to non-logged forests may take as much as 100 to 120 years, which is twice the current felling cycle of 60 years.

Therefore logging the forest once (potentially with high intensities) and then leave it alone as proposed before by *e.g.* Cannon *et al.* 1998b and Rice *et al.* 1998 might be taken in to consideration as well by decision makers. Much would dependent on what happens to the forest after it is abandoned by loggers. Argument against this management option is that forests from which loggers withdraw have higher probabilities of being converted into agricultural land (*e.g.* Pearce *et al.* 2003 and references herein). In Guyana, however, population pressure is very low. Hence large-scale conversion of forest areas to other land-uses like pastures, cattle ranging or oil palm and soy bean plantations is not occurring. Most agriculture is concentrated in the coastal zone where the majority of the less than 800 thousand inhabitants of Guyana live. In the interior of Guyana only small scale agriculture is practised by small indigenous communities. Other problems might arise from a financial perspective. Loggers may be concerned with the total profits that can be made from a certain area of forest. If the total yields from the scenario with the highest %FY over three felling cycles of 60 years are compared with the yield of logging once with a harvest intensity of 12 trees ha^{-1}, the differences appear to be relatively small (54 m^3 h^{-1} vs. 44 m^3 h^{-1}), especially if we take into account higher costs associated with multiple harvests compared to single harvests. Taking into account the rather small long-term effect at logging once 12 trees ha^{-1}, it may be expected that logging once with higher harvest intensities may be possible without major long-term consequence for forest composition. Additional research would be needed to validate this, however.

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Chapter 5

The significance of variable and auto-correlated juvenile tree growth for simulation of tree recruitment: an exploration of the consequences for nine functional groups of rain forest trees in Guyana

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Abstract

Population dynamics models for tropical rain forests rarely include detailed descriptions of regeneration. In this chapter we describe models for juvenile tree (seedlings and saplings < 2 cm DBH) growth and juvenile mortality that were included in a forest simulation model that also includes seed production, seed dispersal and germination. Growth of juvenile trees in relation to competition index was very variable. Many seedlings showed reductions in stem height that are not related to light availability, but probably are the result of falling debris, browsing, herbivory and dieback due to pathogens and pests. These effects can be regarded as rather stochastic processes (from a seedling's point of view). Therefore we developed a modelling approach that can accommodate stochastic variation in growth and temporal auto-correlation. We then evaluate the significance of stochastic variation and auto-correlation for the fraction of recruits that will successfully recruit to 2 cm DBH using simulated growth trajectories and explore the differences between nine functional groups of species.

Faster growing seedlings had a higher probability to survive the time needed to reach 2 cm DBH than slower growing seedlings from the same functional group. Hence the seedlings that reach a size of 2 cm DBH on average have grown faster than the other seedlings. In a traditional modelling approach, however, all seedlings that grow at a certain light availability grow according the average of all seedlings at that light availability. Thus seedlings that normally would grow faster (by chance) and reach 2 cm DBH will then grow slower, which reduces their survivorship and *vice versa* for individuals that normally grow slower because of a random reduction in stem height for instance. Inclusion of the stochastic variation in growth resulted in two clear patterns. For functional groups that had a relatively slow growth rate in relation to their annual mortality probability the inclusion of stochastic mortality resulted in a higher survivorship (increased fraction of the individuals reached 2 cm DBH) than with the average model, while functional groups that had a relatively fast growth rate in relation to their annual mortality probability showed the opposite pattern (decreased survivorship). Hence, allowing stochastic variation in growth rates has important consequences and leads to significantly different results than the average model. Total auto-correlation did significantly affect these patterns, but the degree of auto-correlation comparable with field data had no major affect on the model results. Estimated mean ages for juveniles at 2 cm DBH, based on the growth trajectories including stochastic variation in growth and including mortality, ranged from 7 years for small pioneers to 68 years for the understorey climax group. The 2.5 % fastest growing juveniles reached a size of 2 cm DBH already at 4 and at 45 years, respectively.

1 Introduction

Many individual based models for forest dynamics include spatially explicit distribution of juveniles (seedlings and saplings, *i.e.* trees smaller than 2 cm DBH)) but only few include seedling dynamics (*i.e.* growth and mortality of seedlings). For instance, SORTIE (Deutschman *et al.* 1997) uses spatially explicit dispersal of saplings of a specified size, while other individual based models use spatially dispersed seeds and allocate a certain probability to these seeds to establish as saplings (*e.g.* Chave 1999, Köhler 2000).

The spatial distribution patterns of seeds that are generated by dispersal are important determinants of the spatial arrangement of trees in the forest. In the tropical forest understorey light is generally limiting tree growth. Light availability is spatially and temporally heterogeneously distributed. Differences in survival characteristics and competition for light among individuals with different life-history strategies (Veneklaas & Poorter 1998) will determine which species will attain maturity at a certain spatial position in the forest (Clark & Clark 1992). At places with high light availability fast growing pioneer species generally out-compete juveniles from other groups because they are able to grow faster, while at places with low light availability juveniles from shade tolerant species will be most successful because they have higher survival abilities at low light.

SYMFOR is a software framework for ecological and management models relating to species rich tropical forests (Phillips & van Gardingen 2001a, 2001b, Phillips *et al.* 2002, 2003, 2004, chapter 2). Models within SYMFOR have been applied in Indonesia and Guyana to analyse the sustainability of alternative management scenarios (van Phillips *et al.* 2003, van Gardingen *et al.* 2003, chapter 4). For recruitment these models use an approach, where the probability of a new tree becoming established (*i.e.* appearance at the minimum DBH threshold) in a specific subplot was a function of a competition index (Phillips *et al.* 2003, 2004, chapter 3).

Here we describe the development of models to simulate population dynamics for juvenile tree (<2 cm DBH) in a new recruitment module that is included in a version of SYMFOR for Guyana (van Ulft 2004a). This new recruitment module also includes seed production, seed dispersal (van Ulft 2004a) and germination (van Ulft 2004b), but these processes are not further elaborated in this chapter. Light availability is generally assumed to be the main factor that limits growth of juveniles in forests (*e.g.* Whitmore 1996). But the spatial and temporal pattern of light availability is difficult to quantify. Therefore we model height growth and survival as dependent on a relatively simple competition index as a proxy for light availability. Apart from light availability a number of stochastic processes affect the net realised height growth of juveniles. These include reduction in stem height as a result of falling debris, browse and herbivory and subsequent resprouting (Paciorek *et al.* 2000, Ickes *et al.* 2003). Also differences in genetic background add to variation in growth that cannot be explained by light.

Typically in tree growth models the relation between the explaining variable(s) and growth rate is calibrated by (multiple) regression models. The resulting function then enables the calculation of an average growth rate for each value of the regulating variable. In our case competition index serves as such. This approach, however, neglects the stochastic variation and autocorrelation in growth. Juveniles will then always grow according to the average growth function.

It is often assumed that only faster growing individuals are able to escape high mortality probabilities in the juvenile size classes and reach maturity (Primack *et al.* 1985, Liu & Ashton 1995). The longer an individual takes to reach a certain size, the higher is the cumulative probability that it dies before it reaches that size. Hence, we expect that models that use average growth rated do not provide a realistic picture of the numbers of individuals that will reach a certain size at a certain age. The magnitude of potential under or overestimation of the proportion of seedlings reaching the specified size will depend on the annual average growth rate relative to the annual survival probability of seedlings and saplings.

In this chapter we analyse growth and survival patterns of juveniles that are classified into different functional groups. We describe a growth modelling approach that includes stochastic variation and autocorrelation and we compare the results with a model based on average growth rates. For this comparison we 1) simulate growth trajectories, 2) evaluate differences in ages of juveniles when they reach 2 cm DBH (residence time in juvenile size class), 3) determine cumulative survival probabilities over the residence times and 4) determine the proportion of individuals that actually reach 2 cm DBH when mortality is included in simulations of growth trajectories. Finally we show the consequences for simulated population dynamics and species composition of adult trees, using the different approaches for modelling seedling growth while leaving all other modelled processes equal.

2 Methods

2.1 Study area

For the analyses and model calibration we used data from 15 experimental sample plots (ESP) in the West-Pibiri compartment of Demerara Timbers Ltd.'s logging concession, approximately 50 kilometres south of Mabura Hill in Central Guyana (5°02' N, 58°37' W) (van der Hout 1999). Each ESP measures 140 x 140 m (1.96 ha). The plots were set up in 1993, and covered five different intensities of reduced impact logging: control without intervention, low intensity reduced impact logging (4 trees ha^{-1}), moderate intensity (8 trees ha^{-1}), high intensity (16 trees ha^{-1}) and moderate intensity logging followed by a post-harvest liberation thinning (see van der Hout 1999, 2000 for more details). Reduced impact logging was carried out in 1994. Although the different logging intensities are no direct subject for this current study, they guarantee a wide range of understorey light conditions that match the range from undisturbed to heavily disturbed forests.

The plots are in mixed Greenheart (*Chlorocardium rodiei*) forest (Ek 1997, van der Hout 1999), that is dominated by 8 tree species that account for roughly 45% of the trees with diameter at breast height (DBH, *i.e.* diameter at 1.3 m height) larger than 5 cm (chapter 2). The soils in this area belong to the well drained brown sand series with a moderate to high percentage of clay (Ferralsols) (van der Hout 1999, van Kekem *et al.* 1995). The average annual rainfall in the period 1996-2000 was 2772 mm (van Dam 2001).

2.2 Measurements

In the central 1 ha of each ESP, seedlings and saplings from 0.3 m height to 2 cm DBH were enumerated and measured in 25 subplots of 4 m^2 (totalling 0.01 ha per plot) that were positioned in a fixed pattern (see van der Hout 1999, 2000). The first census took place at the end of 1995 and re-censuses followed after two (1997) and five years (2000). At each census survival was recorded and the height to the highest point was measured without straitening of the seedling and if applicable (*i.e.* saplings > 1.3 m height) the DBH of seedlings was measured at the same point of measurement as in previous years. New recruits > 0.3 m height were enumerated and measured.

2.3 Model introduction

SYMFOR is a spatially explicit individual based modelling framework implemented in visual C++. Below we describe the inference and calibration of height growth and survival models for juveniles (seedlings and saplings up to 2 cm DBH). Using simulated growth trajectories we evaluate three different approaches to model juvenile height growth as function of competition index: (1) average growth model, (2) growth with explicit inclusion of stochastic variation and (3) growth with stochastic variation and auto-correlation explicitly included. The model uses functional groups rather than individual species. To decrease simulation time in SYMFOR all juveniles of a functional group that establish in the same subplot of specifiable area at the same time step will be clumped in one cohort. All juveniles of the same cohort in one subplot will grow with the same rate while mortality reduces the number of individuals in one cohort. When saplings reach a size of 5 cm DBH all remaining individuals in a cohort will become individual trees and randomly get a position within the same subplot where the cohort was in.

2.4 Functional groups

Since most tree species in the forest are very rare it is not possible to calibrate the growth model for all species separately. Therefore species are grouped into functional groups of species with similar ecological characteristics. We subjectively classified all species into nine functional groups based on differences in the following three morphological characteristics: wood density, seed mass and adult stature, which we believe are predictors of species' responses to disturbance in terms of recruitment, survival and growth. Wood density is a good proxy for maximum potential growth rate (Verburg & van Eijk-Bos 2003, ter Steege *et al*. 2003), seed mass is correlated with recruitment success and early survival of a species (*e.g.* Foster & Janson 1985, Hammond & Brown 1995, Boot 1996, Rose & Poorter 2003, but see Grubb 1996), while adult stature is a measure for environmental conditions that are needed for a tree to reproduce. We used wood density and seed mass to quantify three life history strategies (pioneers, long-lived pioneers and climax species) as was done in chapter 2, and we subdivided these life history groups in three subgroups each, depending on adult stature (small, medium and tall stature, which relate to understorey, canopy and emergent positions in closed forests) (table 1).

In the final SYMFOR model that also includes dispersal processes (see van Ulft 2004a) these nine functional groups are again further subdivided in wind and non-wind dispersed groups. Because the combination of small stature and wind dispersal hardly occurs, this classification results in fifteen groups. We assume, however that dispersal type does not affect juvenile growth and survival. Therefore growth and survival functions are the same for functional groups with the same life history and adult stature characteristics, irrespective of dispersal type. In most of this chapter we use the functional groups as outlined in table 1. The full fifteen functional groups only show up in the example simulations in SYMFOR, which illustrate the effect of the different juvenile growth modelling approaches for adult stand dynamics.

Pioneer species are very rare in the studied forest (chapter 2). Even after classification into functional groups there were too few individuals in the medium and tall stature pioneer

Table 1 Limits for wood density (g cm^{-3}, Low: < 0.8 g cm^{-3}, High: ≥ 0.8 g cm^{-3}), seed mass (g, Low < 0.1 g, High: ≥ 0.1 g) and maximum height at maturity (small (understorey): < 25 m, medium (canopy): 25 – 35 m, tall (emergent): ≥ 35 m) for the classification of nine functional groups. The coding is used to facilitate references to the functional groups in other tables and figures. The letters of the codes refer to the life history strategies: Pioneers (P), Long-lived pioneers (LP) and Climax (C), while the accompanying numbers refer to adult stature: small (1), medium (2) and tall (3).

Functional groups		Wood Density (g cm^{-3})	Seed Mass (g)	Max. Height (m)	Coding
Pioneers	small	Low	Low	<25	P1
	medium	Low	Low	25−35	P2
	tall	Low	Low	≥ 35	P3
Long-lived pioneers	small	Low	High	<25	LP1
	medium	Low	High	25−35	LP2
	tall	Low	High	≥ 35	LP3
Climax	small	High	All	<25	C1
	medium	High	All	25−35	C2
	tall	High	All	≥ 35	C3

groups for rigorous calibration of growth and survival functions and for comparisons of mean growth rates and survival probabilities with other functional groups. Therefore we combined the three pioneer groups for these analyses. In the model these three groups will have the same growth and survival properties, but will still differ in allometric and size dependent relations (*e.g.* initial size after germination and height at which a sapling reaches 2 cm DBH).

2.5 Descriptive statistics for growth and survival

For basic understanding of the differences among the functional groups we first calculated for each functional group several descriptive statistics for height growth and survival probability. We determined the mean plus standard error, median and 95-percentile height growth rates based on all height growth observations. We tested for differences in mean growth rates among functional groups using a Kruskal-Wallis test followed by Dunn-type post-hoc tests for nonparametric multiple comparisons with unequal sample sizes and correction for tied ranks (see Zar 1999).

We calculated survival probabilities (P_s) based on observed survival from the first census till the latest census (5 years interval) using the approach proposed by Sheil *et al.* (1995) to get annualised survival probabilities P_s:

$$P_s = \left(\frac{N_S}{N_T} \right)^{\frac{1}{t}} \tag{1}$$

where N_T and N_S are counts of individuals that are alive at the start and end of the census interval with length t (5 years).

We calculated binomial 95% confidence intervals of survival and we tested for differences in survival probabilities among functional groups using Tukey-type multiple comparison tests for proportions with unequal sample sizes (see Zar 1999). We tested the relationship between annual height growth rates and annual survival probabilities of functional groups using product-moment correlation analysis.

Within each functional group we determined the degree of auto-correlation in growth rates between the two growth intervals of individuals through product-moment correlation analyses of growth rates of individuals in the first growth interval against that in the second interval. As auto-correlation is not to be expected for individuals that show negative growth through for example (stochastic) stem breakage, we inferred the degree of auto-correlation by omitting the individuals that showed negative growth in at least one of the two growth intervals.

Table 2 Per functional group the initial height (in m) after germination (H_0) is given, inferred from seed mass through the relation between initial height after germination and average seed mass of species in the functional group as defined by Rose & Poorter (2003) and the height (in m) at which the juveniles reach 2 cm DBH (H_2) based on the allometric height - DBH relation given by chapter 3.

FG	H_0 (m)	H_2 (m)
P1	0.05	3.53
P2	0.06	3.95
P3	0.03	4.88
LP1	0.12	3.53
LP2	0.29	3.95
LP3	0.27	4.88
C1	0.18	3.91
C2	0.28	4.37
C3	0.26	5.72

2.6 Allometry

In the model, after germination (see van Ulft 2004b) seedlings have a certain initial height with which they start growing. Because we have no data on initial sizes after germination, we used a functional relationship between seed mass and initial height based on data from a literature compilation by Rose & Poorter (2003) to determine initial seedling height (table 2).

When saplings reached 2 cm DBH in the field, DBH growth was measured in stead of height growth. This switch is also built in the model. To determine at which height seedlings reach 2 cm DBH we used an allometric function that describes the relationship between DBH and height based on data of trees of all sizes (table 2, see also chapter 3)

2.7 Competition index

An initial evaluation of height growth rates for each functional group showed that height growth did not directly depend on current heights of juveniles. Therefore in the models, juvenile growth is only regulated through an asymmetric competition index that gives a measure for the amount of available light for individuals. We based this index on the assumptions that an individual experiences stronger competition for light (but also other resources) as more and taller neighbours are standing closer by, and that stronger competition, *i.e.* a higher competition index, means less resource availability. Other studies show that the best prediction of growth rates is obtained with distance and size dependent competition indices (*e.g.* Gourlet-Fleury 1998, Moravie *et al.* 1999, de Graaf 2001, Phillips *et al.* 2003)

The competition index (C_G) that we used consists of two parts (equation 2):

$$C_G = G + O \qquad (2)$$

The first part (G) describes the competition effect caused by trees larger than 20 cm DBH, for which we know exact positions in the forest. It is based on the canopy closure index (G) as defined by Lieberman *et al*. (1989, 1995) (equation 3):

$$G = \sum_{j=1}^{n} \left(\frac{H_j - H_i}{d_{ij}} \right) \text{ if } (H_j > H_i \text{ and } D_j \geq 20 \text{ cm}) \tag{3}$$

where n is the number of taller neighbours j within a radius of 15 m with height H_j and DBH D_j, H_i is the height of the subject tree i and d_{ij} is the distance between the top of the subject tree i and the top of its jth taller neighbour. Because for individuals of the smaller size classes no exact coordinates are available we calculated distances with neighbour trees from the centre of the subplot.

