Seeds, Seedlings, and Gaps
Size Matters

A study in the tropical rain forest of Guyana

The Tropenbos Guyana series presents the results of studies and research activities related to the conservation and wise utilisation of forest lands in Guyana. The studies published in this series have been carried out within the Tropenbos Guyana Programme.

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Seeds, seedlings and gaps – size matters

A study in the tropical rain forest of Guyana

Zaden, zaailingen en openingen in het kronendak een kwestie van grootte

een onderzoek in het tropisch regenwoud van Guyana

(*met een samenvatting in het Nederlands*)

Proefschrift

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For my parents

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"If we knew what we were doing, it wouldn't be called research, would it?"

Albert Einstein 1879 - 1955.

CHAPTER 1

INTRODUCTION

Tropical rain forests are one of the richest ecosystems that the world has ever known. The great number of species that form them is the reason for their fascination to people, their value to the biosphere, and the complexity of their proper management. The land that they occupy, and the value of just one of their many useful products - timber - are the reasons why they are rapidly disappearing (Laurance 1999). It has been estimated that 11 million hectares (ha) of mature tropical forests of which 7.5 million ha are rain forests, are converted each year to other uses. The great majority is changed into non-forest uses, only 600,000 ha becoming timber plantations (Gomez-Pompa & Burley 1991). In addition, much tropical forest is degraded every year, perhaps 4.5 million ha through selective logging, the vast majority of this receiving no subsequent active management (Finegan & Camacho 1999). Human disturbance has increased to an alarming level over the last decades and has become a major issue for burgeoning conservation movements (Sizer *et al*.1999).

The belief that rain forests have existed largely unchanged for millions of years is now seen to be a myth. At one end of the temporal spectrum, forests have ebbed and flowed over Asia, Africa and America; at the other, changes due to local disturbances - storms, landslides or the death of individual trees, result in the forest being an ever changing mosaic of gaps, trees growing up in former gaps, and mature forest.

Over the past two decades our understanding of the functioning of the rainforest ecosystem has increased enormously. Many are now convinced that managing these forests for sustainable economic benefit is feasible, and that such management will provide much greater long-term security for people than the present pattern of forest destruction (de Graaf *et al*. 1999). Yet, only a very small proportion of the forest is managed in any real sense of the word, this failure being primarily due to political, administrative and socio-economic causes (Sizer *et al*. 1999).

Disturbance and gaps in tropical forests

The disturbance regime in tropical rain forests, dominated by the fall of one or a few trees, is thought to play a central role in the maintenance of tree species diversity (Brokaw 1985, Denslow 1995). In particular gaps are seen to be important for the establishment and growth of most tree species (Bongers & Popma 1988, Poorter 1998), to produce rare habitats for the high light demanding species (Hubbell & Foster 1990), to promote high growth rates (Coley 1983, Poorter 1998), and to reduce the dominance of competitively superior species (Connell 1978, Huston 1979).

Tree fall gaps produce environmental heterogeneity in establishment sites that could be partitioned by species with different light, temperature, moisture, and/or nutrient requirements (Denslow 1980). So far however, field research has demonstrated the importance of specialisation in only a few light demanding species (Hubbell & Foster 1986, Denslow *et al*. 1990, Newell *et al*. 1993). Tree fall gaps also influence the maintenance of species diversity through effects on plant density. Canopy openings affect species diversity in part because disturbance generally produces a local increase in tree density as a few large trees are replaced with more small trees and stands of higher density usually contain more species. High species richness within gaps is well documented (Brokaw 1985, Uhl *et al*. 1988) although Hubbell *et al*. (1999) disagrees with this.

Importance of gap-size

Size is an important characteristic of gaps because it correlates well with biologically functional parameters. Gap size is commonly measured as the area between the edges of the crowns of peripheral trees projected vertically down to ground level, a definition codified by Brokaw (1982). In practice the vertical projection is not always easy to make precisely. Physical measures of gap size cannot allow for tiny canopy holes and these become increasingly important sources of radiation as the gaps get smaller (Brown & Jennings, 1998). They are also the main source under closed canopies. Accordingly, a distinction can be made between measuring the direct and indirect consequences of a gaps' existence. A direct result of a gap is the destruction of a certain volume of vegetation in the forest canopy. This may be quantified as the area covered by the vertical projection of the hole in the forest canopy. The indirect result can be quantified by the area at the forest floor where environmental conditions are affected by the gap.

During the last decade, at least five different definitions of a gap have been proposed (Brokaw 1982a, Popma *et al*. 1988, Riéra 1982; Runkle, 1981, van der Meer *et al*. 1994). The shortcomings and advantages of these have been tested and argued extensively in literature, and are usually adapted by ecologists based on the objectives their studies. The use of physical gap size as a surrogate for microclimatic variables is undermined by the fact that gaps of the same size do not necessarily experience the same microclimate. Direct measurements of gap microclimates have revealed that gap shape, orientation and topography also play an important role (Brown, 1993). More recent studies have defined gaps in terms of the openness of the canopy (Becker *et al*. 1988, Williams-Linera 1990, Ackerly & Bazzaz 1995, Burton & Bazzaz 1995, Gray & Spies 1996, Pacala *et al*. 1996). Whitmore *et al*. (1993) and Brown and Jennings (1998), both argue that because plants respond to microclimate the most useful measure of gap size is that which most clearly relates to microclimate. Whitmore *et al*. (1993) demonstrated that either canopy openness or proportion of radiation transmitted were better measures of the microclimate than physical gap size**.** (Usually there is a strong correlation between gap size and both of these parameters at the gap centre.) These measures are based on the analysis of hemispherical photographs taken in the centre of the gaps (Brown, 1993). In this study seedling response to gap size is discussed in terms of canopy openness.

Species classification

The ecologically most important result of gap formation is that different species succeed in different sizes of gaps. Tropical tree species have been classified in various ways into guilds, strategies or functional groups based on their differential responses to gaps from as early as 1958 (Poorter 1998). The two classes pioneer and climax, as defined by Swaine and Whitmore (1988) provide the basis for the discussion. These groups are defined on their requirement for light for germination and establishment, and are thought to represent the extremes of a continuum of species responses to light (Osunkoya *et al*. 1994). The shade tolerant species are those which can germinate, grow and survive in low light, and the light demanding species which need a high light environment for establishment.

Although there is general agreement that something falls in between these extremes, there is less agreement on what constitutes the salient features of this intermediate group (Poorter 1998). Despite the amount of speculation, there is little empirical evidence how species can be graded according to their shade tolerance. To date, quite a number of comparative studies have been published describing interspecific variation in plant characteristics for a large number of rain forest species. Generally they have focussed on physiological (Reich *et al*. 1992, Kitajima 1996) and/or morphological (Popma *et al*. 1992, King 1990, Osunkoya 1996) traits as well as on plant performance (Coley 1983, Lieberman *et al*. 1985, Augspurger 1984, Bongers & Popma 1988, Poorter 1998). Few studies have examined these characteristics comparatively between natural species populations and the very controlled experiments in which only a few variables are monitored. In this study an attempt is made to examine these characteristics in common species growing in both natural conditions and controlled experiments.