The second part (O) of the competition index C_G is based on the sum of the height differences with overtopping neighbours smaller than 20 cm DBH that are standing in the same subplot as the subject tree and it was standardised for subplots of 25 m^2 (equation 4):

$$O = \sum_{k=1}^{n} \left[\frac{25}{a_p} \left(H_k - H_i \right) \right] \text{ if } (H_k > H_i) \tag{4}$$

where n is the number of taller neighbours k within the same subplot with height H_k and H_i is the height of tree i and a_p is the area of the subplot

2.8 Growth models

We evaluate the following three different growth-modelling approaches:

1. Average growth rate
   All juveniles grow according to an average growth function. We modelled average seedling height growth (I_μ) as a negative exponential function of competition index (C_G) (equation 5). This negative exponential function was used because this matched relatively well with the data and only uses few parameters in comparison to other more complex statistical functions. It is based on the ecological assumption that growth rate decreases with increasing competition index.

   $$I_\mu = p_0 \cdot \mathrm{e}^{(-p_1 \cdot C)} \tag{5}$$

   where p_0 and p_1 are functional group specific parameters and C is the competition index (C_H for simulations of growth trajectories (see below) and C_G in SYMFOR, also in all following equations that include competition index).

2. Stochastic growth

   In this approach juveniles grow according to a growth rate that is randomly drawn from a Gaussian distribution N($\sigma \mid \mu$) with competition index dependent mean growth rate (I_μ, equation 5) and competition index dependent standard deviation I_σ. We estimated this standard deviation of the growth rate by equation 6 (below) that we fitted through the absolute values of the residuals around the mean growth rate.

   $$I_\sigma = s_0 \cdot \mathrm{e}^{(-s_1 \cdot C)} \tag{6}$$

   where s_0 and s_1 are functional group specific parameters and C is the competition index.

   The actual height growth rate (I) of a modelled individual is then given by equation 7:

   $$I = I_\mu + z \cdot I_\sigma \tag{7}$$

   where z is the z-score (normal deviate) that on every time step is randomly drawn from a standard Gaussian distribution. This z-score tells us how many standard deviations from the mean a specific value is located. For the random draw of the z-score in the model we used the approximation algorithm provided in Press *et al.* (1992) with minor adaptations for use in C++. Because z-scores can vary between –infinity and +infinity also simulated growth rates could vary between –infinity and +infinity. Therefore we restricted z-scores between –3 and +3 (in a normal distribution more than 99% of values lie within $\mu \pm 3\sigma$) to keep growth rates within a realistic range. If drawn z-scores are outside the restricted range they are set to the nearest range limit.

3. Stochastic growth with “auto-correlation”

   Juveniles grow according the stochastic growth function as above, but additionally with explicitly modelled auto-correlation of growth. Again as in the stochastic growth function, at each time step a z-score is randomly drawn from a standard Gaussian distribution. For a newly germinated juvenile the first drawn z-score that results in positive growth forms the basis for the deviation from the average growth rate. If this z-score results in a negative growth rate, then just this z-score is used because we don’t expect auto-correlation of growth if stochastic processes that lead to stem breakage are involved. If the resulting growth rate is positive, this z-score is averaged with the z-score used in the most recent year with positive growth rate. This averaging of z-scores leads to auto-correlation in z-scores between years. We varied the amount of auto-correlation in z-scores by varying the weighting of current year’s z-score in the averaging, *i.e.* we varied how often this year’s z-score is included for calculation of the average z-score. We used the following weighting values of z-scores in relation to that of the previous year with decreasing amount of auto-correlation: zero times (*i.e.* full auto-correlation), 0.5 times, twice and three times. Per functional group we qualitatively evaluated the resulting amount of auto-correlation against the amount of auto-correlation that we found between two growth intervals in the field data. Subsequently for each functional group we use the weighting values for z-scores that give the amount of auto-correlation that best corresponds with the auto-correlation found in the field data as best auto-correlated model.

2.9 Survival model

We derived a competition index dependent function for annual survival probability (*S*) using a logistic regression model in combination with Sheil *et al.*'s (1995) approach, which resulted in equation 8,

$$S = \left(\frac{e^{(m_0 + m_1 C)}}{1 + e^{(m_0 + m_1 C)}} \right)^{\frac{1}{t}} \tag{8}$$

where m_0 and m_1 are functional group specific parameters, C is the competition index and t is the length of the census interval.

2.10 Growth trajectories

To evaluate differences among different growth modelling strategies we simulated growth trajectories (see Lieberman & Lieberman 1985, Lieberman & Lieberman 1987, Korning & Balslev 1994, Zagt 1997) for seedlings between initial height after germination and the height at 2 cm DBH through projection of growth rates. We let virtual juveniles grow with annual increments based on the different growth modelling approaches (average, stochastic, stochastic with full auto-correlation and stochastic with best autocorrelation). Additionally, each time step the survival probability for juveniles is determined based on the survival model. For each growth modelling strategy we simulated 1000 growth trajectories per functional group. To determine the number of juveniles (out of the 1000 that were simulated) that would reach 2 cm DBH we included mortality in the simulations by comparing at each time step the survival probability of a juvenile with a random number between 0 and 1 to determine whether the juvenile would have died. Virtual juveniles that would have died continue to grow to enable comparisons of ages and growth rates between individuals that reach 2 cm DBH alive and those that die before they reach this size.

With these growth trajectory simulations we evaluated, between growth modelling approaches, for each functional group the differences in age at 2 cm DBH (residence time in this size class) and cumulative survival probabilities over the residence times. Additionally we evaluated for each group the differences among the models in numbers of individuals that are alive when they reach 2 cm DBH based on 1000 simulations that included mortality.

For evaluation of differences among growth modelling approaches we repeated each simulation of 1000 growth trajectories 100 times. For each functional group we made comparisons among the different growth modelling approaches for 2.5 percentile, median and 97.5 percentile ages at which juveniles reach 2 cm DBH, based on mean values of these percentiles of 100 runs. We did the same for the cumulative survival probabilities during the residence time in the juvenile size class (<2 cm DBH). Because the average growth modelling approach gives always the same result for the 100 repetitions the mean values of the percentiles will show no variation. Therefore we tested for differences among the groups using the non-parametric Kruskal-Wallis ANOVA with Tukey-type Nemenyi post-hoc tests for multiple comparisons (Zar 1999).

Again based on 100 repeated runs we calculated for each functional group per modelling approach the mean number of individuals that were alive when they reached 2 cm DBH and compared these mean numbers among the modelling approaches. We tested for differences using one-way ANOVA with Tukey HSD post-hoc tests for multiple comparisons.

Because the surrounding forest is not simulated in the growth trajectory simulations, we inferred a functional group specific relation between the height of seedlings and their competition index (C_G) using regression analyses on field data. The underlying assumption is that higher seedlings will generally experience less competition from neighbours, because there are fewer neighbours that are taller. From several statistical functions that we tested, a simple negative exponential function appeared to be the most parsimonious for the relation between competition index (C_H) and height (H):

$$C_H = c_0 \cdot \mathrm{e}^{(-c_1 \cdot H)} \tag{9}$$

where c_0 and c_1 are functional group specific parameters

In SYMFOR trees that die have a certain probability to fall in a random direction. Fallen trees cause additional catastrophic (competition independent) mortality for juveniles below the fallen trunk and crown. This process is not explicitly simulated in the growth trajectory simulations. Based on the field data we determined that on average each year 0.4% of the juveniles were killed by catastrophic events like falling trees and branches. Therefore, for each individual, we subtracted this catastrophic mortality probability from the annually calculated survival that is dependent probability competition index.

2.11 SYMFOR simulations

Finally we evaluate how the four different approaches of modelling juvenile height growth affect the dynamic composition of adult tree populations in simulations with SYMFOR. With each juvenile growth modelling approach we simulated 1 ha of forest for 250 years and repeated this 25 times. Based on these 25 repetitions per modelling approach we determined for each functional group the mean number of trees > 5 cm DBH that were present in the simulated forest at year 250. Subsequently we compared for each functional group the differences in this mean number of trees > 5 cm DBH using one-way ANOVA. Except the juvenile growth functions, all other processes in the model were kept the same for all simulations.

2.12 Statistics

We did most statistical analyses and parameter estimations using the SPSS (2001) statistical software package. Dunn and Nemenyi post-hoc tests for Kruskal-Wallis ANOVA and Tukey-type multiple comparison tests for proportions were carried out using spreadsheets based on Zar (1999).

3 Results

3.1 Descriptive statistics for growth and survival

Descriptive statistics for height growth rates and annual survival probabilities for juveniles of the different functional groups are presented in tables 3 and 4. In figure 1 we plotted the mean height growth rate of functional groups against their annual survival probability. Because of the relatively large variance in mean growth rate and survival probabilities most of the differences among the groups were not significant. Pioneer juveniles (P1-P3), however, grew significantly faster than those of all other groups (figure 1, table 3, Dunn test $P<0.01$), but had a relarively low survival probability (figure 1, table 4). The small and medium sized climax groups (C1 & C2) had the lowest growth rates, followed by the small long-lived pioneer group (LP1) (figure 1, table 3). On the other hand, the smallest climax and long-lived pioneer groups (C1 & LP1) showed the highest annual survival probabilities (figure 1, table 3, Tukey-type test for proportions with unequal sample sizes $P<0.005$).

Table 3 Descriptive statistics and multiple comparisons among the functional groups (FG) for growth rate (m yr^{-1}). For coding of groups, see table 1. The groups P1, P2 and P3 are combined (P1-P3). The descriptive statistics are: mean growth rate ± s.e., range of growth rates from minimum to maximum, median growth rate (50%), 95 percentile growth rate (95%) and total number of growth observations (n). We tested for differences in mean growth rates among groups using a Dunn-type test for nonparametric multiple comparisons with unequal sample sizes and correction for tied ranks. Significant differences (sig.) are marked with different letters ($P<0.01$).

FG	Growth rate (m yr^{-1}) mean ± s.e.	range	50%	95%	sig.	n
P1-P3	0.454 ± 0.054	-0.473 – 2.082	0.223	1.682	d	94
LP1	0.062 ± 0.008	-1.709 – 1.106	0.053	0.375	ac	637
LP2	0.09 ± 0.006	-1.126 – 1.829	0.078	0.462	c	1032
LP3	0.137 ± 0.029	-0.625 – 2.217	0.079	0.761	bc	132
C1	0.052 ± 0.005	-1.078 – 1.108	0.027	0.335	a	1172
C2	0.059 ± 0.003	-1.868 – 1.958	0.053	0.317	ba	3214
C3	0.086 ± 0.016	-0.777 – 1.256	0.053	0.473	ac	204

Table 4 Descriptive statistics and multiple comparisons among the functional groups (FG) for survival probability (yr^{-1}). For coding of groups, see table 1. The groups P1, P2 and P3 are combined (P1-P3). The descriptive statistics for survival probability are: total number of individuals at the start of the census interval (N_T), number of individuals that survived the 5 years long census interval (N_S), survival probability (P_S: $(N_S/N_T)^{1/5}$) and binomial 95% confidence interval (95% CI) for P_s. We tested for differences in survival probabilities among the groups using a Tukey-type multiple comparison test for proportions with unequal sample sizes. Significant differences (sig.) are marked with different letters (P<0.005).

FG	N_T	N_S	P_S (yr^{-1})	95% CI	sig.
P1-P3	41	23	0.891	0.832 - 0.935	a
LP1	300	254	0.967	0.957 - 0.976	bc
LP2	596	363	0.906	0.894 - 0.917	a
LP3	69	38	0.888	0.844 - 0.924	a
C1	534	457	0.970	0.962 - 0.976	c
C2	1719	1152	0.923	0.917 - 0.929	a
C3	98	70	0.935	0.907 - 0.957	ab

There was no significant linear correlation between mean growth rate and survival probability if the combined pioneer groups were included in the analysis (figure 1, r=-0.59, d.f.=5, n.s.). If we, however, omitted the combined pioneer groups (P1-P3) from the analysis, growth and survival were negatively linearly correlated (figure 1, r=-0.83, d.f.=4 and P<0.05). Although there appears to be a trade-off between growth and mortality these results suggests that for pioneer juveniles the survival probability in relation to its growth is relatively higher than expected from the trend in this relation.

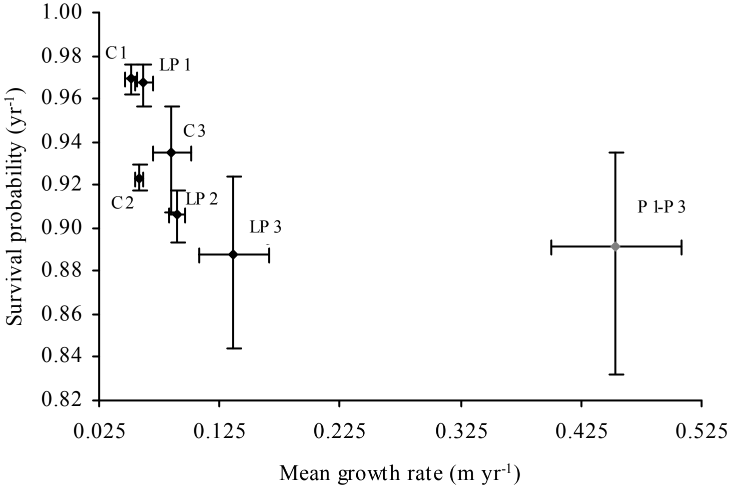

Figure 1 Mean height growth rate (m yr^{-1}) vs. annual survival probability (yr^{-1}) is given per functional group (see table 1 for coding). The three pioneer groups (P1-P3) are combined (see text on functional groups). The vertical error bars show the binomial 95% confidence limits (Zar, 1999) for the survival probabilities and the horizontal error bars represent the standard errors for the mean growth rates.

3.2 Growth models

Growth rates in relation to competition index were very variable, especially at low competition indices. Figure 2 illustrates this for juveniles of the pioneer groups combined (P1-P3) and for the medium stature climax group (C2). Table 5 presents for each functional group the fitted parameters for the average growth (equation 5) and estimated standard deviation (equation 6) models. For the average growth model, the amounts of variation explained by competition index were rather low (R^2 in table 5). In figure 2c we show the corresponding graphs of the fitted average growth parameters for all functional groups together.

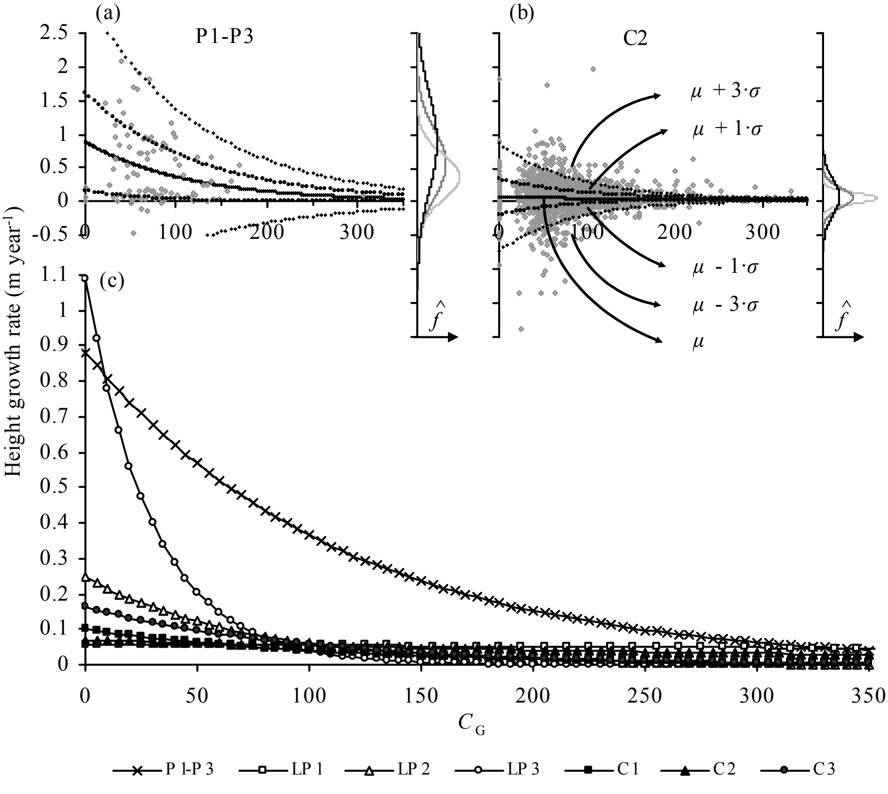

Figure 2 Juvenile height growth rates (m year^{-1}) in relation to competition index (C_G). (a) Shows the result for functional groups P1 to P3 combined (n= 94) and (b) that for group C2 (n=3214) as examples. See table 1 for coding of the groups. Open grey diamonds are field data. In each graph the solid line represents the fitted average growth model (μ, equation 5) and the dashed lines represent $\mu + 3 \cdot \sigma$, $\mu + 1 \cdot \sigma$, $\mu - 1 \cdot \sigma$ and $\mu - 3 \cdot \sigma$ (see equations 6 and 7). To the right of graphs (a) and (b) are the corresponding normal probability density functions for growth rates as used for the random draws of stochastic growth rates at C_G values of 0 (black), 50 (dark grey) and 100 (light grey). Graph (c) shows the average growth rates (μ) in relation to C_G for all groups in one graph for comparison.