Plant responses to gaps

Gaps are widely recognised as important for the establishment and growth of rain forest trees. Hartshorn (1978) suggests that perhaps 75% of the tree species at La Selva Biological Station, Costa Rica are dependent on gaps for germination or growth before and beyond the sapling stage. Similar statements are found in descriptions of forest dynamics in Australia (Hancock *et al*. 1996), Malaysia (Whitmore 1975), West Africa (Jones 1955, 1956) and South America (Denslow 1980). Demographic studies demonstrate greater growth, survival, and reproductions when plants occur in or near canopy openings (Brokaw 1985 & 1987, Clark & Clark 1987, De Steven 1989, Zagt 1997). These examples include canopy, sub canopy, and understorey species across the spectrum of shade tolerant to light demanding physiologies.

Seeds of certain species may germinate only inside a gap, as is the case in many pioneer species. Some pioneer species require the environmental conditions typical of gaps of a certain minimum size to germinate. Species with immediate germination may have formed seedling banks, and when a gap is formed suppressed seedlings may be released by the higher light levels in the gap. Seedlings present before gap creation may take advantage of a gap to grow towards the upper canopy of the forest. The high growth rates of seedlings will lead to increased competition for light and nutrients, which will result in higher mortality rates.

Seed mass

It is widely accepted that in tropical rain forests shade tolerant species have large seeds and strongly light demanding species have small seeds (Ng 1978, Foster & Janson 1985, Foster 1986, Swaine & Whitmore 1988, Clark & Clark 1992). Dissent from this view has been expressed by Putz & Appanah (1987), Ellison *et al*. (1993) and Kelly & Purvis (1993). They have argued that irrespective of seed mass, a species will exhibit different levels of shade tolerance between its seedling and adult stages. Hence the line between shade tolerant and light demanding species is inevitable arbitrary because at one stage of development there is a continuum of tolerance.

A larger seed, with greater energy reserves, could help confer shade tolerance by: 1) allowing radical penetration through the deep litter layers that are often found in the forest understories (Molofsky & Augspurger 1992); 2) allowing the initial establishment of a larger germinant, which would make it less susceptible to smothering by leaf litter and could enable competition with short statured vegetation to be won (Leishman & Westoby 1994); 3) providing reserves for the compensation of leaf loss from damaging agents (Fanshawe 1948, Foster 1986, Armstrong & Westoby 1993). Maximising the relative growth rate (RGR) would allow seedlings to escape the greater risks of small size quickly and out-compete slower growing neighbours (Boot 1996). Several multiple species studies have shown that leaf area ratio (LAR), a strong determinant of RGR in high and moderately low light conditions (Lambers & Poorter 1992, Reich *et al*. 1992), is generally greater in low light for shade intolerant than for shade tolerant species (Kitajima 1994, Popma & Bongers 1988, Reich *et al*. 1998). These patterns suggest that, at all light levels, intolerant species maintain a greater growth potential (i.e. higher LAR) than tolerant species, but this growth potential may be unrealised in conditions of severe light limitations.

Seedlings and exploitation

The study of seedling ecology of tropical tree species is an integral part of the study of forests as a whole. Over the years, the need to enhance forest ecology with seedling studies has been frequently expressed (Lieberman 1996). Indeed, to rely on mature individuals alone to explain the distribution and performance of all size classes of trees is unwise, because many of the processes affecting distribution, structures and dynamics of a population or community may occur very early in a plant's life (Li *et al*. 1996; Zagt & Werger, 1998).

The recruitment, growth and survival of seedlings are critical limiting stages in the population and community structure of tree species (Li *et al*. 1996) and are all addressed in this thesis. Denslow (1980) suggested that the probability that a tree species would persist is a function of its seedling establishment rate. Clark and Clark (1985) stated that long-term seedling demographic studies are necessary to understand the dynamics of forests. Swaine, Lieberman and Putz (1987) indicated that germinated seedlings were the manifestation of the fecundity of the species, and that the inclusion of seedlings in a study of population dynamics is therefore essential. Yet, because seedlings are small and often experience very high mortality rates, much time and effort may be required to monitor sufficient numbers to estimate long-term survival and recruitment to later life-history stages. However for short-term experiments (< 4 years), seedlings are much more advantageous since they show a faster response to changes in environmental conditions than larger sized trees (Zagt & Werger 1998). They are also easier to manipulate and use in experiments and their responses can be quantified precisely.

Exploitation has a number of consequences for the survival and growth of seedlings of tree species. Usually after exploitation there are changes at two levels - the environment and the plant population. The environmental conditions e.g. the light intensity and quality, and the ambient and soil temperature, will change and these influence the nutrient and water cycles (interception and evapo-transpiration) as well as the competitive vigour of plant species, thereby affecting the plant population structure indirectly (Augspurger 1984, Bongers *et al*. 1988, Burslem *et al*. 1995). Further, by the extraction of some species from a stand the absolute and relative abundance of that species (particularly of the mature reproducing (st)age class), is decreased, and this has a direct influence on the remaining plant population (de Graaf *et al*. 1999, van der Hout 1999). The impact of the exploitation varies with its intensity, frequency and spatial extent and also whether the species under consideration is exploited itself, or whether it is simply growing in an area that is exploited for other species.

The effects of exploitation on recruitment growth and/or survival of tree seedlings have been examined during the last decades. Most of the studies have been performed under controlled or intensely manipulated conditions (Augspurger 1984, Bongers and Popma 1988, Denslow *et al*. 1990, Kennedy and Swaine 1992, Osunkoya *et al*. 1993, Cornelissen *et al*. 1994, ter Steege *et al*.1994). In contrast, only a small proportion of studies have been performed in situ, i.e. investigating the effect of exploitation on actual rates of recruitment, growth and survival of naturally occurring seedlings (Prince 1973; Jonkers 1987;

Lieberman and Lieberman 1987; Lieberman *et al*. 1990; Li 1991). While experimental studies may be well suited for addressing species-specific responses, in situ studies on the recruitment, growth and survival of seedlings are essential for an understanding of the population dynamics of tree species in tropical rain forests. This should be followed by studies on subsequent sapling growth and survival and by studies focusing on later stages in the tree's life cycle (van der Hout 1999). This study attempts to describe the potential establishment, survival and growth capacity of tropical rain forest species using manipulated seedling populations, and eventually to compare this to what these species actually achieve in natural seedling populations.

Tropenbos-Guyana Programme

The Tropenbos Foundation is a Dutch initiative established to address the complex question of the sustainable management of tropical rain forests. It is an independent, internationally oriented organisation that works for and with tropical countries to conduct research and development activities. The Foundation seeks to contribute to the conservation and wise use of tropical rain forests by generating knowledge, developing methodologies, and strengthening local research institutions and capacity. In pursuit of this, it has identified four main objectives, all of which take account of indigenous communities: land-use planning; biodiversity conservation in protected areas; sustainable production of forest products; and restoration and use of degraded forest.