Table 5 Per functional group (FG) parameter values for the average growth model (I_μ, equation 5), the standard deviation for this growth model (I_σ, equation 6), the logistic survival model (*S*, equation 8) and the height depended competition model (C_H, equation 9) are given. Next to the parameters of each model are the associated goodness of fits (R^2) and numbers of data points (n) used for parameterisation.

FG	I_μ			I_σ			I_μ & I_σ
	p_0	p_1	R^2	s_0	s_1	R^2	n
P1-P3	0.8838	0.0088	0.07	0.7293	0.0077	0.16	91
LP1	0.0591	0.0007	0.00	0.3199	0.0151	0.06	600
LP2	0.2471	0.0142	0.02	0.4050	0.0173	0.10	973
LP3	1.0882	0.0334	0.12	0.8009	0.0227	0.13	123
C1	0.0991	0.0092	0.01	0.2782	0.0134	0.08	1112
C2	0.0699	0.0026	0.00	0.2644	0.0118	0.06	3065
C3	0.1625	0.0105	0.01	0.4937	0.0181	0.15	193

Table 5 Cont'd

FG	*S*				C_H			
	m_0	m_1	R^2	n	c_0	c_1	R^2	n
P1-P3	1.720	-0.016	-	40	103.499	0.288	0.15	135
LP1	2.839	-0.011	0.04	277	118.399	0.286	0.35	660
LP2	1.288	-0.009	0.04	541	119.190	0.309	0.24	1325
LP3	1.697	-0.016	0.10	61	91.023	0.203	0.15	185
C1	2.404	-0.008	0.02	499	115.542	0.262	0.35	1239
C2	1.819	-0.012	0.07	1626	120.728	0.263	0.19	3697
C3	2.439	-0.016	0.08	90	109.866	0.224	0.28	232

3.3 Survival model

In table 5 we also give the fitted parameters for the survival probability (*S*) in relation to the competition index (equation 8). The logistic regression model, however, did not yield a significant result for the combined pioneer groups. As there were only few (n=40) juveniles present at the start of the first census. Because it is rather unlikely that competition index (or light) does not affect survival of pioneers we used an alternative approach for this life-history group. For this we assumed that pioneer seedlings with no competition would have a survival probability close to 1 (0.97) and that pioneers with median competition index would have the average survival probability (P_s) as calculated before, *i.e.* 0.89. We further assumed that the pioneer juveniles cannot survive beyond the 95 percentile competition index for pioneers as, except one outlier, no seedlings were found at higher competition index values. Based on these assumptions we inferred the parameters for a declining logistic function between a competition index of zero and median competition index (see table 5, no R^2 because it is not directly based on data). From the median competition index onwards the survival probability declines linearly with increasing competition index until it becomes zero at the 95 percentile competition index.

3.4 Growth trajectories

For the simulations of growth trajectories we estimated the competition index for juveniles of each functional group from their height. This estimate was based on a relationship between height and the competition index C_G (see equation 9) for which the fitted parameters are given in table 5. Except at the smallest heights, the pioneer juveniles had lower competition index values (more light available) in comparison to the other groups at the same heights. This means that on average the pioneer juveniles experienced less competition than other groups, *i.e.* they occur on average in lighter patches than the other groups.

After simulations of growth trajectories we first determined for each functional group the amount of auto-correlation in growth rates between two subsequent time intervals for the different growth modelling approaches and compared these with those found for field date (table 6). Obviously the average model and the stochastic model with full auto-correlation of z-scores explicitly included showed full auto-correlation (coefficients of determination are 1) and the fully stochastic model showed the lowest amount of autocorrelation. For the stochastic growth model with auto-correlation explicitly included we selected for each functional group those weighting values of z-scores that showed auto-correlation values that were closest to those found for the field data (table 6).

Table 6 Per functional group (FG), coefficients of determination for the product-moment correlations of growth rates between two subsequent census intervals, *i.e.* auto-correlation, are given as found for data and growth trajectory simulations with the average growth model (Avg.), the stochastic growth model (stochastic) and the stochastic growth model with auto-correlation explicitly included (stochastic & auto-correlation). The weights at the subdivision of the stochastic & auto-correlation results refer to the weighting of the latest year's z-score in relation to the previous year's z-score for the averaging of z-scores (see materials and methods section): 0: only previous z-score, *i.e.* full auto-correlation: 0.5: latest z-score taken 0.5 times … 3: taken 3 times (with increasing weighting of the latest z-score for growth the z-score in the previous time interval becomes less important and thus auto-correlation in growth rates will become less). For each functional group the amount of auto-correlation that is closest to that found in the data is shown as "best" auto correlation. The amount of auto-correlation in the growth data for the three pioneer groups is based on analyses of all three pioneer groups combined. All auto-correlations were highly significant at P<0.001.

FG	Data	Avg.	Stochastic	Stochastic & auto-correlation		
				0 (full)	Best	Weight
P1	0.82	1	0.09	1	0.83	1
P2		1	0.08	1	0.84	1
P3		1	0.11	1	0.84	1
LP1	0.45	1	0.10	1	0.47	2
LP2	0.68	1	0.22	1	0.72	1
LP3	0.86	1	0.28	1	0.89	0.5
C1	0.41	1	0.12	1	0.39	3
C2	0.42	1	0.09	1	0.44	2
C3	0.71	1	0.18	1	0.70	1

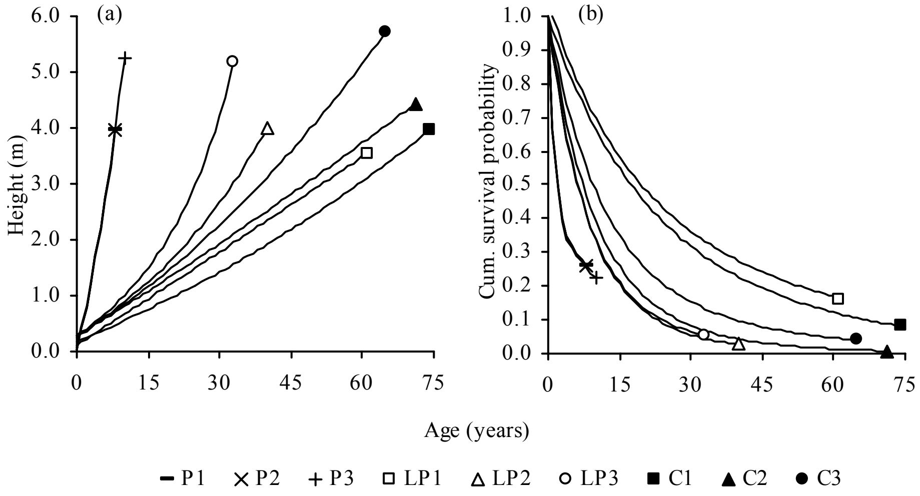

Figure 3 Results from the growth trajectory simulations using the average growth modelling approach. For the nine functional groups, height (m) (a) and cumulative survival probability (b) with increasing ages of juveniles that grow with average growth rate are given. The symbols mark the point at which the seedlings reach 2 cm DBH. The different types of symbols refer to different functional groups (see legend, and see table 1 for coding of groups).

Figure 3a shows the growth trajectories for the different functional groups based on simulations with the average model only. Because all individuals of the same functional group have the same height growth rates, all individuals per functional group also follow the same growth trajectory. In figure 3b we give the cumulative survival probabilities with increasing age for each functional group. The three pioneer groups were youngest (8 to 10 years old) when they reached a size of 2 cm DBH while the climax groups took longest to reach this size (65 to 74 years). Within each main life-history group (P, LP and C) the age at which juveniles reached 2 cm DBH increased with decreasing adult stature. The three pioneer groups had the highest cumulative survival probability over the whole residence time in the juvenile size class (< 2 cm DBH). Of the other life-history groups, the small stature groups had the highest cumulative survival probability, while the medium stature groups had the lowest (figure 3b).

The growth projections with the stochastic modelling approaches do show variance in growth trajectories of functional groups. Therefore in figure 4 we only give for each functional group the mean percentiles (2.5, median and 97.5) of ages at which the juveniles reached 2 cm DBH for the four different growth modelling approaches. In figure 5 we do the same for the cumulative survival probability over the residence time in the juvenile size class. The observed patterns are more important than the exact values for each percentile.

For all functional groups the mean 2.5 percentile (mean of 100 repetitions of 1000 trajectories each) ages at 2 cm DBH were significantly lower for the three stochastic models than the ages with the average growth model (figure 4). Among the stochastic modelling

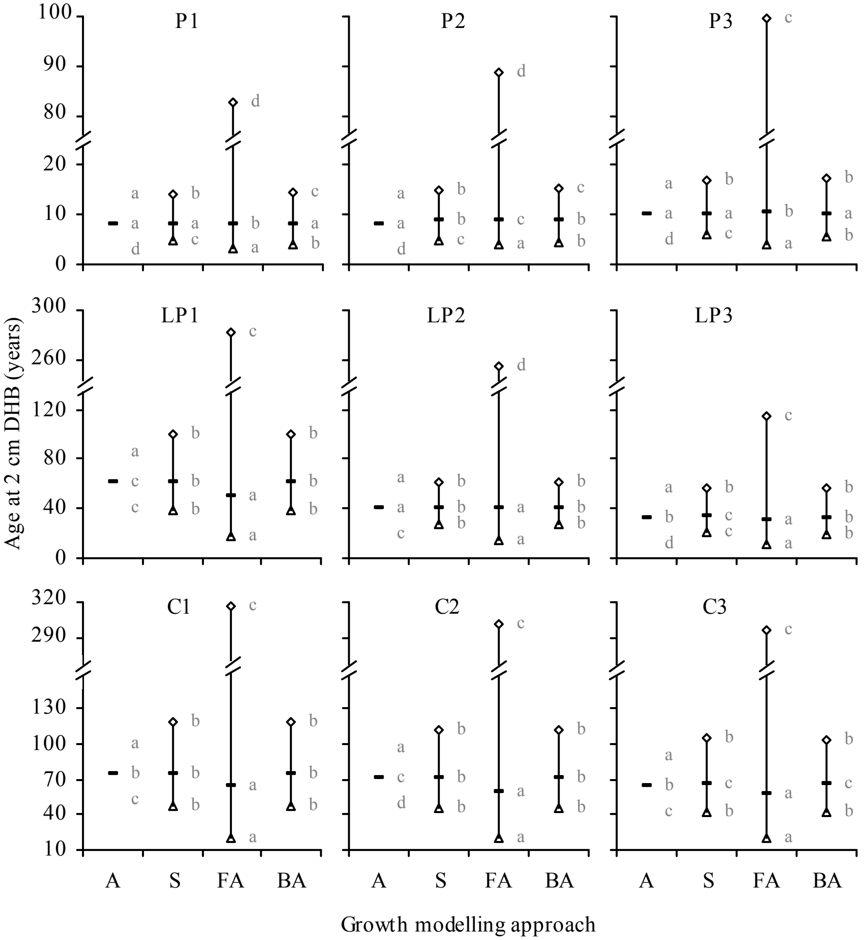

Figure 4 Results of growth trajectory simulations. Per functional group (see table 1 for coding) the mean 2.5 percentile (triangles), mean median (bars) and mean 97.5 percentile (diamonds) ages at 2 cm DBH are given for the 4 different growth modelling approaches (A: Average growth, S: Stochastic growth, FA: stochastic growth with Full Autocorrelation, BA: stochastic growth with Best Autocorrelation). Mean percentiles and medians were calculated from 100 repetitions of 1000 growth trajectories. Per functional group we tested each mean percentile for differences among the different modelling approaches using Kruskal-Wallis ANOVA followed by nonparametric Tukey-type multiple comparisons using a Nemenyi test (Zar, 1999). Significant differences among modelling approaches are given by different letters ($P<0.01$). There is no variation in ages for the average modelling approach. Note the differences of scale on the y-axes among the functional groups.

approaches the simulations that included full auto-correlation had the lowest mean 2.5 percentile of ages. The mean 2.5 percentile ages at 2 cm DBH for the three pioneer groups and the tall long-lived pioneer group were significantly lower with the best auto-correlated stochastic model than with the fully stochastic model. For instance for the medium stature climax group all juveniles needed 71 years to reach 2 cm DBH with the average model while the fastest growing 2.5 percent of the juveniles needed less than 45 years with the fully stochastic and best auto-correlated stochastic models and only 20 years with the fully auto-

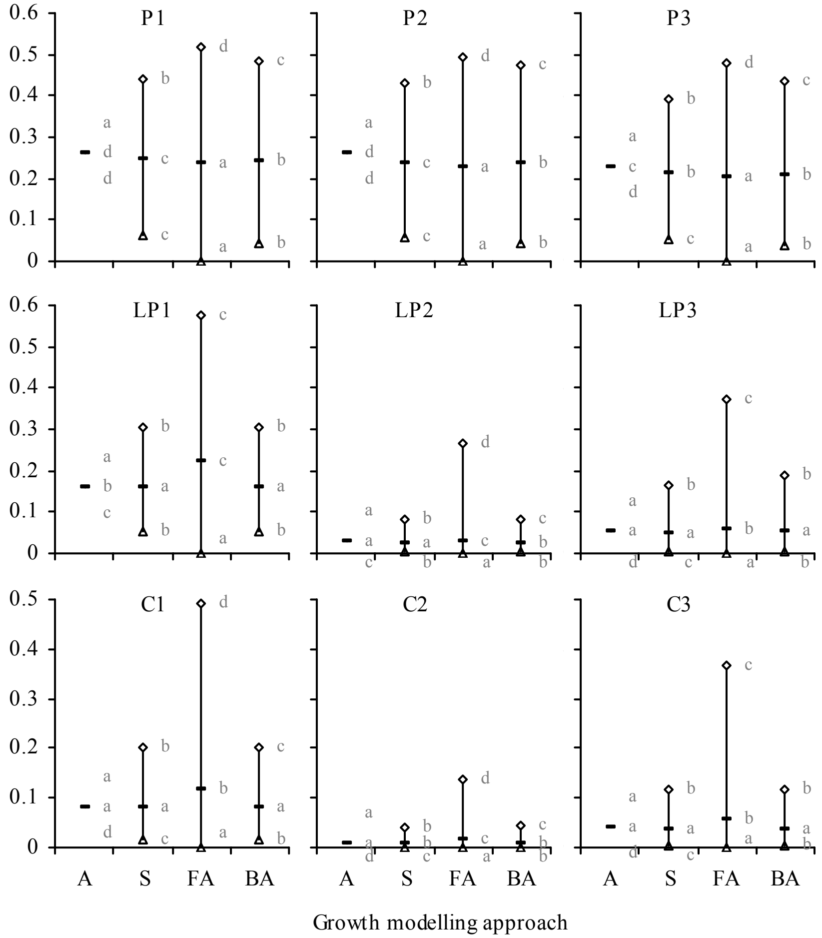

Figure 5 Results of growth trajectory simulations. Per functional group (see table 1 for coding) the mean 2.5 percentile (triangles), mean median (bars) and mean 97.5 percentile (diamonds) cumulative survival probabilities for juveniles at 2 cm DBH are given for the 4 different growth modelling approaches (A: Average growth, S: Stochastic growth, FA: stochastic growth with Full Autocorrelation, BA: stochastic growth with Best Autocorrelation. Means of the percentiles and median were calculated from 100 repetitions of 1000 growth trajectories. Per functional group we tested each percentile for differences among the different modelling approaches using Kruskal-Wallis ANOVA followed by nonparametric Tukey-type multiple comparisons using a Nemenyi test (Zar, 1999). Significant differences are given by different letters (P<0.01). There is no variation in cumulative survival probability for the average modelling approach.

correlated model. For the differences among the modelling approaches in mean median and mean 97.5 percentile ages we refer to figure 4.

For all functional groups the mean 97.5 percentile cumulative survival probabilities for growth trajectories with the stochastic models were significantly higher than the cumulative survival probabilities of al juveniles with the average model (figure 5). Among the stochastic modelling approaches for each functional group the mean 97.5 percentile cumulative

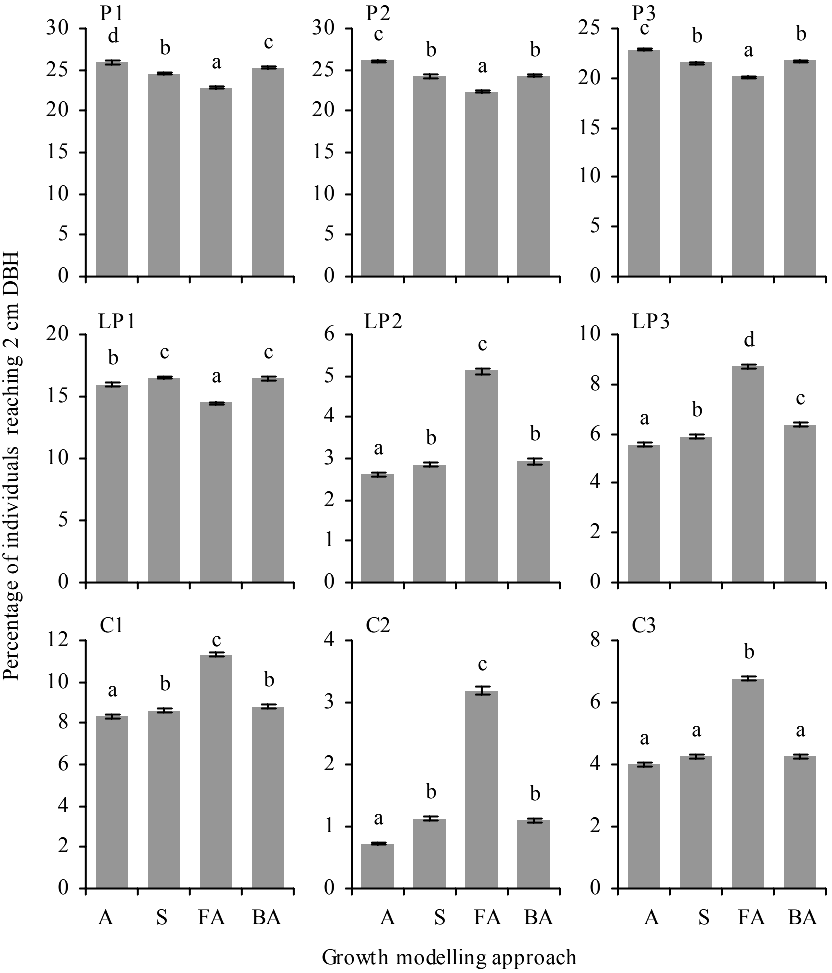

Figure 6 Results of growth trajectory simulations with mortality included. Per functional group (see table 1 for coding) the mean ± s.e. numbers of juveniles that reach 2 cm DBH alive are given for the 4 different growth modelling approaches (A: Average growth, S: Stochastic growth, FA: stochastic growth with Full Autocorrelation BA: stochastic growth with Best Autocorrelation). The means are based on 100 replicate simulations that started with 1000 juveniles. Per functional group we tested differences among the different modelling approaches using one-way ANOVA followed by multiple comparisons using the Tukey test. Significant differences among modelling approaches are given by different letters ($P<0.01$). Note the differences of scale on the y-axes among the functional groups.

survival probability increased with increasing amount of auto-correlation in growth. The differences between the fully stochastic model and the best auto-correlated stochastic model, however, were generally small (figure 5). For the differences among the modelling approaches in mean median and mean 2.5 percentile cumulative survival probability we refer to figure 5.

In figure 6 we present per functional group the mean number of juveniles that reach 2 cm DBH for the four different growth modelling approaches based on 100 repetitions of 1000

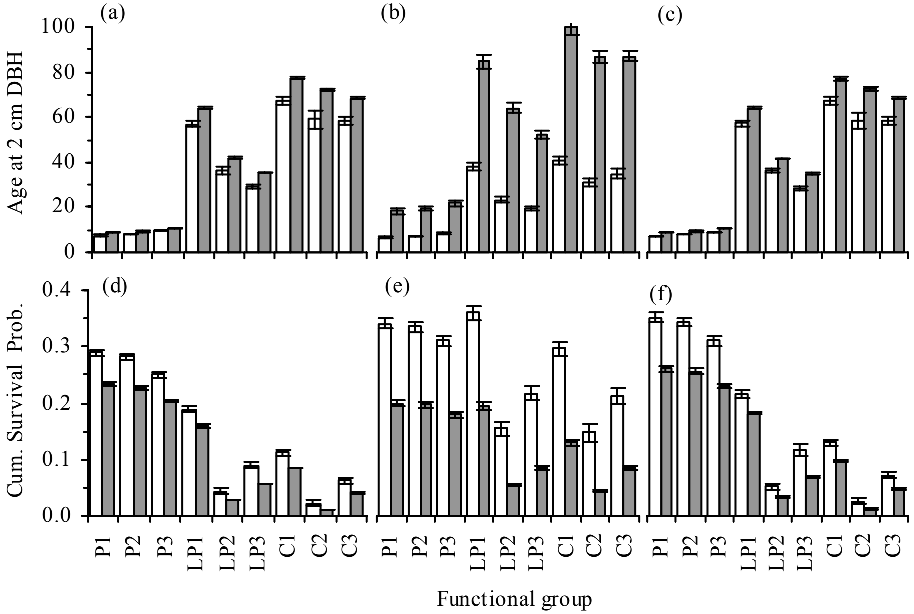

Figure 7 Results for growth trajectory simulations with mortality included. Per functional group the mean ages (years) at 2 cm DBH (a-c) and mean cumulative survival probability (d-f) are given for individuals that were alive when they reached 2 cm DBH (white bars) and individuals that would have died in the course of time (grey bars). Graphs (a) and (d) show results for the stochastic growth model, graphs (b) and (e) for the stochastic growth model with full auto-correlation and graphs (c) and (f) for the stochastic model with best auto-correlation. The error bars represent standard deviations. All comparisons between juveniles that were still alive and those that would have died were significantly different ($P<0.01$).

trajectories with mortality included. For the three pioneer groups (P1-P3) and the smallest long-lived pioneers (LP1) the simulations with fully auto-correlated stochastic growth resulted in the lowest number of juveniles reaching 2 cm DBH, while for the pioneer groups simulations with the average model had the highest number of juveniles reaching 2 cm DBH. For the other groups this was just the other way around with the average model resulting in the lowest numbers and the fully auto-correlated stochastic model resulting in the highest numbers of juveniles reaching 2 cm DBH. Except for the smallest long-lived pioneer group, the results of the other two modelling approaches were in between those of the average and fully auto-correlated models (figure 6). Figure 7 shows that in the simulations that include mortality in the stochastic models, juveniles that actually were alive when they reached 2 cm DBH grew faster than the juveniles that would have died before they reached 2 cm DBH.

3.5 SYMFOR simulations

For the simulations in SYMFOR we extended the previously used functional groups with a further sub-division into wind dispersed (w) and non-wind dispersed (nw). For the pioneer groups with medium and tall adult stature and most wind dispersed sub-divisions of groups there were not sufficient numbers of individuals > 5 cm DBH for evaluation of differences among groups. For the extended functional groups with sufficient numbers we show the results of multiple SYMFOR simulations with the four different juvenile growth modelling approaches in figure 8. For most functional groups the differences among the different juvenile growth modelling approaches in the number of trees > 5 cm DBH at year 250 roughly show the same pattern as found for the equivalent groups without dispersal sub-division for the growth trajectories with mortality included (figure 6).

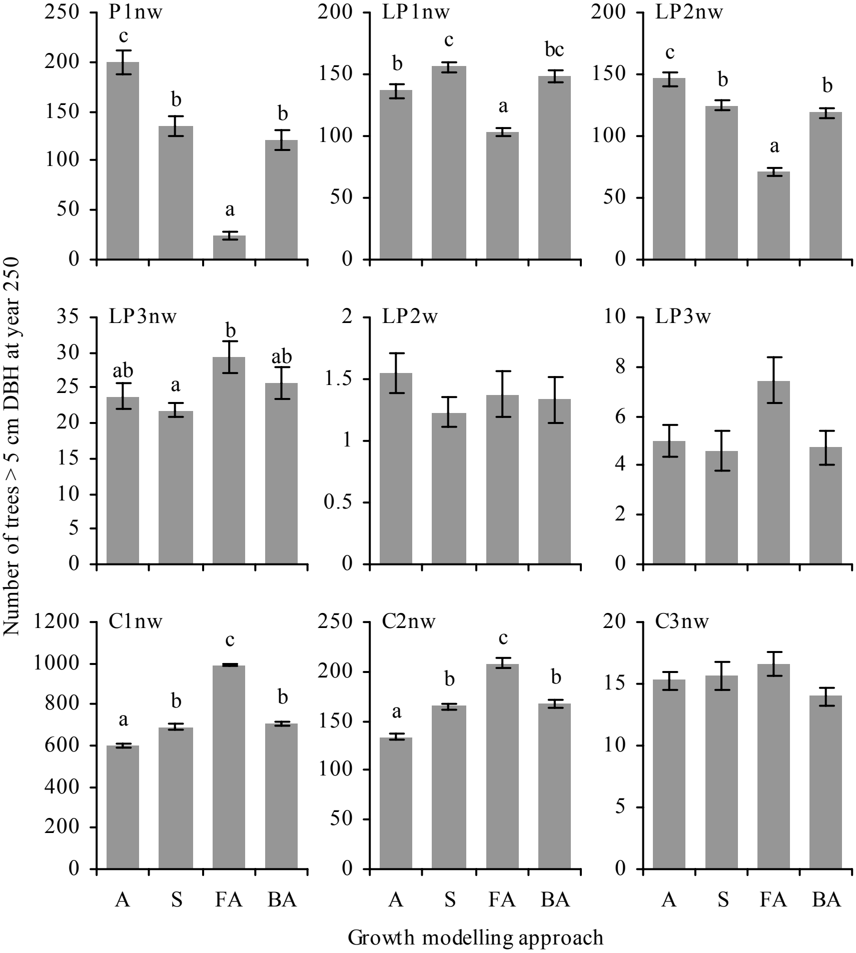

Figure 8 Results of multiple SYMFOR simulations. For the functional groups with sufficient individuals in the simulated forest, the mean ± s.e. numbers of trees > 5 cm DBH at year 250 are given for the 4 different growth modelling approaches (A: Average growth, S: Stochastic growth, FA: stochastic growth with Full Autocorrelation BA: stochastic growth with Best Autocorrelation). See table 1 for coding of functional groups with additional coding referring to non-wind dispersed (nw) and wind dispersed (w) sub-divisions of functional groups (see main text on functional groups). The means are based on 25 replicate simulations per growth modelling approach. Per functional group we tested differences among the different modelling approaches using one-way ANOVA followed by multiple comparisons using the Tukey test. Significant differences among modelling approaches are given by different letters ($P<0.01$). Note the differences of scale on the y-axes among the functional groups.

4 Discussion

4.1 Growth models

Although the goodness of fit of the average growth models were rather low, they are in the same order as found in other studies using competition indices based on neighbourhood effects (*e.g.* Gourlet-Fleury 1998, Ferment *et al.* 2001, Uriarte *et al.* 2004). Except the pioneer groups all functional groups showed distributions of growth rates that were more or less similar to that of the medium sized climax group as shown in figure 2b. This means that variation in growth rates was symmetrically around the mean and that it was highest at small competition indices. Also the strongest negative growth rates appeared at the lower competition indices. From this, in combination with the low values for the coefficients of determination for the average growth model, we argue that the used competition index limits the extreme values of the growth rate distribution rather than that it is good predictor of actual growth rates in models that include stochastic variation. Lower competition index values (higher light availability) allow higher potential growth rates, but these are not realised by all seedlings growing with that value of competition index because for instance growth is inhibited by other resources or physical damage. Our stochastic modelling approaches make it possible to fully capture variation in growth and to simulate the whole distribution of growth variation.

4.2 Growth trajectories

The results of the growth trajectory simulations using only average growth models showed that pioneers reached 2 cm DBH much faster than the other functional groups. Although the pioneers had a low annual survival probabilities (figure 1), more pioneers recruited to 2 cm than the other groups. Because their residence time as seedlings is short due to high growth rates, they realised higher cumulative survival probabilities at reaching 2 cm DBH than other functional groups.

4.3 Significance of stochastic variation

Obviously if stochastic variation in growth rate is included in growth models, the resulting growth trajectories for juveniles will show variation. For each functional group the simulated 2.5 percentage ages and 97.5 percentile survival probabilities are achieved by the individuals that grow fastest. Note that even these fastest growing individuals will never have a cumulative survival probability close to 1. In comparison with the average growth model, the models with stochastic variation had lower numbers of juveniles that ultimately reached 2 cm DBH for all pioneer groups, while for most other functional groups they showed the opposite trend (figure 6). This can be explained as follows. Pioneer seedlings that grow with the average growth rate all have a reasonable probability to survive and reach 2 cm DBH (figure 3 and 5). With the models that include stochastic variation in growth roughly 50% of the pioneer juveniles will faster reach 2 cm DBH (figure 4) and have higher cumulative survival probabilities (figure 5) than with the average model while the other 50% will take longer and have lower cumulative survival probabilities. Many of the 50% of pioneers that survived and reached 2 cm faster than average, would also have survived with the average growth model while many of the 50% of pioneer juveniles that now take longer and have lower cumulative survival probabilities do not survive while they would have with the average growth model.

Most of the slower growing groups have very low probabilities to survive the time needed to reach 2 cm DBH with the average growth model (figures 3 and 5). For these groups the effect of inclusion of stochastic variation in growth has the opposite effect as we saw for the pioneer group.

When using an average growth model the inherent assumption made on population level is that the effect of individuals with a positive growth variance is balanced by the effects of individuals with a negative growth variance. Above we show that positive and negative growth variances don’t have a symmetrical effect on cumulative survival. Consequently the effects of individuals that show different amounts of variance in growth rate are not balanced. The magnitude of these effects will depend on how well the juveniles survive with the average growth model in relation to the degree of observed variance in growth data. Therefore our results obtained with the growth models that included stochastic variation are regarded more realistic than those with the average model. The average model leads to an underestimation of surviving juveniles if average growth rate is relatively slow in comparison to annual survival probability while it leads to an overestimation of surviving juveniles when growth rates are relatively fast.

4.4 Significance of auto-correlation

Our results show that the ranges of ages at which juveniles reached 2 cm DBH and of cumulative survival probabilities increased with increasing auto-correlation (figures 4 and 5). With the fully auto-correlated model juveniles consistently grew faster or slower while with the not-explicitly auto-correlated approach they can grow very fast one year and grow slow the next year. The best auto-correlated modelling approach stands somewhere in between these two. Due to the wider ranges of ages and cumulative survival probabilities at 2 cm DBH the inclusion of auto-correlation in the outcome of growth models with stochastic variation will amplify the effect of variation in growth rate on numbers of juveniles reaching 2 cm DBH as discussed above and as shown in figure 6. Although the results with the fully auto-correlated model show that it potentially can play an important role in growth models, for most functional groups the differences between the fully stochastic and the best auto-correlated modelling approaches were rather small.

4.5 Effects on results of forest simulation models

The results of the SYMFOR simulations using the different growth modelling approaches show that the effects on juvenile dynamics are propagated to the adult size classes. The way of modelling juvenile growth thus has major consequences for the results obtained with forest simulation models.

It is important to realise that the competition index as used for the simulations of growth trajectories was an average for juveniles of that functional group at a certain height. For pioneers this average competition index is lower (more light) than for the other groups. In the forest and in the SYMFOR simulations on average the competition index values are higher than the average for pioneers. Therefore in the SYMFOR simulations pioneers perform worse relative to other groups than would be expected from the results with the growth trajectories that not necessarily simulate widely occurring competition indices.

We expect that our findings may also be relevant for other types of models that use juvenile growth, like for instance matrix models. The proportion of individuals that reached 2 cm DBH in our simulations of growth trajectories can be directly translated to a transition probability to 2 cm DBH. If transition probabilities of the bigger size classes remain the same, this effect will then continue throughout the bigger size classes in the matrix model.

4.6 Conclusions

In this chapter we clearly show that the stochastic variation in growth rates has significant effects for modelling juvenile population dynamics. This variation is also found in observed growth data and therefore should not be neglected in growth models for tropical trees. Auto-correlation in growth rates potentially affects results of growth models (*e.g.* our full auto-correlated model), the inclusion of the observed levels of auto-correlation in models with stochastic variation (*e.g.* the best auto-correlated model) does not result in significantly different results.

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Chapter 6

General discussion and summary

Since only a small area of Guyana's forests can be protected and because timber harvesting is an important source of income, logged forests will play an important role in the conservation of biodiversity in Guyana. As in other tropical countries, sustainable forest management should result in sustained timber yields over long periods of time to provide lasting revenues and to secure livelihoods, while on the other hand also diversity should be conserved as much as possible. To be able to define criteria for sustainable forest management, information on the long-term effects of logging is needed.

The aim of the investigations described in this thesis was to elucidate the long-term effects of logging on tree population dynamics, forest composition and tree diversity and to evaluate the sustainability of alternative forest management scenarios for both future yields and biodiversity conservation. The main results are summarised and discussed in this chapter.

Functional groups

The abundance of many species in sample plots is too low for statistically meaningful analyses of demographic processes like growth, mortality and recruitment. Therefore species were objectively classified into functional groups with similar ecological characteristics and responses to logging, based on differences in three morphological characteristics: wood density, seed mass and adult stature, which are predictors of species' responses to disturbance in terms of growth, recruitment and survival. Wood density and seed mass were used to quantify three life history strategies (pioneers, long-lived pioneers and climax species). In chapter 2 this classification of three groups was used, while for use in the other chapters these three life history groups were subdivided in three subgroups each, depending on adult stature (small, medium and tall stature, which relate to understorey, canopy and emergent positions in closed forests). This combination of life history and adult stature groups results in nine functional groups. Trees belonging to different functional groups were expected to respond differently to changes in light climate caused by logging.

Observed short-term effects of logging

In chapter 2, the short term (5-6 years) effects of logging on population dynamics, species composition and biodiversity were studied for two different areas in Guyana. Based on the

Pibiri plots in central Guyana, the main study area in this thesis, short-term (six years) effects of logging on light availability and population dynamics of saplings (2-5 cm DBH) and poles (5-20 cm DBH) were studied for species classified in three functional groups (pioneer, long-lived pioneer and climax). The 12 plots that were used contained 4 treatments of reduced impact logging (RIL) with harvest intensities of 0 (control), 4, 8 or 16 trees ha^{-1} that each were repeated three times (see van der Hout 1999, van der Hout 2000). The tree community before logging appeared to be adapted to low intensity and infrequent disturbance events with climax species as the most abundant group (> 50 % of all individuals), while pioneers constituted less than 1%. Dawkin's canopy illumination index (CII), which is determined visually on an ordinal scale, was used to determine differences in light availability. For the Pibiri area and additionally for plots from Northwest Guyana (only divided in logged and not logged) shifts in composition of functional groups and changes in tree diversity were evaluated for time series after logging.

Six years after logging light availability for saplings and poles were still significantly related to logging. The proportion of saplings and poles in better light climates increased with increasing harvest intensity. In general, all three functional groups showed increased growth rates with increased light availability, suggesting a positive effect of logging on growth rates of all species. Yet, in the higher light classes the growth rates of pioneer poles and saplings were faster than for the other two groups. Notably highly increased recruitment (in-growth) rates (47% yr^{-1}) resulted in fast net population gain rates for pioneer saplings (44 % yr^{-1}) in high light conditions. Pioneers were also found standing relatively more often in high light conditions than species from the other functional groups.