Tropenbos-Guyana was developed in 1989 on a research base established by the University of Guyana and Utrecht University in the Netherlands, and focuses on the development of a forest management system for sustainable production of timber, non-timber forest products and services. The programme is being realized through the joint efforts of researchers from the National Agricultural Research Institute, the University of Guyana, the Guyana Forestry Commission, the Department of Lands and Surveys, Hydromet, the University of Utrecht in the Netherlands, the Imperial College from the United Kingdom, the 'Centre Technique Forestier Tropicale' from France, and the U.S. Forest Products Laboratory.

The programme is executed primarily in the concession area of the Demerara Timbers Limited Company, in the lowland tropical rain forest of the Mabura Hill District (5°13' North 58°48' West), 230 km South of the capital

Georgetown (Figure 1). The research activities have focussed mainly on acquiring knowledge of natural resources, physical environment, biodiversity and timber characteristics, development of parameters for sustainable forest management. A smaller and more recent site has been established in the North West District, which focuses on the significance of non-timber forest products for indigenous communities and the impact of forest exploitation on the life styles of these communities.

By the end of the first phase of the programme in 1993, the integrated results led to the formulation of a set of recommendations for sustainable forest management and suggestions for further research (ter Steege *et al*. 1996). The second and final phase of the programme will be completed in December 2001.

Guyana

Guyana is situated on the northeastern coast of South America between 0°45' and 8°38' north latitude and 56°32' and 61°22' west longitude. The area of Guyana is 214,970 km^2, and the population is strongly concentrated on the narrow strip along the coast. The climate is tropical with a mean temperature of 26°C. Annual rainfall is approximately 2700 mm/year and is concentrated in two periods: May - August and December - February.

Tropical rain forests cover approximately 16 million hectares of the country's land area. These forests may be classified as swamp forest on the coast and rain, seasonal and dry evergreen forest in the interior (Fanshawe 1952) (Figure 1). Deforestation rates in Guyana rank among the lowest in the world although several large forest concessions have been granted to Asian companies since the early 1990's (Sizer *et al*. 1999).

The tropical rain forests in Guyana are exceptional in the sense that large parts are dominated by a few or one species (ter Steege 2000). Dominance may result in clearly identifiable forest types. Forest types are locally described by the dominant species, such as *Chlorocardium rodiei* 'Greenheart' forests, *Mora excelsa* 'Mora' forest, *Mora gonggrijpii* 'Morabukea' forest, *Eperua falcata* 'Soft wallaba' forest and *Eperua grandiflora* 'Ituri Wallaba' forest. Co-dominant species may differ, especially in Greenheart forests, which makes a typological classification in plant communities difficult (ter Steege *et al*. 1993).

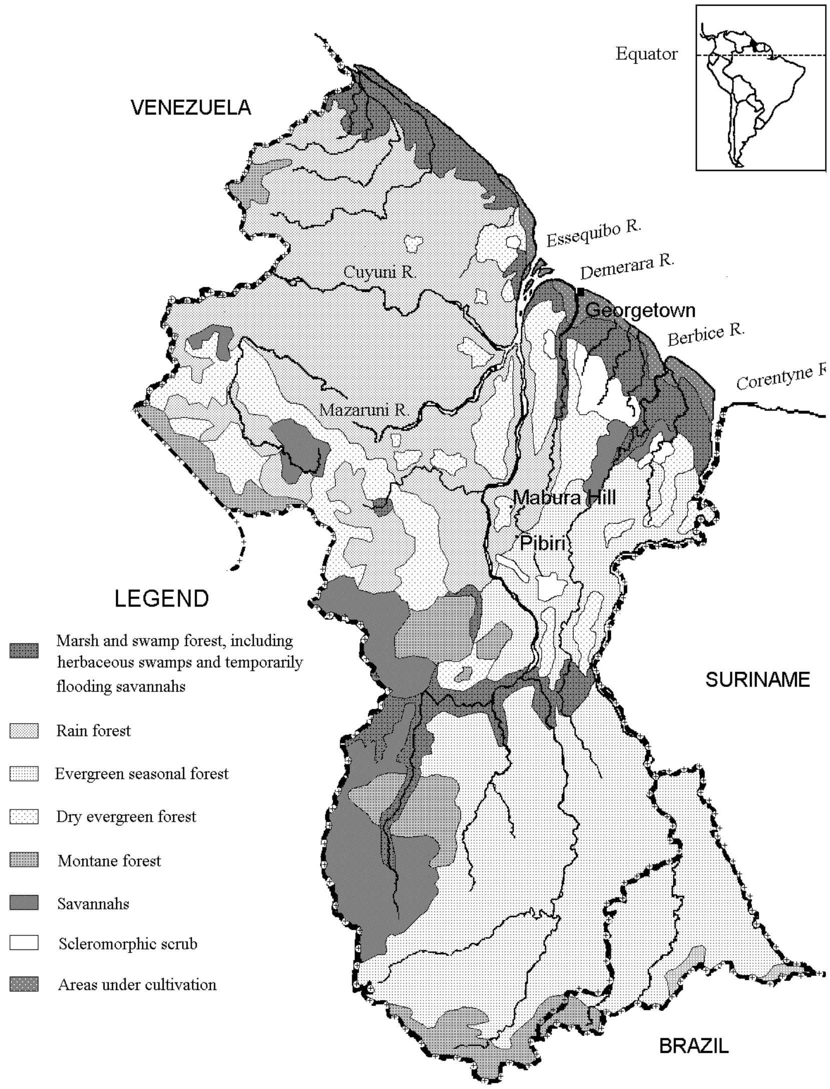

Figure 1 *Map of Guyana indicating the different forest types and the two main Tropenbos research sites.*

Aim and outline of this thesis

This study moves gradually from experiments carried out under controlled conditions (Chapter 2 - 4) to studies carried out in natural conditions (Chapter 5 & 6) where plants were exposed to the vagaries of the forest environment. In the earlier chapters the emphasis is on the potential survival and growth of selected species whereas in the later chapters the realised survival and growth of all naturally occurring species are discussed.

Chapter 2 seeks to parameterise the simple competition model of Boot (1996), by growing seedlings of eight species under five different canopy openness levels. The differences in initial plant size and the ability of small seeded species to increase their RGR with an increase in light much more than large seeded species are addressed.

Chapter 3 follows up on the heels of the previous chapter by trying to define the canopy openness levels at which species will maximise their growth rates. In this case the survival and growth of eight species distinguished by their seed mass and grown in seven different gap sizes ranging from 50 m^2 to 3200m^2 is addressed.

Chapter 4 focuses on survival in relation to gap size but at the leaf level. Leaf life spans of the same eight species in the previous chapter are studied for almost two years in seven gap sizes.

Chapter 5 switches from the controlled experimental conditions to the natural field situation. Here the recruitment, mortality and the species composition are investigated in selectively logged forest. Tree seedling responses are discussed in the context of canopy openness and seed mass, providing here the link with the previous chapters.