In the Northwest, the abundance of pioneers in logged plots increased from 1% to 7% for saplings and from 2% to 8% for poles. In Pibiri only in the plots with the highest harvest intensity, the pioneer saplings increased from 0% to 6.2%, while in the other treatments no significant changes occurred. The timing and magnitude of the changes in functional group composition after logging differed between the two study areas. In the Northwest, there was already a notable increase in abundance of pioneer saplings within 2 to 3 years after logging, while in Pibiri this was seen only after 4 to 6 years. Furthermore, the relative abundance of pioneer poles in the Northwest increased within 5 years after logging, but in Pibiri this was not as yet the case within 6 years after logging. These differences are associated with a difference in mean pioneer growth rates between the two areas (likely due to differences in nutrient availability between the soil types in the two areas). Hence in the Northwest recruits of the pioneer species would have been able to achieve sapling size more quickly than in Pibiri.

In all cases the increased relative abundance of pioneers goes together with lower relative abundances of climax species. In both forest areas, tree α-diversity of saplings, calculated as Fisher's α, increased with increasing harvest disturbance (relative reduction of basal area).The results of this study are consistent with the predictions of the intermediate disturbance hypothesis for forests at the low intensity end of the disturbance range. Logging increased light availability and created more suitable habitat conditions for successful regeneration of pioneer species that were previously virtually absent. Yet the magnitude of the changes is rather small and no large scale proliferation of the pioneers occurred. This was probably due to the low abundance of mature pioneer trees in the primary (pre-logging) forest, which limits seed input.

How to study long-term effects of logging?

Tropical trees are slow growing and may live for several centuries. Therefore the consequences of changes in present day demographic trends caused by logging can only be empirically assessed after a long period of time. The full impact of logging on species composition will only become apparent many years later. Few post harvest monitoring data are available that have been collected during a sufficiently long period of time and with those few available data sets one of the problems that arises is that harvesting in old times is often not comparable with current logging practises. Hence these long-term monitoring studies provide generally little insight in the effects of current logging practises. Novel forest simulation models are therefore needed to make instantaneous projections of the long-term effects. In this study a new population dynamics model for forests in central Guyana was developed and implemented within the SYMFOR modelling framework (Phillips & van Gardingen 2001a, 2001b, Phillips *et al*. 2003, 2004, chapter 3). Subsequently this model was used to evaluate alternative scenarios for sustainable timber harvesting in these forests of central Guyana and their effects on functional diversity.

Model

The ecological model (chapter 3) was developed based on data from permanent sample plots of a reduced impact logging experiment in central Guyana. The model is individual-based and spatially explicit, meaning that all trees are individually represented and occupy a unique spatial position in the simulated forest stand. It represents the three main demographic processes in populations of forest trees, namely, *growth*, *mortality* and *recruitment*. The rates of these processes for individual trees depend on the size (growth) of the trees and their competition, mainly for light, with other trees (growth and mortality) and were parameterised from data for nine functional groups of species. Competition among individuals is represented as a distance and size dependent competition index that is explicitly derived from the data. Each tree has a diameter at breast height (DBH) that is updated each time-step using a diameter-growth function. Other allometric properties such as height and crown width of the trees are determined using allometric functions of DBH that were derived from data. Trees that die from natural causes as determined by a semi-stochastic mortality function, have a certain probability to fall in a random direction and damage smaller neighbour trees within their damage area. The recruitment function describes the appearance of new trees at the minimum DBH threshold, which was 2 cm. The probability of recruitment of a new tree in a grid-square of 25 m^2 depends on the light availability (competition index) in that grid-square. The model runs with annual time-steps.

From the parameterised functions we could determine some differences between the demographic rates of the functional groups. As might be expected, the pioneer groups had the fastest diameter increment rates for trees smaller than 20 cm dbh, while that of the climax species was generally slowest. Since the dbh-height relationships for the smaller trees (<20 cm DBH) were similar for all groups, pioneers also grew fastest in height. The two tallest long-lived pioneer groups had the strongest response to increased light availability while that of the pioneers was rather low. This is in contrast to expectations that response would be strongest for the light demanding pioneer species. This can be explained, however, by the fact that in forests pioneers are usually only found in sites with high light availability. Pioneers intrinsically have a high whole plant light compensation point. Hence, they will die in shaded conditions because reduced photosynthesis cannot compensate for loss of biomass and inherently high respiration (*e.g.* Popma & Bongers 1988, Veneklaas & Poorter 1998, Poorter 1999). The average value for competition index was much lower for pioneers than for the other groups. This indicates that pioneers indeed occurred at higher light (low competition index) sites in the forest. Because only a small gradient in competition index was measured for pioneers in the field, their response in terms of growth is inevitably limited. The pioneers did, however, show very strong increase in mortality probabilities with increasing competition index. Thus, more trees growing under a high competition index died in the course of a given census interval and were consequently not included in the growth analysis. Additionally the pioneer groups had very low recruitment probabilities at low light, but that rapidly increased with increasing light availability. This is in accordance with the general notion about pioneer species that they need high light conditions for regeneration (*e.g.* Brokaw 1987, Alvarez-Buylla & Martínez-Ramos 1992, Ellison *et al.* 1993, Peña-Claros 2003 and results from chapter 2).

Long runs (1000 years) of the model without simulated management showed that the abundance of some of the functional groups changed over time. Within 250 years all groups had reached a stable number of stems per hectare of simulated forest. Although for one group the abundance increased with a factor 2.5 at stable state, all simulated abundances remained within the ranges of abundances that also occurred in the sample plots. In chapter 3 some potential causes for these simulated changes will be discussed.

An extensive sensitivity analysis of the model showed that the model is rather robust for changes in tested model components (growth, mortality, recruitment and three parameters that directly affect these components). Exceptions are the pioneer groups, which showed very large changes in abundance and especially basal area when model components were changed. The model results were most sensitive to mortality and recruitment, which are also the components that had the highest uncertainty. This result is consistent with findings of other studies (Kammesheidt et al. 2001, Phillips et al. 2003). Since the high uncertainties for mortality and recruitment mainly reflect small sample sizes, this indicates that future research should concentrate more on mortality and recruitment, especially for pioneer species. This means that compared to growth, data on mortality and recruitment have to be collected either on larger sample areas or over longer periods of time since their recordings are rare and infrequent.

Scenarios for sustainable forest management

In chapter 4 the long-term effects of different logging scenarios on abundances of nine functional groups, (functional) species composition, timber yields and the times needed to recover were evaluated. To do this we used the ecological model described in chapter 3 in combination with an existing management model within SYMFOR. This management model simulates the felling of trees, the removal of harvested trees through heavy machinery (skidders) and the involved damage to the remaining forest. Parameter settings of the management model followed the code of practice for timber harvesting in Guyana. Directional felling and planning of skid-trails were simulated to represent at least some degree of reduced impact logging. Similar to the functional groups that were used in the ecological model, the management model used utility groups that contain species with similar commercial values. The evaluated scenarios differed in combinations of harvest intensity (HI: 4, 8 or 12 trees ha^{-1}), minimum felling diameter (MFD: 35 or 60 cm DBH) and felling cycle (FC: 25, 40, or 60 years between two subsequent harvests). The simulations were based on the three control plots as input for the forest in the model.

After logging once, commercial volumes returned to base-line values in all scenarios. This indicates that sustainable harvesting, in principle, is possible. At high harvest intensities, however, the two commercially most valuable utility (timber) classes needed approximately 100 years to fully recover. This is substantially longer than the currently advised felling cycle of 60 years. As a result, the commercial volumes over time declined even for the management scenarios with the lowest harvest intensity and longest felling cycle. The yields at the second and third harvest as percentage of the first yield (henceforth referred to as: % first yield) increased with increasing length felling cycle, while within each felling cycle class the highest percentages were achieved at the lowest harvest intensities. For the scenarios with the longest felling cycle (60 yrs) these yields were generally > 90 % of the first yield, while with the shortest felling cycle (25 yrs) this ranged from 37 to 79 %. Highest total yields over three harvests were achieved for the scenarios with the highest harvest intensity, independent of felling cycle. The highest average annual yield for three subsequent harvests was achieved, however, by the scenario with the shortest felling cycle, lowest minimum felling diameter and highest maximal harvest intensity (the heaviest treatment). At the same time this heaviest treatment led to a rapid depletion of the commercial volume.

After logging once, the abundances of all functional groups returned in all scenarios to values similar to that of base-line simulations without logging. Shifts in species composition within functional groups may have occurred, but could not be tested with the current model. Generally the return times for abundance increased with increasing logging intensity. The longest return times were found, however, for the small pioneers, the small climax species and medium sized climax species. The small pioneers rapidly increased in abundance after logging. Depending on the harvest intensity, they need approximately 82 to 113 years to decrease back to base-line values. The two climax groups, however, greatly decreased in abundance after logging and needed 111 to 161 years (small climax species) and 83 to 120 years (medium sized climax species) to recover the loss of individuals due to logging.

Because the felling cycles of all scenarios were shorter than the abundance recovery times of the functional groups, the pioneer groups further increased after each logging event, while the climax groups further decreased. This effect increased with increasing maximal harvest intensity and decreased with increasing length of felling cycle. Because the number of trees that could actually be harvested decreased over time (yields were not sustained) the effect slightly declined after some harvests in the scenarios with high harvest intensity and short felling cycle.

After three harvests the composition in almost all scenarios of functional groups had significantly changed. Only in the scenarios with FC 60 and HI4 this was not the case. All long-term changes came down on an increase of the pioneer groups and a decrease of the climax groups, which is consistent with the observed changes in chapter 2. In the most affected scenario, however, the total abundance of the three pioneer groups increased from 0.3% to 3.5%, while at the same time the total abundance of all climax groups decreased from 72 to 64 %.

The results of this study can be used to rank the scenarios for each of the results obtained (*e.g.* total yields, average annual yields, % first yield, effects on functional group composition). Forest managers and decision makers can use these results as input for multiple criteria analysis to decide on what would be the most desirable logging practises. Important deliberations have to be made then on how to value each of the silvicultural and ecological aspects and what would be the costs and socio-economic effects.

The results of this study show that it is possible manage the forest in a way that results in relatively small changes in functional composition and still achieves more or less sustained yields. From scenarios with a felling cycle of 60 years, all would more or less qualify. Yet within this set of scenarios there is still a trade-off between productivity and sustainability, *i.e.* scenarios with highest total yields have the lowest % first yield and strongest effects on functional group composition. On the long term functional group composition appeared to be not much affected by logging. Hence, it can be concluded that logged forests in Guyana still have high conservation values.

Nevertheless, the times after logging needed to return to commercial volumes and abundances of functional groups that would be similar to non-logged forests may take as much as 100 to 120 years, which is twice the currently advised felling cycle of 60 years. Therefore logging the forest once (potentially with high intensities) and then leave it alone as proposed before by *e.g.* Cannon *et al.* (1998) and Rice *et al.* (1998) might be taken into consideration as well by decision makers. Much would dependent on what happens to the forest after it is abandoned by loggers. Argument against this management option is that forests from which loggers withdraw have higher probabilities of being converted into agricultural land (*e.g.* Pearce et al. 2003 and references herein). In Guyana, however, population pressure is very low. Hence large-scale conversion of forest areas to other land-uses like pastures, cattle ranging or oil palm and soy bean plantations is not occurring. Most agriculture is concentrated in the coastal zone where the majority of the less than 800 thousand inhabitants of Guyana live. In the interior of Guyana only small scale subsistence agriculture is practised by small indigenous communities. Other problems might arise from a financial perspective. Loggers may be concerned with the total profits that can be made from a certain area of forest. If the total yields from the scenario with the highest % first yield over three felling cycles of 60 years are compared with the yield of logging once with a harvest intensity of 12 trees ha^{-1}, the differences appear to be relatively small (55 m^3 h^{-1} vs. 44 m^3 ha^{-1}). Taking into account the rather small long-term effect at logging once 12 trees ha^{-1}, it may be expected that logging once with higher harvest intensities may be possible without major long-term consequence for forest composition.

A major threat for sustainable management of the forests in Guyana may come from conflicting land-use utilisation between forestry and mining (gold and diamonds). Mining is locally much more destructive for the forest than selective harvesting of timber. Forest areas may be cleared and soil and surface water are polluted. To the Government of Guyana gold mining has priority above forestry, as the revenues for gold are much higher than for timber. The forests in the interior of the country are vast and uninhabited, while most of its borders are unattended. This makes it very difficult to regulate and control mining operations and to prevent illegal mining. Yet, gold mining, both legal and illegal, regularly frustrates and damages investments and efforts of the forestry industry in Guyana to develop sustainable management practices and, reduces its willingness to do so.

Recruitment in models

In the simulation model that was described in chapter 3, and many other models described in literature, recruitment is often modelled as the probability of appearance (in-growth) of new trees at a specific minimum size threshold (2 cm in this study). This neglects the seedling stage, whereas that plays an important role in determining the future of the forest and is likely most affected by logging. In addition to neglection of the seedling stages, the number of recruits is generally modelled independent of the number of conspecific adult trees in the area, which is also the case in previous models in SYMFOR and the one described and used in this study. The reason why it was not done in this study is that no relation was found between the number of recruiting individuals of 2 cm DBH and the number of adults in the same plot. In chapter 5 it was estimated that the 2.5 % fastest growing seedlings would need approximately 4 for pioneer groups to 45 for climax groups years to grow from seed to 2 cm DBH, while slower growing individuals from the climax groups could need more than 68 years. This means that individuals when first recorded in the field as recruits at 2 cm DBH had their origin somewhere between 45 and 68 years earlier. This long time-lag obviously obscures the relation between the current number of adult trees and number of recruits at 2 cm DBH.

During logging most often the large and reproductive trees are harvested. This may have important implications for the regeneration of the forest after logging. Omission of the relation between numbers of adults and of numbers of recruits will, over time, lead to an underestimation of the effect of the logging disturbance on abundances and commercial volumes. If, for instance, some of the adult trees of a climax group have been removed or killed in logging simulations, 45 years after simulated logging the probability of recruitment in a subplot with a certain competition index is still the same as before logging. In the real forest, however, after logging the number of dispersed seeds would have decreased, which in turn would lead to a reduction in the number of recruits over the subsequent period of 45 years. If sufficient pre-adult trees are available in the forest this reduction in recruitment can be expected to last only a few years until the number of adult trees is recovered, but otherwise this may have important consequences for the total abundance of trees form that particular functional group.

Therefore, in addition to the model described in this study, a new model with detailed descriptions of the regeneration process was developed and implemented within the SYMFOR modelling framework. This model is described in van Ulft (2004). In addition to the model in this study, that model explicitly included the processes of seed production, seed dispersal, germination and growth and mortality of seedlings. When seedlings reached a size of 2 cm DBH, the model procedures become the same as in the model used in this study. Seed production, dispersal and germination are described in detail in van Ulft (2004), while the growth and mortality of seedlings is described in chapter 5 of this thesis.

In chapter 5 it is shown that growth of the seedlings in relation to competition index was very variable. Many seedlings showed reductions in stem height that are not related to light availability, but probably are the result of falling debris, browsing, herbivory and dieback due to pathogens and pests. These effects can be regarded as rather stochastic processes (from a seedling's point of view). In chapter 5 it is further shown that the probability to reach 2 cm DBH is higher for faster growing seedlings than for slower seedlings from the same functional group. Hence the seedlings that reach a size of 2 cm DBH on average have grown faster than the other seedlings. In a traditional modelling approach, however, all seedlings that grow at a certain light availability grow according the average of all seedlings at that light availability. Thus seedlings that normally would grow faster (by chance) and reach 2 cm DBH will now grow slower in the simulations and thus reduces their survivorship. As a consequence the total recruitment of this functional group will be lower than if some individuals were allowed to grow faster. Therefore we developed an approach that takes into account the stochastic variation and show the consequences for the nine functional groups. The modelling approach that includes this stochastic variation is then used in the model described in van Ulft (2004).

With this new SYMFOR model, it was not possible, however, to get realistic projections of forest structure and compositions of functional groups within a reasonable period of working time. In van Ulft (2004) potential problems are highlighted. Major problem with that model is its complexity. It contains over 1000 parameters and many processes are related, which makes it rather difficult to analyse the problems with the model.

Having read all this, one should keep in mind that simulation models merely reflect an extrapolation of current knowledge and assumptions rather than that they give “true” predictions. The scenario studies using the simulation model described in this thesis provide best educated guesses regarding the future of managed forests in central Guyana. Careful interpretations of model results can guide discussions on sustainable forest management and can be used for “evidence based” management planning. When in the future models can be improved due to additional data availability and increased understanding of forest dynamics, management planning can be adjusted accordingly.