Chapter 6 presents an analysis of the first four years of height growth after selective logging for a suite of species ranging in shade tolerance and seed mass. The differences between the height growth of 'old' (seedlings established prior to the study) and 'new' (seedlings established during the course of the study) seedlings is discussed.

Finally Chapter 7 discusses the aspects of seedling establishment, survival and growth in the context of controlled and natural conditions, identifying key factors that may be used in identifying/defining species strategies. The importance of gap size and seed mass in future forest management practices is also discussed.

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"I find that a great part of the information I have, was acquired by looking up
something and finding something else on the way"

Anonymous

CHAPTER 2

THE IMPORTANCE OF SEED MASS AND CANOPY OPENNESS FOR THE EARLY GROWTH RESPONSES OF TREE SEEDLINGS OF EIGHT TROPICAL RAIN FOREST SPECIES

with Nico Houter & Hans ter Steege

Abstract

Growth rates of seedlings of eight tropical rain forest tree species were compared under five different canopy openness levels (FU and 50, 200, 800, 3200 m^2 gaps). RGR exhibited a positive relation with canopy openness with species attaining their highest RGR at the 800 m^2 (4 species) or 3200 m^2 (3 species) gaps. Seed mass and RGR were negatively related. The increase in RGR between small and large gaps was highest for small seeded species, with these species more than doubling their RGRs. The RGR of most large seeded species remained relatively constant over all gaps. Canopy openness had opposing effects on NAR and LAR for most species. Usually as LAR decreased, NAR increased with decreasing canopy openness. However, this resulted in only marginal decreases in RGR. Small seeded species sharply increased their NAR compared with marginal increases in large seeded species. This ability of small seeded species to greatly increase their NAR is what results in their RGR being more than double that of large seeded species in the same gap size.

Keywords

Seed mass, canopy openness, growth analysis, tropical rain forest

Introduction

Seed mass varies considerably among species in different habitats and different successional stages (Foster & Janson 1985, Mazer 1989, Susko & Lovett-Doust 2000) and there have been suggestions that seed mass may be related to dispersal capacity, seedling establishment, seedling size, relative growth rate and competitive ability (Westoby *et al*. 1992; Thompson *et al*. 1993).

Rainforest tree species have generally been categorised into shade intolerant (pioneers or long-lived pioneers) and shade tolerant (climax) according to their response to light conditions (Denslow 1980, Whitmore 1989). The former typically have small widely dispersed seeds from which juveniles establish only in gaps although they may germinate in low light conditions (Swaine *et al*. 1997, Peña-Claros 2000). The shade tolerant species generally have larger seeds and can germinate and persist as suppressed juveniles beneath the forest canopy (Foster 1986, Boot 1993).

The primary advantage of large seed mass appears to be enhancement of survival in shade (Osunkoya *et al*. 1994, Boot 1993, Saverimutuu & Westoby 1996). Several hypotheses attempt to explain how a larger seed reserve leads to a survival advantage in the shade. One view is that a large seed provides a longer period of support of carbon to the seedlings. This hypothesis assumes that seedlings in the shade generally have a negative carbon budget (Raich & Gong 1989). Another view is that a large seed creates a large seedling and thus an important initial size advantage (Westoby *et al*. 1992, Leishman & Westoby 1994, Boot 1996). This initial difference in seedling size may however soon disappear at high light availability, owing to the different growth rates among seedlings of different species (Zimmerman & Weis 1983, Boot 1996).

Boot (1996) developed a simple model to explain differences in plant sizes and thus competitive hierarchy in small and large gaps, for species differing in seed mass. The model predicts that in small gaps the 'lag time' for seedlings of small seeded species to attain similar heights as seedlings of large seeded species is much longer than in large gaps. This is primarily because in small gaps growth rates of all species are low because assimilation rates are limited by low light availability. Hence, the initial size hierarchy based on seed size will be preserved in time. On the other hand, in large gaps small seeded species can attain much higher relative growth rates than large seeded ones. Hence, ultimately at some point in time, the small seeded species will attain larger plant sizes than the large seeded species.

This study sought to parameterise this model for seedlings of eight species in the tropical rain forest in Guyana. The following hypotheses were tested:

- Large seeded species produce seedlings with a larger initial size than small seeded species;
- Small seeded species can attain higher relative growth rates in large gaps, compared to large seeded ones in the same light environment;
- The net assimilation rate contributes more to the changes in relative growth rates than the leaf area ratio.

Eight tropical rain forest species differing largely in seed mass were grown in four different gap sizes and the forest understorey. Their growth was analysed from the time the seed reserves were exhausted until they had tripled their biomass or five months later.

Materials and Methods

Study site and species

The study was conducted from August 1997 to January 2000 in the Pibiri Research Area. The area is located about 40 km south of the Mabura Hill Township and approximately 250 km south of the capital, Georgetown, Guyana, between 5° 05' and 5° 10' latitude and 58° 25' and 58° 35' west longitude. The climate in the region is characterised by a mean annual temperature of 27 °C and a mean annual rainfall of about 2700 mm.

Eight species were included in the study, five of them being important timber species (Table 1). Species selection was based on seed mass and presumed light requirements. Species ranged from shade tolerant species such as *Mora gonggrijpii* to pioneers such as *Cecropia obtusa*. Henceforth species will be referred to by their generic name only.

Table 1. *Species studied. Strategy refers to plant strategy (P = pioneer, LLP = long-lived pioneer, S = shade tolerant). Seed weights refer to average fresh weights. (* Fresh weight extracted from Hammond & Brown 1995.)*

Scientific name	Family	Strategy	Seed-wt (g)(ave.)
Cecropia obtusa	Moraceae	P	0.00014*
Goupia glabra	Celastraceae	LLP	0.0014
Sclerolobium guianense	Caesalpinioideae	LLP	0.101
Ormosia coccinea	Papilionoideae	S	0.87
Hymenaea courbaril	Caesalpinioideae	LLP	3.72
Carapa guianensis	Meliaceae	LLP	22.01
Catostemma fragrans	Bombacaceae	S	32.83
Mora gonggrijpii	Caesalpinioideae	S	72.33

Gap size and growth experiment

Five light conditions - four gaps and a forest understorey site - were selected for the study (Table 2). Within each site, a hexagonal area that allowed for the equidistant placement of seedlings was demarcated. The available area per individual varied between the gaps and ranged from 0.45 m^2 in the FU and 50 m^2 gap to 0.6 m^2 in the largest gap (Table 2). In larger gaps, where growth rates were expected to be higher, plants were allocated larger areas to prevent competition between seedlings. The soil in each area was turned over to a depth of 20 cm, and all roots and stumps removed. To homogenise the soil within the plot, the topsoil layer was thoroughly mixed. Lime [$CaCO_3$] was added to increase the soil pH from 3 to 4.5. Slow release nutrients (Osmocote plus; 15:10:12:2 - N, P, K, Mg with micro nutrients) were added to avoid nutrient stress. The estimated release time was approximately 4 months hence fertiliser was added at 3-month intervals during the course of the experiment.