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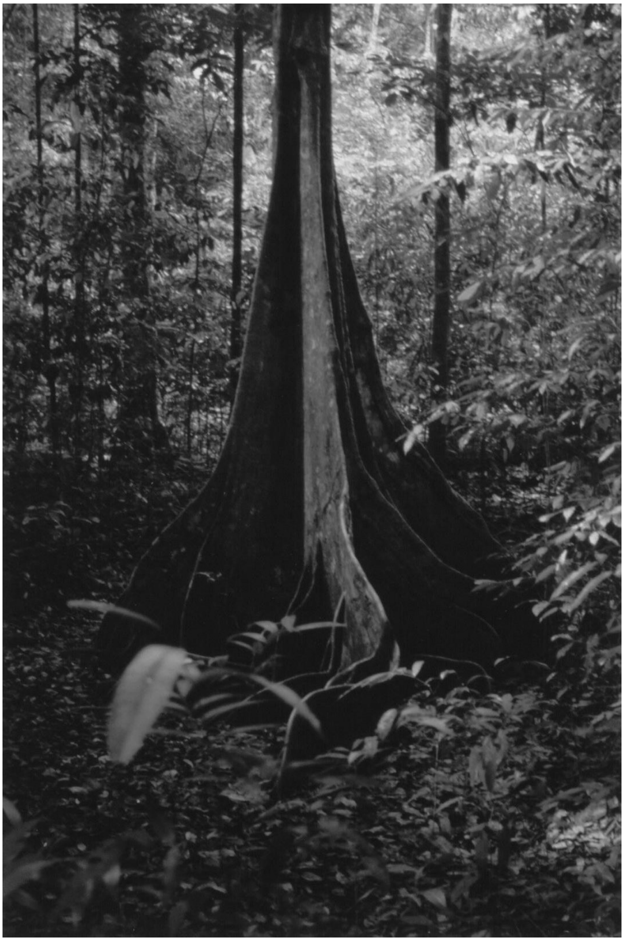

Appendix A Classification into functional groups of tree species occurring in 15 sample plots in Pibiri

Appendix A The classification into functional groups (FG) of tree species occurring in the 15 experimental sample plots in Pibiri. The letters in the coding of functional groups refer to the life-history strategy of the species in that group (P: Pioneer species, LP: Long-lived Pioneer species and C: Climax species), while the numbers refer to adult stature (1: small (understorey) < 25 m, 2: medium (canopy) 25 – 35 m, 3: tall (emergent) ≥ 35 m).

FG	Species	Familiy	Vernacular name
P1	*Ambelania acida*	Apocynaceae	Makoriro
	Casearia sp.	Flacourtiaceae	Kibihidan
	Cecropia obtusa	Moraceae	Congo pump, common
	Faramea quadricostata	Rubiaceae	Kamadan, green flower
	Miconia hypoleuca	Melastomataceae	Wakaradan
	Miconia lepidota	Melastomataceae	Waraia, lepidota
	Miconia punctata	Melastomataceae	Waraia, punctata
	Palicioura crocea	Rubiaceae	Kamadan, red/orange flower
	Palicioura guianensis var. *occidentalis*	Rubiaceae	Kamadan, yellow flower
	Picramnia guianensis	Simaroubaceae	Hikuribianda, like
	Pouteria trigonosperma	Sapotaceae	Kamahora, medium leaf
	Psychotria capitata / P. puberulenta	Rubiaceae	Kamadan, white flower
	Touroulia guianensis	Quiinaceae	Fern tree
	Zanthoxylum apiculata	Rutaceae	Sada
P2	*Apeiba petoumo*	Tiliaceae	Duru
	Hyeronima alchorneoides var. *alchorneoi*	Euphorbiaceae	Suradan
	Jacaranda copaia subsp. *copaia*	Bignoniaceae	Futui
	Simarouba amara	Simaroubaceae	Simarupa
	Vochysia surinamensis var. *surinamensis*	Vochysiaceae	Iteballi
P3	*Goupia glabra*	Celastraceae	Kabukalli
	Laetia procera	Flacourtiaceae	Warakairo
	Parkia pendula	Leguminosae (M)	Hipanai
	Xylopia nitida	Annonaceae	Kuyama, white
	Xylopia pulcherrima	Annonaceae	Kuyama, red
LP1	*Alchornea* sp.	Euphorbiaceae	Kanakudiballi
	Anaxagorea dolichocarpa	Annonaceae	Kurihikoyoko
	Aniba kappleri	Lauraceae	Gale, ginger
	Aparisthmium cordatum	Euphorbiaceae	Mababalli
	Cordia nodosa	Boraginaceae	Hurueréroko
	Endlicheria punctulata	Lauraceae	Yekoro
	Guatteria sp.	Annonaceae	Arara, smooth skin
	Ilex martiniana	Aquifoliaceae	Kakotaro

FG	Species	Familiy	Vernacular name
LP1	*Panopsis sessilifolia*	Proteaceae	Mahoballi
	Paypayrola guianensis / P. longifolia	Violaceae	Adebero
	Protium guianense var. *guianense*	Burseraceae	Haiawa
	Simaba multiflora	Simaroubaceae	Hachiballi
	Tabernaemontana spp.	Apocynaceae	Pero-ishi-lokodo
	Trichilia sp.	Meliaceae	Yuriballi
	Unonopsis sp.	Annonaceae	Arara, broad leaf
LP2	*Anacardium giganteum*	Anacardiaceae	Ubudi
	Aniba citrifolia	Lauraceae	Gale, almond
	Aniba excelsa	Lauraceae	Gale, greenheart
	Aniba hypoglauca	Lauraceae	Silverballi, yellow
	Bocageopsis multiflora	Annonaceae	Arara, fine leaf
	Carapa guianensis	Meliaceae	Crabwood
	Cassia cowanii var. *guianensis*	Leguminosae (C)	Warua
	Catostemma fragrans	Bombacaceae	Baromalli, sand
	Chaunochiton kappleri	Olacaceae	Hiwaradan
	Cordia exaltata var. *exaltata*	Boraginaceae	Table tree
	Couepia guianensis cf.	Chrysobalanaceae	Kauta, fine leaf
	Dulacia guianensis	Olacaceae	Hishirudan
	Helicostylis tomentosa	Moraceae	Ituri-ishi-lokodo
	Himathanthus articulatus	Apocynaceae	Mabwa
	Hymenolobium sp.	Leguminosae (P)	Koraroballi
	Inga alba	Leguminosae (M)	Maporokon
	Inga lateriflora	Leguminosae (M)	Shirada
	Inga spp.	Leguminosae (M)	Warakosa
	Ocotea acutangula	Lauraceae	Silverballi, pear leaf
	Ocotea canaliculata	Lauraceae	Silverballi, sawari skin
	Ocotea cf. floribunda	Lauraceae	Silverballi, pea's leaf kereti
	Ocotea glomerata	Lauraceae	Silverballi, kurahara
	Ocotea oblonga	Lauraceae	Silverballi, poor kereti
	Ocotea puberula	Lauraceae	Silverballi, kereti
	Ormosia coccinea	Leguminosae (P)	Barakaro
	Ormosia coutinhoi	Leguminosae (P)	Korokororo
	Pourouma guianensis subsp. *guianensis*	Moraceae	Buruma
	Protium decandrum	Burseraceae	Kurokai
	Protium tenuifolium	Burseraceae	Haiawaballi
	Tachigali rusbyi	Leguminosae (C)	Yawaredan
	Tapirira obtusa	Anacardiaceae	Duka
LP3	*Aberema jupunba* var. *trapezifolia*	Leguminosae (M)	Huruasa
	Antonia ovata	Loganiaceae	Inyak
	Catostemma commune	Bombacaceae	Baromalli, swamp
	Couratari guianensis	Lecythidaceae	Wadara

FG	Species	Familiy	Vernacular name
LP3	*Enterolobium cf. barbebianum*	Leguminosae (M)	Devil grandfather's ear
	Enterolobium cyclocarpum	Leguminosae (M)	Devil's ear
	Hymenolobium flavum	Leguminosae (P)	Darina
	Ocotea guianensis var. *guianensis*	Lauraceae	Silverballi, shirua
	Parahancornia fasciculata	Apocynaceae	Dukali
	Parkia ulei var. *surinamensis*	Leguminosae (M)	Uya
	Pouteria caimito	Sapotaceae	Asepokoballi, fine leaf
	Pouteria speciosa	Sapotaceae	Suya
	Pseudopiptadenia suavolens	Leguminosae (M)	Manariballi, like
	Ruizterania albiflora	Vochysiaceae	Muneridan
	Sclerolobium guianense var. *guianense*	Leguminosae (C)	Kaditiri
	Sterculia pruriens	Sterculiaceae	Maho, smooth leaf
	Sterculia rugosa	Sterculiaceae	Maho, rough leaf
	Swartzia jenmanii	Leguminosae (P)	Parakusan
	Trattinickia demerarae	Burseraceae	Ulu, rough skin
	Trattinickia rhoifolia	Burseraceae	Ulu, smooth skin
	Virola sebifera	Myristicaceae	Dalli, like
C1	*Amaioua guianensis* var. *guianensis*	Rubiaceae	Komaramaraballi
	Calyptranthes forsteri	Myrtaceae	Kakirio
	Cheiloclinium cognatum	Hippocrateaceae	Monkey syrup
	Cupania cf. scrobiculata	Sapindaceae	Kulishiri, black
	Cupania hirsuta	Sapindaceae	Kulishiri, hairy black
	Duguetia neglecta	Annonaceae	Yari yari
	Duguetia yeshidan	Annonaceae	Yeshidan
	Duroia eriophila var. *eriophila*	Rubiaceae	Komaramara
	Eugenia coffeifolia	Myrtaceae	Banyaballi
	Eugenia conjuncta	Myrtaceae	Konoko shrub
	Eugenia patrisii	Myrtaceae	Hichu
	Heisteria cauliflora	Olacaceae	Makarasali
	Hirtella cf. caduca	Chrysobalanaceae	Fire tree
	Hirtella racemosa var. *hexandra*	Chrysobalanaceae	Unknown Hirtella
	Ixora aluminicola	Rubiaceae	Coffeeballi
	Marlierea schomburgkiana	Myrtaceae	Akarako
	Matayba cf. oligandra	Sapindaceae	Kulishiri, white
	Mouriri sp.	Melastomataceae	Mamuriballi
	Myrcia sp.	Myrtaceae	Ibibanaro
	Oxandra asbeckii	Annonaceae	Karishiri
	Quiina guianensis	Quiinaceae	Okokonshi, fine leaf
	Rheedia benthamiana	Guttiferae	Asashi
	Sandwithia guianensis	Euphorbiaceae	Unknown A
	Siparuna decipiens	Monimiaceae	Shitwood
	Siparuna sp.	Monimiaceae	Muniridan
	Sloanea cf. eichleri	Eleocarpaceae	Aruadan, broad rough leaf

FG	Species	Familiy	Vernacular name
C1	*Sloanea guianensis*	Eleocarpaceae	Aruadan
	Tapura guianensis	Dichapetalacea	Waiaballi
	Tovomita spp.	Guttiferae	Awasokule
C2	*Aspido*sperma *album*	Apocynaceae	Shibadan, smooth leaf
	Balizia pedicellaris	Leguminosae (M)	Manariballi, common
	Brosimum guianense	Moraceae	Tibokushi
	Brosimum rubescens	Moraceae	Dukaliballi
	Byrsonima aerugo	Malpighiaceae	Arikadako
	Byrsonima stipulacea	Malpighiaceae	Kanoaballi
	Caryocar nuciferum	Caryocaraceae	Sawari
	Chaetocarpus schomburgkianus	Euphorbiaceae	Ruri
	Chlorocardium rodiei	Lauraceae	Greenheart
	Chrysophyllum pomiferum	Sapotaceae	Paripiballi
	Chrysophyllum sanguinolentum	Sapotaceae	Barataballi
	Clathrotropis brachypetala var. *brachypetala*	Leguminosae (P)	Aromata
	Couepia cf. exflexa	Chrysobalanaceae	Aruadan
	Dipteryx odorata	Leguminosae (P)	Tonka bean
	Emmotum fagifolium	Icacinaceae	Manobodin
	Eschweilera coriacea	Lecythidaceae	Kakaralli, smooth leaf
	Eschweilera sagotiana	Lecythidaceae	Kakaralli, black
	Eschweilera wachenheimii	Lecythidaceae	Kakaralli, thick skin
	Geissospermum sericeum	Apocynaceae	Manyokinaballi
	Hebapetalum humiriifolium	Linaceae	Shiballidan
	Lecythis confertiflora	Lecythidaceae	Wirimiri
	Lecythis corrugata	Lecythidaceae	Wina
	Lecythis holcogyne	Lecythidaceae	Haudan
	Lecythis zabucajo	Lecythidaceae	Monkey pot
	Licania alba	Chrysobalanaceae	Kautaballi
	Licania cf. canescens	Chrysobalanaceae	Marishiballi
	Licania heteromorpha	Chrysobalanaceae	Buruburuli
	Licania heteromorpha var. *perplexans*	Chrysobalanaceae	Kairiballi
	Licania hypoleuca	Chrysobalanaceae	Unikiakia
	Licania laxiflora / L. persuadii	Chrysobalanaceae	Kauta
	Maytenus myrsinoides	Celastraceae	Kaiarima
	Micropholis venulosa	Sapotaceae	Kudibiushi
	Minquartia guianensis	Olacaceae	Wanania
	Mora gongrijpii	Leguminosae (C)	Morabukea
	Neea sp.	Nyctaginaceae	Mamudan
	Pentaclethra macroloba	Leguminosae (M)	Trysil
	Pouteria cf. filipes	Sapotaceae	Kamahora, fine leaf
	Pouteria cf. venosa subsp. *amazonica*	Sapotaceae	Kamahora, broad leaf
	Pouteria cladantha	Sapotaceae	Aiomorakushi
	Pouteria coriacea	Sapotaceae	Moraballi

FG	Species	Familiy	Vernacular name
C2	*Pouteria egregia*	Sapotaceae	Kokoritiballi, fine leaf
	Pouteria guianensis	Sapotaceae	Asepoko
	Quiina cf. obovata / Q. indigofera	Quiinaceae	Okokonshi
	Swartzia benthamiana var. *benthamiana*	Leguminosae (P)	Itikiboroballi
	Swartzia oblanceolata	Leguminosae (P)	Serebedan
	Swartzia spp.	Leguminosae (P)	Itikiboroballi, others
	Talisia squarrosa	Sapindaceae	Moroballi
	Trymatococcus paraensis	Moraceae	Pasture tree
	Vouacapoua macropetala	Leguminosae (C)	Sarebebeballi
C3	*Aspido*sperma *cruentum*	Apocynaceae	Shibadan, boat leaf
	*Aspido*sperma *exselsum*	Apocynaceae	Yaruru
	Diplotropis purpurea var. *purpurea*	Leguminosae (P)	Tatabu
	Eperua falcata	Leguminosae (C)	Wallaba, soft
	Glycydendron amazonicum	Euphorbiaceae	Devildoor tree
	Hymenaea courbaril var. *courbaril*	Leguminosae (C)	Locust
	Licania cf. micrantha	Chrysobalanaceae	Marishiballi, high bush
	Licania majuscula	Chrysobalanaceae	Kautaballi, fine leaf
	Licania sp.	Chrysobalanaceae	Konoko
	Licaria cannella	Lauraceae	Silverballi, brown
	Mora excelsa	Leguminosae (C)	Mora
	Parinari campestris	Chrysobalanaceae	Burada
	Peltogyne sp.	Leguminosae (C)	Purpleheart, saka
	Peltogyne venosa subsp. *densiflora*	Leguminosae (C)	Purpleheart
	Pouteria reticulata subsp *surinamensis*	Sapotaceae	Kokoritiballi, common
	Sacoglottis guianensis var. *guianensis*	Humiriaceae	Dukuria
	Swartzia leiocalycina	Leguminosae (P)	Wamara
	Terminalia amazonia	Combretaceae	Fukadi
	Zygia racemosa	Leguminosae (M)	Tureli

Samenvatting

Tropische regenbossen herbergen heel veel soorten en zijn dus waardevol om te behouden. Toch worden deze belangrijke ecosystemen met name de afgelopen decennia steeds meer door grootschalige ontbossing en onzorgvuldige houtkap bedreigd. Selectieve houtkap - waarbij slechts enkele bomen worden gekapt en het bos als geheel overeind blijft - kan een goede manier zijn om het bos te gebruiken zonder het te vernietigen. In Guyana is hardhout, verkregen uit selectieve kap, een belangrijke bron van inkomsten. Om dit op een duurzame manier te doen, moeten zowel de houtopbrengst als de natuurwaarde van het bos op termijn gehandhaafd blijven.

Selectieve houtkap richt zich in Guyana vooral op een aantal hardhoutsoorten, waarvan een deel van de gezonde, en vaak de grootste, individuen geoogst worden. Hoewel meestal maar een paar bomen per hectare geoogst worden, kan de schade aan het omliggende bos lokaal aanzienlijk zijn, als gevolg van onzorgvuldig vellen van bomen en uitslepen met zware machines. Verder ontstaan door selectieve houtkap gaten in het kronendak van het bos en is er dus onderin het bos meer licht. Hierdoor kunnen sommige boomsoorten - de "pioniers" - veel sneller groeien. Op termijn kan dit tot een verandering van de soortensamenstelling in het bos leiden. Het doel van het onderzoek beschreven in dit proefschrift was om de gevolgen van selectieve houtkap voor de samenstelling van het bos en de toekomstige houthoeveelheden te bepalen. Hiertoe is in het kader van het Tropenbos-Guyana programma veldonderzoek in gekapt en ongestoord bos in Guyana gedaan. Daarnaast is een simulatiemodel opgesteld om de lange-termijn effecten te kunnen inschatten. Dit model simuleert de groei, overleving en regeneratie van bomen en doet voorspellingen van de bossamenstelling en de hoeveelheid hardhout in de loop van decennia. De belangrijkste resultaten worden verder in de volgende paragrafen samengevat en bediscusieerd.