Seeds of all species were collected in the West-Pibiri Area and the fresh weights recorded (Table 1). Large seeds (*Catostemma, Mora and Carapa*) were placed directly in the plots to germinate, whilst the other species were germinated in the shade house. This was done to prevent the smaller seeds from being washed away by rain or dislodged by high winds. Germination was defined as the protrusion of the radical and when this was observed, germinated seeds were transferred from the shade house to the plots. The individual plant positions were first identified and marked within the plots with short pieces of sticks and aluminium tags respectively. Ten individuals per species per treatment were randomly positioned in the plots.

Table 2. *The sites used, the demarcated study areas and the area per plant within each site.*

Gap size	Study area (m^2)	Area per ind (m^2)	Ave. canopy openness (%)
Understorey	87	0.40	5.9
50 m^2	87	0.40	8.3
200m^2	98	0.45	13.5
800 m^2	119	0.55	17.1
3200 m^2	130	0.60	36.8

At a peripheral distance of 1 m away from the actual plot, a drain of 60 cm was dug and lined with a triple layer of thick plastic sheeting to prevent the in-growth of roots from surrounding trees. The area was then fenced to prevent the entry of larger herbivores. Seedlings were watered twice daily (in the absence of rain), to avoid drought stress and sprayed regularly with an insecticide (Sevin) to prevent insect attacks. To prevent excessive evaporation, the soil surface was covered with a homogeneous layer of leaf litter. Naturally occurring plants and weeds were removed weekly.

Two harvests were taken. For each species and treatment, an initial harvest was carried out once the seedlings had exhausted their cotyledon reserves. This was detected by the falling-off or shrivelling of the cotyledons. At this harvest, pairs of conspecific individuals of the same size were identified of which one was harvested and the second was left the second harvest. The second harvest was done either when plants had tripled their biomass since the first harvest or five months after this first harvest when growth was very slow as in the forest understorey and small gaps. This double criterion was used because it was possible for the faster growing species to dramatically increase their plant biomass (esp. in the large gaps) by as much as 100 fold. The first criterion therefore limits the size range over which biomass and growth rates of species would be compared. However, where this criterion could not be practically met (e.g. FU and small gaps), then the second criterion would be used and thus time would be the determining factor. In this way, the time at which plants would be compared would be reasonably objective. Summarising, the experiment contained 8 species * 5 sites * 2 harvests * 10 individuals = 800 seedlings.

At each harvest, the stem lengths and leaf area were determined. Leaf area was measured using a LiCor 3100 leaf area meter (Lincoln Inc Nebraska). Plants were then separated into leaves, stem plus branches and petioles, and roots, and oven dried at 70°C for 72 hours after which the dry weights were determined.

Abiotic measurements

Canopy openness at the sites was estimated using hemispherical photographs. Photographs were made at 6-month intervals under overcast conditions, at a height of 1-m above each of the sites. Photographs were made with a digital Fujix-Nikon DS505^{TM} 35-mm camera with Sigma 8-mm Fish-eye lens mounted on a tripod. From the photographs, canopy openness was calculated with Winphot 5 (ter Steege 1997).

Analysis

From the primary data, the following variables were derived; leaf mass ratio (LMR, leaf mass per unit plant mass g g^{-1}); stem mass ratio (SMR, (including stem, petioles and branches) mass per unit plant mass g g^{-1}); root mass ratio (RMR, root mass per unit plant mass g g^{-1}); leaf area ratio (LAR, leaf area per unit plant mass m^2 kg^{-1}); specific leaf area (SLA, leaf area per unit leaf mass m^2 kg^{-1}); relative growth rate (RGR = $(\ln W_2 - \ln W_1)/(t_2 - t_1)$ g $g^{-1}day^{-1}$). Mean RGR and NAR were calculated with formulas given by Hunt (1978). The formula for the calculation of the net assimilation rate (NAR g $m^{-2}day^{-1}$) is only valid if leaf area and plant dry mass are linearly related (Hunt 1978). For all species-gap combinations this condition was met; mean r^2 of the linear regression of leaf area against plant mass was 0.93.

Statistical analysis

Plant responses (size and morphology) were evaluated using a two-way ANOVA, with light and seed mass as independent variables. Dependent variables (with the exception of the mass ratios) were transformed to natural logarithms before the analysis to homogenise the variances and to meet the assumption of ANOVA that effects of independent variables are additive (Sokal & Rohlf 1995). Analyses were carried out using SPSS 8.0 (SPSS Inc 1997). The hypothesis that the response of species to gap size would depend on seed mass would be revealed by a significant interaction between seed mass and light.

Results

The importance of light and seed mass

The results of the two-way ANOVA using light and seed-mass as main effects at both harvest intervals indicates that seed-mass had a much stronger influence on the growth and biomass allocation patterns than light (Table 3, Appendix 1). At the first harvest, light had a significant effect only on a few variables whereas the seed mass effect was always highly significant. This was probably because plants were only in their respective conditions for a short period. Thus, they had not had their full development after germination there. Seed mass continued to have a significant effect at the final harvest, and light became increasingly important for plant growth (Table 3). Significant canopy openness * seed mass interactions for plant variables indicated that species followed different ontogenetic trajectories. The explained variation by the ANOVA model was high (mean 0.86, range 0.52-0.99). Most species survived well to at least 37% canopy openness conditions. Only *Cecropia* and *Goupia*; the two smallest seeded species in the experiment, did not survive in the FU and the 50 m^2 gap where light availability was lowest.

INITIAL SIZE

As would be expected, stem length and plant mass were positively related with seed mass at the initial harvest (Figure 1).

GROWTH RATES: LAR, NAR AND RGR.

In general, RGR exhibited a positive relation with canopy openness (Figure 2) with most species attaining their maximum RGR at 17 % canopy openness (800-m^2

Table 3. *Results of a two-way ANOVA with canopy openness (n=5) and seed mass (n=8) as fixed effects. F-values, significance (P), and the coefficient of determination (r^2) are shown. The dependent variables were In-transformed prior to the analysis. (P>0.05, NS; P<0.05, *; P<0.01, **; P<0.001, ***)*

	Canopy op.		**Seed mass**		**Canopy op.*seed mass**		
Variable	**F**	**P**	**F**	**P**	**F**	**P**	**r^2**
Harvest 1							
Stem length	3.95	*	456.94	**	292.00	***	0.99
Root length	3.69	*	67.85	**	44.60	***	0.95
Leaf weight	2.57	NS	188.15	**	122.38	***	0.98
Stem mass	2.36	NS	432.38	**	278.95	***	0.99
Root mass	3.41	*	198.51	**	137.32	***	0.98
Total plant mass	2.92	*	248.89	**	161.64	***	0.99
Leaf mass ratio	1.60	NS	8.06	**	5.75	**	0.71
Stem mass ratio	3.60	*	3.67	**	3.40	***	0.59
Root mass ratio	1.23	NS	14.53	**	9.61	***	0.80
Leaf area	1.82	NS	186.86	**	121.08	***	0.98
Specific leaf area	2.29	NS	23.11	**	15.68	***	0.87
Leaf area ratio	2.38	NS	6.45	**	17.82	***	0.88
Harvest 2							
Stem length	4.35	*	50.32	**	32.90	***	0.94
Root length	4.04	*	12.53	**	9.09	***	0.82
Leaf mass	17.08	***	40.80	**	31.04	***	0.94
Stem mass	14.42	***	59.68	**	41.81	***	0.95
Root mass	12.72	***	51.61	**	36.28	***	0.95
Total plant mass	10.06	***	24.98	**	18.68	***	0.90
Leaf mass ratio	1.80	NS	4.93	**	4.10	**	0.67
Stem mass ratio	3.47	*	2.98	*	3.48	**	0.63
Root mass ratio	1.15	NS	10.32	**	7.01	***	0.79
Leaf area	10.16	***	24.51	**	19.23	***	0.91
Specific leaf area	7.86	***	15.99	**	12.25	***	0.86
Leaf area ratio	0.44	NS	3.02	*	2.16	*	0.52
Net assimilation rate	7.71	***	2.76	**	3.25	**	0.73
Relative growth rate	6.16	***	3.85	**	15.29	**	0.87

gap). There was a negative relationship between seed mass and RGR, with smaller seeded species having the higher RGRs when compared to the larger seeded species. The two smallest seeded species had their highest RGRs at 17 % canopy openness and the decline in RGR between the 17 and 37 % canopy openness levels was strongest for these two species, *Goupia* and *Cecropia*. *Mora* was the only species that exhibited a negative RGR in the two darkest sites. Along with *Ormosia, Mora* was the only species that exhibited maximum RGR in the largest gap (Figure 2).

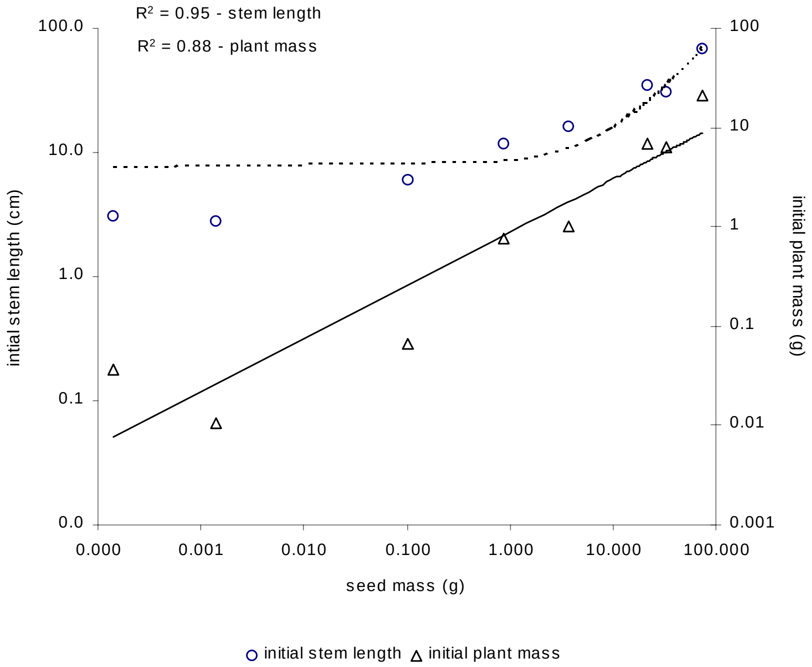

Figure 1 *The initial stem length and the initial plant mass (broken lines) as a function of seed mass.*

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For most species, LAR declined sharply with an increase in canopy openness until 17% and thereafter remained somewhat constant (Figure 2). This trend was usually accompanied by an increase in NAR. Maximum NAR for most species was also recorded at the 17% canopy openness level. For all species, the pattern of RGR followed closely that of NAR.

The ratio of LAR, NAR and RGR in the the largest gap - 3200 m^2 gap - and the 200 m^2 gap (the smallest gap size where RGR could be calculated for all species) was calculated for all species and regressed with seed mass (Figure 3). As seed mass increased ratios decreased for NAR and RGR and increased for LAR. Whilst small seeded species more than doubled their RGRs, the RGR of most large seeded species remained the same (Figure 3).

Discussion

The influence of seed mass on initial seedling size

The positive correlation between seed mass and initial size (both length and mass) illustrates that large seeded species produce the biggest seedlings. This finding confirms the conclusions of several other studies (Howe & Richter 1982; Gross 1984; McConnaughay & Bazzaz 1987; Jurado & Westoby 1992; Boot 1996). The initial large seedling size may provide seedlings with a competitive advantage especially in areas where light is a limiting resource (e.g. dense understorey). The taller the seedling, the greater its' ability to shade other seedlings and further to intercept incoming light. However, in large gaps (high light environments) there is usually no long-term advantage of this initial large seedling size. In these areas the growth rates of small seeded species is much higher than species having a larger seed mass, and it enables them to outgrow these larger seedlings in a very short time (Chapter 1).