Functionele groepen

In tropische bossen komen veel boomsoorten in zulke lage dichtheden voor dat statistische analyses van demografische processen, zoals groei, mortaliteit en rekrutering vaak niet erg zinvol zijn. Daarom zijn in dit proefschrift boomsoorten objectief in negen functionele groepen met vergelijkbare ecologische eigenschappen en responsen op houtkap ingedeeld. De indeling was op drie morfologische kenmerken gebasseerd: houtdichtheid, zaadgewicht en hun statuur (de potentiële hoogte die bomen in het kronendak bereiken). Dit zijn goede voorspellers van de responsen van bomen op verstoring in termen van groei, mortaliteit en regeneratie. Een combinatie van houtdichtheid en zaadmassa is gebruikt om drie 'life-history'-strategieën te klassificeren (pioniers, lang-levende pioniers en climaxsoorten). In hoofdstuk 2 wordt alleen deze indeling in drie functionele groepen gebruikt, terwijl in de andere hoofdstukken ieder van deze drie 'life-history'-groepen weer in drie sub-groepen wordt onderverdeeld op basis van de statuur van volwassen bomen (klein, intermediair en lang, hetgeen in bos met een gesloten kronendak overeenkomt met respektievelijke kroonposities in de ondergroei, in het kronendak en boven het kronendak uitstekend). Van bomen in de verschillende functionele groepen wordt verwacht dat ze verschillend op veranderingen in de lichtbeschikbaarheid, veroorzaakt door selectieve houtkap, reageren.

Geobserveerde korte termijn effecten

In hoofdstuk 2 worden de korte termijn (5 tot 6 jaar) effecten van selectieve houtkap op populatiedynamiek, soortensamenstelling en soortendiversiteit van bomen voor twee verschillende gebieden in Guyana bestudeerd. Met de data van proefvlakken in Pibiri in centraal Guyana, het belangrijkste onderzoeksgebied voor dit proefschrift, zijn de korte termijn effecten van houtkap op lichtbeschikbaarheid en populatiedynamiek van 'saplings' (boomopslag met 2-5 cm diameter op borsthoogte, DBH) en 'poles' (opgroeiende bomen met 5-20 cm DBH) bestudeerd. Hiervoor zijn de boomsoorten in drie functionele groepen (pioniers, langlevende pioniers en climaxsoorten) ingedeeld. De twaalf gebruikte en experimenteel, met een schadebeperkend oogstsysteem, gekapte permanente proefvlakken in Pibiri ondergingen 4 verschillende kapintensiteiten. De gebruikte kapintensiteiten waren: 0 (contole), 4, 8 of 16 bomen per hectare, die steeds in drie proefvlakken herhaald werden (voor een uitgebreide beschrijving zie: van der Hout 1999, van der Hout 2000).

De boomgemeenschap in niet gekapt bos lijkt aan een lage intensiteit en lage frequentie van verstoring te zijn aangepast. De meeste bomen in deze bossen behoren tot de climaxsoorten (meer dan 50% van de bomen), terwijl de pioniers minder dan 1% van de bomen in het bos vertegenwoordigen. Als maat voor de verschillen in lichtbeschikbaarheid is de Dawkin's kroonbelichtingsindex gebruikt. Deze index wordt visueel op een ordinale schaal afgeschat, waarbij lichtbeschikbaarheid in een vijftal klassen wordt ingedeeld. Verder werden voor de proefvlakken in Pibiri en additioneel voor proefvlakken in het noordwesten van Guyana (alleen gekapte en niet gekapte proefvlakken zij daar onderscheiden) veranderingen in de functionele-groepen-samenstelling van het bos en de boomsoortendiversiteit op verschillende momenten na kap bestudeerd.

Zes jaar na kap was de lichtbeschikbaarheid voor 'saplings' en 'poles' nog steeds aan de kapintensiteit gerelateerd. Het aandeel van saplings' en 'poles' met een hogere Dawkin's index nam met toenemenende intensiteit van de houtkap toe. Over het algemeen nam de groeisnelheid van bomen uit alle functionele groepen toe met toenemende kapintensiteit. Dit suggereert, dat in principe alle soorten van de toegenomen lichtbeschikbaarheid na kap profiteren. In de hoogste lichtbeschikbaarheidsklassen zijn de groeisnelheden van de pioniersoorten echter veel hoger dan van bomen uit de andere twee functionele groepen. Daarnaast leidde op plekken met een hoge lichtbeschikbaarheid met name de sterk toegenomen rekruteringssnelheid van de pioniersoorten (47% per jaar) tot een snelle toename (44% per jaar) van de boompopulatie van deze functionele groep. Over het algemeen werden de pioniersoorten relatief vaker op plekken met een hoge lichtbeschikbaarheid dan bomen uit beide andere functionele groepen aangetroffen.

In de gekapte proefvlakken in het noordwesten nam het relatieve aandeel van de pioniersoorten toe van 1% tot 7% voor ‘saplings’ en van 2% tot 8% voor de ‘poles’. In de Pibiri proefvlakken nam het relatieve aandeel van de pioniersoorten in de proefvlakken met de hoogste kapintensiteit (16 bomen per hectare) toe van 0% tot 6,2% voor de ‘saplings’, terwijl er bij de overige behandelingen en bij de ‘poles’ geen significante veranderingen optraden. De ‘timing’ en de omvang van de veranderingen verschilden tussen beide onderzoeksgebieden. In het noordwesten was na 2 tot 3 jaar de toename van het aandeel van ‘saplings’ van pioniersoorten al merkbaar, terwijl dit in de plots in Pibiri 4 tot 6 jaar duurde. Ook nam in de plots in het noordwesten binnen 5 jaar het aandeel van ‘poles’ van de pioniersoorten toe, terwijl in de Pibiri plots zelfs na 6 jaar nog geen significante verandering optrad. De verschillen tussen beide gebieden kunnen door de hogere groeisnelheden van pioniersoorten in de proefvlakken in het noordwesten worden verklaard, die waarschijnlijk het gevolg zijn van een hogere nutrientenbeschikbaarheid in de bodem van de proefvlakken in het noordwesten. Hierdoor zullen zaailingen in het noordwesten sneller de grootte-ondergrens van de ‘sapling’-grootteklasse bereiken.

In alle gevallen gaat de toename van het relatieve aandeel van pioniersoorten samen met een afname van het relatieve aandeel van de climaxsoorten. In beide onderzoeksgebieden neemt voor de ‘saplings’ de alfa-diversiteit, berekend als Fisher’s alfa, toe met toenemende mate van verstoring (uitgedrukt als relatieve afname van de totale stamoppervlakte (‘basal area’)) als gevolg van selectieve houtkap. Deze resultaten zijn in overeenstemming met de “intermediaire verstoringshypothese” die voorspelt dat in bossen met weinig verstoring en een relatief lage diversiteit, zoals die in Guyana voorkomen, meer verstoring tot een hogere boomsoortendiversiteit zal leiden. Selectieve houtkap verhoogt lokaal de lichtbeschikbaarheid en schept daardoor meer geschikte habitatplekken voor succesrijke verjonging van pioniersoorten die voor de houtkap vrijwel afwezig waren. Toch is de omvang van de toename van het aantal pionierbomen in absolute zin tamelijk gering en breiden ze zich niet op grote schaal uit. Dit komt zeer waarschijnlijk door de zeer lage dichtheid van volgroeide pionierbomen in het ongekapte bos waardoor de aanvoer van zaden beperkt blijft.

Hoe kunnen lange termijn effecten worden bestudeerd?

Veel tropische bomen groeien erg langzaam en kunnen wel tot enkele eeuwen oud worden. Daardoor kunnen de consequenties van veranderingen in hedendaagse demografische trends, zoals die door selectieve houtkap veroorzaakt worden, pas na een lange tijdsperiode empirisch vastgesteld worden. De volle omvang van de invloed van houtkap op soortensamenstelling zal daarom veelal pas na lange tijd duidelijk worden. Er zijn nog maar weinig empirische gegevens voorhanden die gedurende een voldoende lange tijdsperiode na kap zijn verzameld. Als deze data al voorhanden zijn, dan is het probleem vaak dat kappraktijken in het verleden niet meer met moderne houtkap vergelijkbaar zijn. Daarom verschaffen bestaande data die gedurende lange tijd zijn verzameld vaak weinig inzicht in de effecten van de huidige houtkappraktijken. Nieuwe simulatiemodellen voor tropische bossen zijn daarom de aangewezen wijze om instantane projecties van de effecten van houtkap voor de lange termijn (decennia tot eeuwen) te maken. Voor het onderzoek in dit proefschrift is een simulatiemodel van de populatiedynamiek voor de bossen in centraal Guyana opgesteld en binnen het SYMFOR modelleer-raamwerk geïmplementeerd (zie Phillips & van Gardingen 2001a, 2001b, Phillips *et al*. 2003, 2004, hoofdstuk 3). Vervolgens is dit model gebruikt om voor de bossen in centraal Guyana de duurzaamheid van verschillende alternatieve houtkapscenarios te evalueren en hun effecten op de bossamenstelling op lange termijn te bepalen.

Model

Het ecologische model (hoofdstuk 3) is aan de hand van data van de experimenteel met een schadebeperkend oogstsysteem gekapte, permanente proefvlakken in Pibiri in centraal Guyana opgesteld. Het model is op individuele bomen gebaseerd en ruimtelijk expliciet. Dit houdt in dat bomen individueel vertegenwoordigd zijn en een unieke ruimtelijke positie in het gesimuleerde bos innemen. In dit proefschrift wordt een ondergrens voor de grootte van gesimuleerde bomen van 2 cm DBH gehanteerd en worden altijd bosoppervlakten van één hectare gesimuleerd.

Het model simuleert de drie belangrijkste demografische processes in boompopulaties, namelijk groei, mortaliteit en rekrutering. Voor individuele bomen hangen de snelheden van deze processen van de eigen grootte van de individuele boom (bij groei) en concurrentie, voornamelijk om licht, met andere bomen af. De functies, die de demografische processen beschrijven, zijn met behulp van data voor negen functionele groepen afgeleid en geparameteriseerd. Concurrentie tussen individuele bomen wordt door middel van een afstands- en grootte-afhankelijke concurrentie-index, die direct met waargenomen velddata afgeschat is, gesimuleerd. Iedere boom heeft een DBH, die gebruikmakend van een diameter-groei-functie, tijdens iedere tijdstap aangepast wordt. Andere allometrische eigenschappen van de bomen, zoals de diameter van de kroon en de hoogte van de boom worden vervolgens aan de hand van allometrische functies bepaald die zijn afgeleid van een regressie met DBH. Iedere tijdstap wordt, aan de hand van een deels stochastische mortaliteitsfunctie, voor iedere boom bepaalt of de boom doodgaat of overleeft. Bomen die doodgaan hebben een bepaalde kans om in een willekeurige richting om te vallen en zo buurbomen te beschadigen of te doden. De functie voor rekrutering beschrijft het verschijnen van nieuwe bomen met een DBH van 2 cm. De kans dat een nieuwe boom in een gridcel van 25 m^2 in het gesimuleerde bos wordt gerekruteerd hangt van de lichtbeschikbaarheid in het betreffende kwadraat af. Het model draait met jaarlijkse tijdstappen.

Aan de hand van de voor het model geparameteriseerde functies konden verschillen tussen de demografische snelheden van de verschillende functionele groepen bepaald worden. Zoals zou kunnen worden verwacht, hadden de pioniergroepen de snelste diametergroei voor bomen met een DBH kleiner dan 20 cm, terwijl de climaxgroepen de langzaamste groeisnelheid hadden. Omdat de relaties tussen DBH en hoogte voor bomen kleiner dan 20 cm DBH voor alle functionele groepen vergelijkbaar waren, kan worden geconcludeerd dat pioniersoorten ook sneller de hoogte in groeiden. De twee grootste langlevende-pioniergroepen lieten de sterkste toename in groeisnelheid bij een toename van de lichtbeschikbaarheid zien. Dit is in tegenstelling tot de verwachting, dat deze reactie het sterkst zou optreden bij de lichtbehoeftige pioniergroepen. Dit zou echter verklaard kunnen worden door het feit dat pionierbomen over het algemeen alleen op plekken worden gevonden waar de lichtbeschikbaarheid al hoog is. Deze soorten hebben intrinsiek een hoog lichtcompensatiepunt voor de fotosynthese versus ademhaling van de gehele plant. Daarom hebben ze een grotere kans om op beschaduwde plekken dood te gaan, waar gereduceerde fotosynthese voor verloren gegane biomassa en de inherent hoge ademhaling niet kan kompenseren (zie bijvoorbeeld Popma & Bongers 1988, Veneklaas & Poorter 1998, Poorter 1999). De gemiddelde waargenomen waarde voor de concurrentie-index was dan ook veel lager voor individuen uit de pioniergroepen. Dit wijst er op, dat pionierbomen inderdaad vooral op plekken voorkomen waar de lichtbeschikbaarheid hoger (concurrentie-index lager) is. Daarbij komt nog dat er slechts een kleine bandbreedte in concurrentie-indexwaarden voor de pionierbomen gevonden was, waardoor hun groei-response op een toename van de lichtbeschikbaarheid onvermijdelijk slechts gering kan zijn.

De pionierbomen lieten daarentegen wel een zeer sterke toename van de mortaliteitskans met toenmende concurrentie-index (meer beschaduwing) zien. Op plekken met een hoge concurrentie-index gaan er dus gedurende een meetinterval meer pionierbomen dood en derhalve kunnen deze niet in de groei-analyse betrokken worden. Daarnaast hadden de pioniersoorten op plekken met een hoge concurrentie-index ook een zeer lage kans om daar met succes een nieuw individu te rekruteren. Deze kans op rekrutering nam voor pioniers echter met afnemende concurrentie-index (toenemende lichtbeschikbaarheid) zeer sterk toe. Deze resultaten zijn in overeenstemming met de algemeen geldende opvattingen, dat pioniersoorten veel licht nodig hebben voor succesvolle rekrutering (zie bijvoorbeeld

Brokaw 1987, Alvarez-Buylla & Martínez-Ramos 1992, Ellison *et al.* 1993, Peña-Claros 2003 en de resultaten in hoofdstuk 2).

In modelsimulaties zonder houtkap met een gesimuleerde tijdsperiode van 1000 jaar veranderde de abundantie van sommige van de functionele groepen gedurende de gesimuleerde tijd. Binnen 250 jaar hadden alle functionele groepen echter een stabiel aantal bomen per hectare gesimuleerd bos bereikt. Hoewel dit stabiele aantal bomen per hectare voor de kleinste climaxgroep zelfs 2,5 keer hoger lag dan het aantal bomen in de uitgangssituatie, bleven alle gesimuleerde abundanties binnen de spreiding van de in de permanente proefvlakken geobserveerde variatie in abundanties. In hoofdstuk 3 worden mogelijke oorzaken voor de in de simulaties geobserveerde veranderingen in abundanties bediscussieerd.

Een uitgebreide gevoeligheidsanalyse van het model toonde aan dat het model behoorlijk robuust is voor kleine veranderingen in de waarden van geteste modelcomponenten (groei, mortaliteit, rekrutering en drie parameters die deze processen direct beïnvloeden). Een uitzondering hierop vormden de groepen van pioniersoorten waarvoor, na kleine veranderingen in de waarden van met name mortaliteits- en rekruteringskansen, relatief grote veranderingen in zowel abundanties als totale stam oppervlakte (‘basal area’) gevonden werden. Over het algemeen zijn de modelresultaten vooral gevoelig voor mortaliteit en rekrutering. Dat zijn tevens de modelcomponenten die met de grootste onzekerheid zijn afgeschat. Deze resultaten van de gevoeligheidsanalyse zijn in overeenstemming met de resultaten van andere studies (Kammesheidt et al. 2001, Phillips et al. 2003). Omdat de hoge onzekerheid in het afschatten van mortalities- en rekruteringskansen grotendeels door relatief kleine steekproefgrootte veroorzaakt worden, zou toekomstig onderzoek zich met name op de mortaliteits- en rekruteringsprocessen moeten richten. Dit betekent dat, in vergelijking met metingen aan groeisnelheden, rekening houdend met de relatieve zeldzaamheid van mortaliteit en rekrutering, gegevens over deze processen in grotere proefvlakken of over langere tijdsperioden verzameld moeten worden.

Scenario’s voor duurzaam bosbeheer

In hoofdstuk 4 zijn de lange-termijn effecten van verschillende houtkapscenario’s bepaald op abundanties van bomen ingedeeld in negen functionele groepen, soortensamenstelling, houtopbrengsten en de tijd nodig om na kap te herstellen. Hiervoor is van het ecologische simulatiemodel, dat in hoofdstuk 3 wordt beschreven, gebruik gemaakt, in combinatie met een hieraan gekoppeld bosbeheersmodel in het SYMFOR modelleer-raamwerk.

Het bosbeheersmodel simuleert de houtkap, het uitslepen van gekapte bomen met behulp van zware machines (“skidders”) en de daarmee gepaard gaande schade aan het omliggende bos. De parameters in het model zijn zo gekozen dat de gesimuleerde houtkap zoveel mogelijk de regelgeving in Guyana volgt. Daarnaast werden het gericht vellen van bomen en gecontroleerde uitsleep gesimuleerd om een zekere mate van schadebeperkende houtoogstmethoden na te bootsen. Op een vergelijkbare wijze als de functionele groepen in het ecologsiche model gebruikt worden, maakt het bosbeheersmodel gebruik van gebruiksgroepen. In deze gebruiksgroepen worden soorten met een vergelijkbare commerciële waarde en beheersvoorschriften samengevoegd. De geëvalueerde bosbeheersscenario's verschillen in combinaties van kapintensiteit (KI: 4, 8, of 12 bomen per hectare), minimale kapdiameter (MKD, de DBH die een boom minimaal moet hebben voordat hij gekapt mag worden: 35 of 60 cm DBH) en kapcyclus (FC, de tijd tussen twee opeenvolgende keren kappen: 25, 40 of 60 jaar). De beginsituaties van de uitgevoerde simulaties waren gebaseerd op gegevens uit de drie permanente proefvlakken die niet gekapt waren.