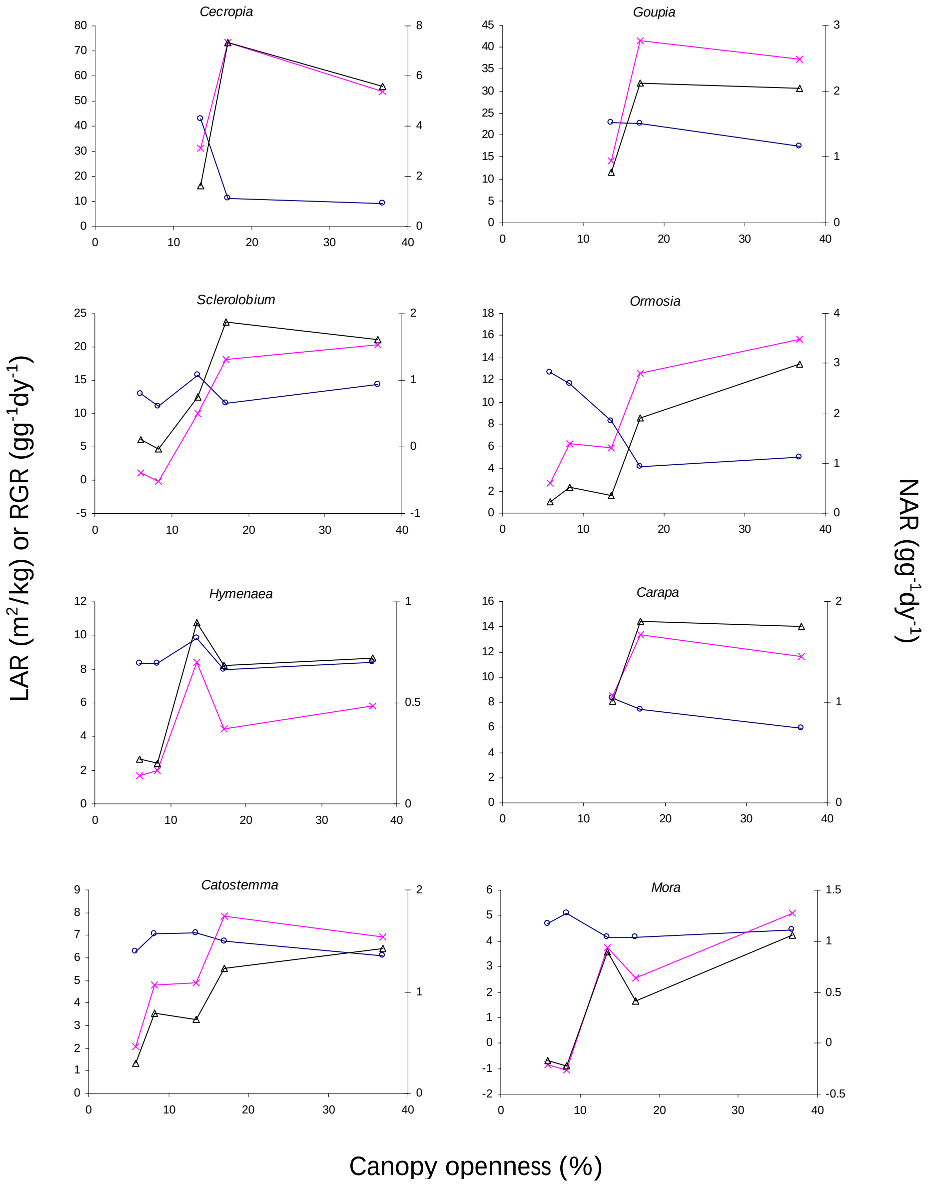

Figure 2. *The responses of NAR, LAR and RGR to canopy openness for all species. Species plots are shown in order of increasing seed mass. Note the scaling differences between plots.* (△ NAR; ○ LAR; X RGR)

Hence, if they are present soon after gap formation, small seeded species may have an advantage over the larger seeded species (McConnaughay & Bazzaz 1987).

In small gaps or in the forest understorey, the success of seedlings is not only dependent on the initial seedling size but also first on the ability of that seedling to survive and establish in these light limiting conditions. In this study, the smallest seeded species experienced 100% mortality rates in the forest understorey and the 50-m^2 gaps, a finding similar to that of McConnaughay & Bazzaz (1987). For eight species comprising a range of seed masses, grown in artificially created disturbances, they found limited establishment of all species in the forest understorey and no survival in the understorey and the smallest gap for the two smallest seeded species. Therefore, in the light limiting conditions survival may be more important than large initial seedling size in determining a species success.

The interaction of seed mass, gap size and species growth rates

For 4 out of 8 species (*Cecropia*, *Goupia*, *Carapa*, *Catostemma*), RGR reached a peak at the intermediate gap size (800 m^2 gap) above which it declined (Figure 2). The RGR responses of plants to canopy openness can be explained by underlying patterns in LAR and NAR. With an increase in light, NAR increases, basically due to an increase in photosynthesis per unit leaf area. At the same time LAR decreases, however resulting in a stimulation of RGR far less than expected from the photosynthetic rate values (Poorter & van der Werf 1998). However, Figure 2 indicates that this is not always the case and only four species (*Cecropia*, *Goupia*, *Ormosia* and *Carapa*) showed this trend. This suggests that there was not a very clear trend with seed mass.

Some authors have noted that the decrease in LAR is mainly due to a decrease in SLA (Pons 1977, Hunt & Halligan 1981). This is supported by all species in this experiment (Appendix 1), however unlike the results of Poorter & van der Werf (1998) LMR did not remain constant. The reduction in RGR at the largest gap size can be due to the high light and temperatures associated with this gap size (especially around midday). This may have led to reduced stomatal conductance, reduced carbon fixation rates, and perhaps even photoinhibition (Huc *et al*. 1994; Chazdon *et al*. 1996). *Sclerolobium*, *Ormosia*, and *Mora* seemed unaffected by these stress factors and exhibited their highest RGR's in the largest gap.

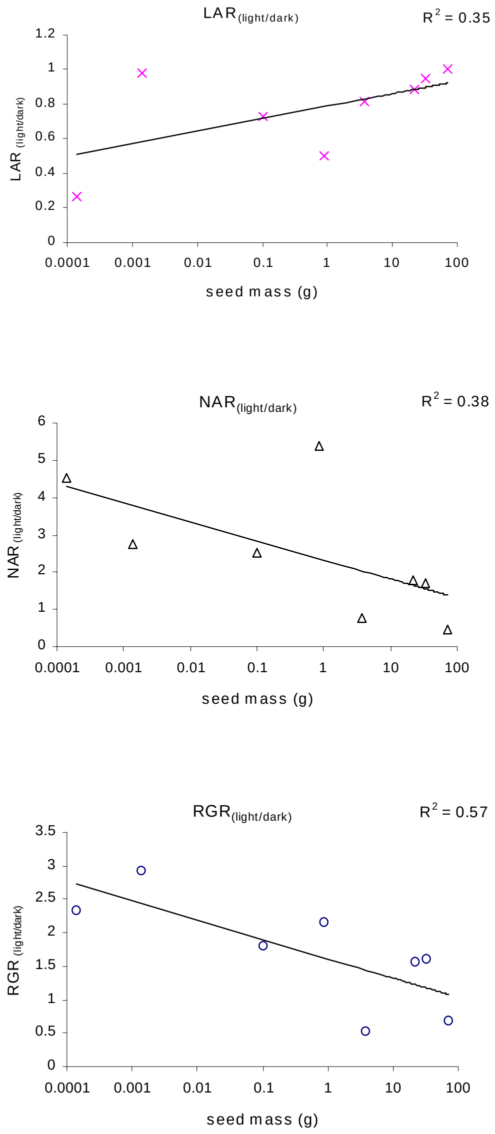

Figure 3. *The relationship between seedmass and the ratio of LAR, NAR and RGR in the 3200m^2 (light) and 200m^2 (dark) gaps.*

Generally, small seeded species exhibited higher RGRs than large seeded species in all the gaps where they survived (Figure 3), a finding that supports the second hypothesis (Popma & Bongers1988, Poorter 1999). Thus, over the course of the experiment these species were able to compensate for their initial smaller size. The data indicate that the maximum RGR of small seeded species, attained in the 800-m^2 gap, was almost triple that in the 200-m^2 gap. Large seeded species exhibited hardly any increase in RGR between these two gaps (Figure 3) and neither over the entire gap size range. This implies that at their maximum the small seeded species were growing twice to thrice as fast as the large seeded and indeed in time would be able to outgrow these large seeded species, as suggested by Boot (1996).