Na één keer kappen herstelden, bij simulaties van alle combinaties van kapintensiteit en minimale kapdiameter, de comerciële volumes zich tot waarden die vergelijkbaar waren met controle-simulaties zonder houtkap. Bij de hoogste kapintensiteiten hadden de twee meest economisch waardevolle gebruiksgroepen meer dan 100 jaar nodig om de kapbare hourvolumes weer te herstellen. Dit duurt substantieel langer dan de huidige in Guyana geadviseerde lengte van een kapcyclus van 60 jaar. Als gevolg hiervan namen de kapbare volumes hardhout met verloop van tijd zelfs nog bij de scenario's met de laagste kapintensiteit (4 bomen ha^{-1}) en de langste lengte van de kapcyclus (60 jaar) af.

De houtopbrengsten van de tweede en derde kap als percentage van de houtopbrengst van de eerste kap namen met toenemende lengte van de kapcyclus toe. Als binnen kapcycli van gelijke duur de verschillende kapintensiteiten met elkaar vergeleken worden, blijkt dat het hoogste percentage gerealiseerd wordt bij de laagste kapintensiteiten. Voor de scenario's met de langste kapcyclus (60 jaar) waren de opbrengsten van de tweede en derde kap over het algemeen 90% of meer van de houtopbrengsten die tijdens de eerste kap werden behaald, terwijl de percentages bij de kortste kapcyclus (25 jaar) varieerde van 37% tot 79% ten opzichte van de eerste kap. De totale houtopbrengst van drie keer kappen is het hoogst bij de beheersscenario's met de hoogste kapintensiteit, onafhankelijk van de lengte van de kapcyclus. De hoogste gemiddelde jaarlijkse houtopbrengsten worden echter met de kortste lengte van kapcyclus, de laagste minimale kapdiameter en de hoogste kapintensiteit (het meest ingrijpende scenario) behaald. Deze combinatie van hoge kapintensiteiten en korte kapcyclus leidde echter ook tot een snelle uitputting van de beschikbare hoeveelheid hardhout in het bos waardoor er tijdens opeenvolgende kapcycli steeds minder hout geoogst kan worden.

Na één keer kappen herstelden, bij simulaties van alle combinaties van kapintensiteit en minimale kapdiameter, ook de abundanties van de functionele groepen zich weer tot waarden die vergelijkbaar waren met controle-simulaties zonder houtkap. Hoewel er binnen functionele groepen een verschuiving van soortensamenstelling kan optreden, kan dit met het huidige model niet worden onderzocht. Over het algemeen genomen nam de tijd nodig voor herstel van de abundanties van de functionele groepen met toenemende kapintensiteit toe. De langste hersteltijden werden gevonden voor de kleinste pioniersoorten, de kleinste climaxsoorten en de climaxsoorten van intermediaire grootte. De kleinste pioniers namen na kap in eerste instantie sterk toe, waarna 82 tot 113 jaar (afhankelijk van de kapintensiteit) nodig was voordat de abundanties weer tot waarden vergelijkbaar met de controle simulaties afgenomen waren. De twee climaxgroepen daarentegen namen door de kap sterk af in abundanties en hadden 111 tot 161 jaar (kleinste climaxgroep) en 83 tot 120 jaar (intermediaire climaxgroep) nodig om het verlies van individuen door kap weer aan te vullen.

Omdat de kapcycli van alle gesimulleerde kapscenario’s korter waren dan de hersteltijden voor de abundanties van de verschillende functionele groepen, nemen de abundanties van de pioniers na iedere opeenvolgende kap verder toe, terwijl de abundanties van de climaxgroepen daarentegen steeds verder afnemen. Dit effect was kleiner voor de langere kapcycli, maar was sterker naarmate de kapintensiteit hoger was. Omdat in gesimuleerde scenario’s met een hoge kapintensiteit en een korte kapcyclus na verloop van tijd het aantal bomen dat tijdens opeenvolgende kapcycli gekapt kan worden afneemt (hoge opbrengsten konden niet volgehouden worden), vlakte in simulaties ook het effect van kappen na verloop van tijd af.

Na drie keer kappen was in bijna alle gesimuleerde scenario’s de samenstelling van het bos significant veranderd. Alleen voor de scenario’s met een kapcyclus van 60 jaar en een kapintensiteit van 4 bomen per hectare was dit niet het geval. Alle lange termijn veranderingen in de samenstelling van het bos kwamen op een toename van het relatieve aandeel van de pioneersoorten en een afname van het relatieve aandeel van de climaxsoorten neer. Dit is in overeenstemming met de in het veld geobserveerde korte termijn veranderingen. Echter, zelfs in het scenario met de meeste intensieve vorm van houtkap (kapcyclus van 25 jaar met een kapintensiteit van 12 bomen ha^{-1}) waren deze veranderingen nog steeds redelijk gering. Hierin nam het relatieve aandeel van de drie pioniergroepen toe van 0,3% tot 3,5%, terwijl tegelijkertijd het relatieve aandeel van de climaxgroepen van 72% tot 64% gereduceerd werd.

De resultaten van deze scenario-studie kunnen nu worden gebruikt om de verschillende houtkapscenario’s te rangschikken voor wat betreft hun houtopbrengsten (totale houtopbrengst, gemiddelde jaarlijkse houtoprengst), de duurzaamheid van de houtwinning (houtopbrengst als percentage van de eerste kap) en effecten op de natuurwaarde van het bos (soortensamenstelling en bosstructuur). Bosbeheerders en beleidsmakers in Guyana kunnen deze resultaten dan, in combinatie met gegevens over de economische haalbaarheid van de scenario’s, weer gebruiken in een multipele criteria-analyse om normen en criteria voor duurzaam bosbeheer vast te stellen. Daarvoor zullen dan wel nog belangrijke (politieke en economische) afwegingen over een eventuele weging van de verschillende factoren gemaakt moeten worden.

De resultaten van deze studie laten verder zien, dat het mogelijk is om de bossen in centraal Guyana op een manier te beheren die enerzijds leidt tot relatief kleine veranderingen in de bossamenstelling en anderzijds ook leidt tot een duurzame houtwinning. Hiervoor zouden waarschijnlijk alle bosbeheerspraktijken met een kapcyclus van 60 jaar in aanmerking komen. Naarmate de kapintensiteiten hoger zullen liggen, zullen de negatieve effecten op bossamenstelling en bosstructuur sterker zijn en de duurzaamheid van de houtwinning lager, maar de houtopbrengsten zullen daarentegen dan juist weer hoger zijn. Doordat de samenstelling van functionele groepen na kap niet heel drastisch verandert, kan geconcludeerd worden dat de gekapte bossen in Guyana nog steeds een hoge natuurwaarde hebben.

Niettemin duurt het 100 jaar en langer voordat, na houtkap, de kapbare houtvolumes en de abundanties van de functionele groepen zich weer hersteld hebben. Dit is erg lang en bijna twee keer zo lang dan de huidige in Guyana geadviseerde kapcyclus met een lengte van 60 jaar. Daarom zouden beleidsmakers zeker ook moeten overwegen om slechts één houtkap, mogelijkerwijs met hoge kapintensiteiten, toe te staan waarna het bos weer volop (meer dan 100 jaar) de gelegenheid gegeven wordt om volledig te herstellen. De haalbaarheid hiervan zal in belangrijke mate afhangen van wat er na de houtkap met het bos gaat gebeuren en dit scenario heeft alleen zin als het bos daarna ook echt verder met rust wordt gelaten.

Een belangrijk argument dat vaak tegen zo een bosbeheerspraktijk wordt aangevoerd is, dat gekapt bos, dat niet meer door bosbouwbedrijven in gebruik is, vaak een grotere kans heeft om tot landbouwgrond omgegevormd te worden. In Guyana is de populatiedruk van mensen echter zeer gering. Daardoor komt grootschalige conversie van tropisch regenwoud naar landgebruik als bijvoorbeeld weiland of oliepalm- en sojaboonplantages nauwelijks voor. De meeste landbouw wordt bedreven in een smalle strook langs de kust van Guyana, waar ook het merendeel van de ongeveer achthonderduizend inwoners woont. In het binnenland van Guyana wordt door kleine indianengemeenschappen slechts op kleine schaal landbouw ten behoeve van het eigen levensonderhoud bedreven.

Andere argumenten tegen het toestaan van het slechts één keer kappen van een bepaald bosgebied zouden vanuit een financieel oogpunt aangevoerd kunnen worden. Houtkapbedrijven zijn mogelijk bezorgd over de financiële winst die uit een bepaald bosgebied gehaald kan worden. Echter, als de totale houtopbrengst van drie keer kappen bij het beheersscenario met de hoogste duurzaamheid van de houtwinning (dus bij tweede en derde kap de hoogste houtopbrengst als percentage van de eerste kap) vergeleken wordt met één keer kappen met een intensiteit van 12 bomen per hectare, blijken de verschillen in houtopbrengst redelijk mee te vallen (55 m^3 h^{-1} tegen 44 m^3 h^{-1}). Gezien het feit dat na één keer kappen met 12 bomen per hectare de lange termijn effecten van kap gering bleken, zouden bij één keer kappen waarschijnlijk zonder al te ingrijpende negatieve effecten ook meer bomen per hectare gekapt kunnen worden, waardoor het opbrengstverschil nog geringer wordt.

Momenteel is conflicterend landgebruik tussen enerzijds houtkap en anderzijds mijnbouw (goud en diamanten) waarschijnlijk de belangrijkste bedreiging voor duurzaam bosbeheer in Guyana. Hoewel mijnbouw veelal op een kleinere schaal plaatsvindt, kan het lokaal veel destruciever voor het bos zijn dan selectieve houtkap. Voor mijnbouw worden stukken bos volledig ontbost en het leidt vaak tot vervuiling van grond- en opppervlaktewater. Voor de overheid in Guyana heeft mijnbouw prioriteit boven houtkap, omdat de relatieve opbrengsten uit mijnbouw vaak hoger liggen dan bij hout. De bossen in het binnenland zijn erg uitgestrekt en zeer dunbevolkt en de landsgrenzen zijn grotendeels onbewaakt. Dat maakt het erg moeilijk om de regulaties over mijnbouwwerkzaamheden goed te controleren en zo illegale mijnbouw tegen te gaan. Daardoor frustreert en vernielt zowel legale als illegale mijnbouw vaak de investeringen en inspanningen van houtkapbedrijven om duurzame bosbeheersmethoden te gebruiken waardoor de bereidheid hiervoor afneemt.

Regeneratie in modellen

In het simulatiemodel dat in hoofdstuk 3 is gepresenteerd en bij veel ander modellen beschreven in de literatuur, wordt regeneratie vaak gemodelleerd als een kans dat een nieuwe boom met een bepaalde DBH in het gesimuleerde bos verschijnt (2 cm DBH in deze studie). Hierbij wordt het zaailingenstadium vaak overgeslagen, terwijl dit stadium wel een belangrijke rol speelt in het bepalen van de toekomstige struktuur en samenstelling van het bos. Daarnaast is in het hier beschreven model, net als in voorgaande ecologische modellen in het SYMFOR modelleer-raamwerk, het aantal nieuwe individuen dat jaarlijks gerekruteerd wordt onafhankelijk van het aantal ouderbomen van dezelfde soort. De reden hiervoor is dat in deze studie geen verband gevonden was tussen het aantal nieuw gerekruteerde bomen van 2 cm DBH en het aantal volwassen bomen in dezelfde proefvlakken. In hoofdstuk 5 is geschat, dat de 2,5% snelstgroeiende zaailingen (kleiner dan 2 cm DBH) ongeveer tussen de 4 jaar, voor pioniersoorten, en 45 jaar, voor climaxsoorten, nodig hebben om van net gekiemde zaailing tot een DBH van 2 cm op te groeien, terwijl langzamer groeiende individuen behorende tot de climaxsoorten daar zelfs meer dan 68 jaar voor nodig kunnen hebben. Dit betekent dat individuen van deze climaxsoorten, als ze voor het eerst geobserveerd worden met een DBH van 2 cm, hun oorsprong ergens 45 tot 68 jaar daarvoor hebben liggen. Deze lange tijdspanne tussen kieming en rekrutering bij een DBH van 2 cm verdoezelt overduidelijk het verband tussen aantal ouderbomen en aantal rekruten met een DBH van 2 cm.

Bij houtkap worden over het algemeen voornameijk grote en vaak reproductieve bomen geoogst. Uiteindelijk kan dit belangrijke implikaties voor de regeneratie in het bos na houtkap hebben. Weglating van een verband tussen aantal ouderbomen en aantal rekruten in het gebruikte model zal dus waarschijnlijk leiden tot een onderschatting van de effecten van houtkap op abundanties van bomen en commerciële houtvolumes. Als bijvoorbeeld tijdens gesimuleerde houtkap een aantal bomen uit een climaxgroep worden geoogst of gedood, zal in het gesimuleerde bos bij een bepaalde waarde van de concurrentie-index in een gridcel de kans op rekrutering niet veranderen. In het daadwerkelijke bos zal hierdoor het aantal geproduceerde en verspreide zaden afnemen, hetgeen uiteindelijk voor de betreffende soort of functionele groep vanaf 45 jaar na kap tot een reduktie in de rekrutering van bomen bij 2 cm DBH zal leiden. Als voldoende adolescente individuen voorhanden zijn zal deze reduktie in rekrutering maar een paar jaar duren totdat het aantal reproductieve bomen weer is aangevuld door groei van deze tijdens de houtkap niet gekapte en nog net niet reproductieve bomen. Voor functionele groepen die in lage dichtheden voorkomen kan dit echter verregaande consequenties voor de abundanties van bomen hebben.

Daarom is in aanvulling op het model dat in dit proefschrift is beschreven nog een nieuw model opgesteld, waarin de regeneratieprocessen op een gedailleerde wijze zijn opgenomen. Dat model is uitgebreid beschreven in van Ulft (2004). Hierin worden, in aanvulling op het model in dit proefschrift, de processen van zaadproduktie, zaadverspreiding, kieming van zaden en de groei en mortaliteit van zaailingen tot een DBH van 2 cm expliciet uitgewerkt. Vanaf het moment dat een zaailing een DBH van 2 cm bereikt heeft, volgt de betreffende boom verder de functies zoals beschreven in hoofdstuk 3 van dit proefschrift. De processen van zaadproduktie, zaadverspreiding en kieming worden gedetaileerd in van Ulft (2004) behandeld, terwijl de groei en mortaliteit van zaailingen tot een DBH van 2 cm in hoofdstuk 5 van dit proefschrift beschreven worden.

De resultaten in hoofdstuk 5 laten zien, dat de groei van zaailingen in relatie tot een concurrentie-index erg variabel was. Veel van de in de proefvlakken opgemeten zaailingen vertoonden een reduktie in stamhoogte die niet aan lichtbeschikbaarheid gerelateerd is, maar veel waarschijnlijker het gevolg is van vallende takken, vraat door dieren en door het afsterven van plantendelen door ziekten. Deze oorzaken kunnen als toevalsprocesses (vanuit het oogpunt van de zaailing) beschouwd worden. Verder wordt in hoofdstuk 5 aangetoond dat de kans om te overleven tot een DBH van 2 cm, hoger is voor sneller groeiende individuen dan voor langzamer groeiende individuen behorende tot dezelfde functionele groep. Anders geformuleerd betekent dit dus dat individuen die een DBH van 2 cm bereiken over het algemeen harder hebben gegroeid dan andere individuen. Bij een traditionele manier van modelleren, waarbij gebruik wordt gemaakt van regressiemodellen, zullen alle individuen bij een bepaald lichtklimaat echter met eenzelfde snelheid groeien, die gelijk is aan de gemiddelde groeisnelheid van alle individuen bij dat lichtklimaat. Zo kan het met dat soort modellen gebeuren, dat zaailingen die in werkelijkheid door toeval net iets harder groeien dan het gemiddelde en daardoor overleven tot een DBH van 2 cm, nu in het model met de gemiddelde groeisnelheid groeien waardoor hun kans om een DBH van 2 cm te bereiken afneemt. Als een gevolg hiervan zal de totale gesimuleerde rekrutering bij een

DBH van 2 cm voor de betreffende functionele groep lager zijn dan wanneer het een deel van de zaailingen was toegestaan om harder te groeien. Daarom is in hoofdstuk 5 een manier van modelleren ontwikkeld waarbij met de stochastische variatie in de groeisnelheid van zaailingen rekening wordt gehouden. In hoofdstuk 5 worden tevens de consequenties hiervan nader belicht. Deze nieuwe manier van modelleren is vervolgens toegepast in het aangepaste simulatiemodel waarin regeneratieprocessen gedetailleerd zijn uitgewerkt (zie van Ulft 2004)

Met dat nieuwe simulatiemodel was het echter niet mogelijk om realistische projecties van de bosstructuur en samenstelling van functionele groepen te verkrijgen. In van Ulft (2004) worden mogelijke oorzaken hiervoor verder toegelicht. Het belangrijkste probleem lijkt de grote complexiteit van het model te zijn. Het bevat meer dan 1000 parameters en veel processen in het model zijn met elkaar verbonden waardoor het zo goed als onmogelijk is om de waargenomen problemen te analyseren.

Na dit allemaal te hebben gelezen moet men zich realiseren dat simulatiemodellen eerder een extrapolatie van de huidige kennis en aannamen weergeven dan dat ze absoluut “ware” voorspellingen geven. De scenariostudie, die in dit proefschrift met behulp van het beschreven simulatiemodel is uitgevoerd, geven wel de best onderbouwde schatting aangaande de toekomstige ontwikkelingen van het met verschillende houtoogsmethoden beheerde bos in centraal Guyana. Zorgvuldige en voorzichtige interpretaties van de resultaten uit de modelsimulaties kunnen discussies over duurzaam bosbeheer ondersteunen en kunnen voor bosbeheersplanning gebruikt worden. Als in de toekomst de modellen kunnen worden verbeterd, doordat meer en nieuwe gegevens beschikbaar komen, inzichten veranderen, of het berip van de bosdynamiek toeneemt, dan kan het bosbeheer navenant aangepast worden.

Referenties

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