Conclusions

A high LAR is an advantage in the understorey and small gap environments, where interception of light is of primary importance. However as gap size and thus light increases a high NAR is more important, to enable plants to fully benefit from a high photosynthetic capacity. In large gaps, large seeded species that are usually shade tolerant are constrained by an inherently lower photosynthetic capacity (Strauss-Debenedetti & Bazzaz 1996) whereas small seeded species can realise high photosynthetic rates (Raaimakers *et al*. 1995). Poorter & van der Werf (1998) showed that there was a close relationship between photosynthetic rates and NAR. It follows therefore that differences in the photosynthetic rates of species will be reflected in their NAR. Hence from small to large gaps, light availability increases, thus photosynthetic rates and consequently NAR increases. However, in the largest gaps at the highest light intensities, the slow growing large seeded species with their low photosynthetic capacity cannot achieve the high photosynthetic rates as the small seeded species with their high capacity. There will be corresponding increases in NAR, and species will show similar differences in NAR as with their photosynthetic rates. Small seeded species will sharply increase their NAR compared with marginal increases in large seeded species. It is this ability to greatly increase its' NAR that results in the more than doubling in RGR of these small seeded species.

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Appendix 1. Mean plant dry mass and the ratio of leaves, stem and roots with plant mass at harvest 1 and 2.

Harvest 1

	Cecropia		*Goupia*		*Sclerolobium*		*Ormosia*		*Hymenaea*		*Carapa*		*Catostemma*		*Mora*	
	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
total plant mass (g)																
FU	0.030	0.018	0.007	0.035	0.061	0.012	0.273	0.053	0.917	0.189			3.016	0.960	12.280	7.801
50	0.023	0.012	0.008	0.040	0.083	0.027	0.379	0.111	0.971	0.122			4.652	2.137	18.729	7.19
200	0.079	0.043	0.013	0.067	0.064	0.010	0.689	0.241	0.954	0.164	6.297	2.961	6.268	2.057	16.423	3.176
800	0.027	0.011	0.016	0.010	0.056	0.016	0.975	0.434	1.109	0.310	4.187	4.858	8.130	4.028	30.855	22.912
3200	0.022	0.090	0.007	0.005	0.068	0.022	1.517	1.467	1.103	0.281	10.075	7.529	9.041	5.136	28.206	14.117
leaf mass ratio (g/g)																
FU	0.360	0.170	0.410	0.153	0.460	0.148	0.500	0.111	0.510	0.057			0.400	0.108	0.350	0.0539
50	0.340	0.179	0.300	0.125	0.430	0.135	0.540	0.060	0.490	0.041			0.430	0.079	0.360	0.0523
200	0.450	0.138	0.480	0.226	0.460	0.102	0.540	0.069	0.520	0.038	0.460	0.067	0.440	0.108	0.310	0.11
800	0.410	0.222	0.320	0.132	0.510	0.051	0.530	0.059	0.410	0.047	0.390	0.098	0.420	0.088	0.380	0.102
3200	0.390	0.135	0.330	0.152	0.560	0.113	0.550	0.055	0.480	0.050	0.500	0.066	0.430	0.124	0.440	0.032
stem mass ratio (g/g)																
FU	0.250	0.131	0.280	0.120	0.290	0.105	0.280	0.078	0.360	0.057			0.320	0.081	0.300	0.0601
50	0.290	0.172	0.340	0.141	0.310	0.078	0.270	0.035	0.350	0.047			0.290	0.050	0.300	0.0714
200	0.210	0.101	0.220	0.195	0.350	0.084	0.250	0.022	0.310	0.039	0.310	0.102	0.260	0.038	0.310	0.124
800	0.290	0.158	0.290	0.142	0.290	0.066	0.200	0.046	0.330	0.062	0.310	0.040	0.220	0.058	0.220	0.0279
3200	0.300	0.093	0.280	0.062	0.260	0.116	0.200	0.044	0.300	0.030	0.300	0.056	0.200	0.053	0.200	0.0744
root mass ratio (g/g)																
FU	0.390	0.175	0.310	0.150	0.250	0.111	0.220	0.057	0.140	0.028			0.280	0.074	0.350	0.0789
50	0.370	0.134	0.360	0.148	0.260	0.137	0.200	0.047	0.170	0.065			0.280	0.076	0.340	0.0693
200	0.340	0.144	0.300	0.131	0.190	0.083	0.220	0.066	0.170	0.028	0.230	0.058	0.300	0.103	0.380	0.104
800	0.300	0.079	0.390	0.195	0.200	0.077	0.270	0.023	0.250	0.076	0.290	0.079	0.340	0.120	0.350	0.0656
3200	0.320	0.135	0.390	0.157	0.180	0.129	0.250	0.053	0.210	0.053	0.180	0.064	0.360	0.159	0.330	0.0601
specific leaf area (m^2 kg-1)																
FU	25.283	21.158	49.708	20.320	17.488	6.201	27.754	4.822	20.780	1.300			17.922	5.676	13.695	1.276
50	37.957	24.842	83.753	31.657	16.796	7.067	24.437	3.421	17.504	1.900			14.604	1.950	13.134	0.508
200	39.091	10.567	31.519	5.502	20.577	11.439	19.680	3.456	17.658	1.483	19.635	12.186	14.206	1.772	14.896	62.8
800	29.699	8.062	39.889	12.908	18.632	4.031	14.767	3.288	13.441	4.191	16.959	3.037	13.577	7.756	12.204	0.826
3200	27.949	11.943	67.950	34.263	15.359	5.789	12.463	1.441	14.779	1.224	15.127	0.644	11.096	1.793	12.558	0.652
leaf area ratio (m^2 kg-1)																
FU	10.330	3.488	22.191	8.154	8.455	1.597	13.617	4.128	10.517	1.253			7.314	1.337	4.955	0.63
50	12.947	6.096	25.866	9.410	7.673	2.691	13.183	2.267	8.562	1.640			6.383	1.423	4.814	0.746
200	16.980	8.455	15.468	8.012	9.626	1.410	11.129	3.038	9.249	0.413	10.438	4.232	6.281	2.038	4.612	0.941
800	12.206	6.225	14.300	6.311	9.815	1.680	8.156	1.719	5.741	1.732	7.401	2.312	5.978	3.516	4.657	1.343
3200	10.613	4.241	22.225	5.406	9.253	2.661	7.127	1.030	7.210	0.823	7.684	0.644	4.934	1.374	5.491	0.474

Appendix 1. cont'd

Harvest 2

	Cecropia		*Goupia*		*Sclerolobium*		*Ormosia*		*Hymenaea*		*Carapa*		*Catostemma*		*Mora*	
	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
total plant mass (g)																
FU					0.075	0.034	0.446	0.179	1.302	0.486			4.591	1.890	9.367	3.756
50					0.074	0.029	0.967	0.418	1.310	0.123			8.167	3.096	17.701	10.976
200	0.287	2.705	0.046	0.025	0.334	0.194	1.869	1.369	4.125	1.579	26.244	16.056	15.268	8.732	30.142	9.916
800	0.107	0.648	0.061	0.130	0.653	0.279	7.800	4.824	2.099	0.521	32.662	41.937	31.193	12.484	39.761	17.815
3200	0.076	2.649	0.039	0.096	2.199	2.390	18.026	19.764	3.895	3.390	69.022	44.683	34.553	25.038	80.435	48.710
leaf mass ratio (g/g)																
FU					0.510	0.101	0.480	0.117	0.440	0.096			0.390	0.079	0.360	0.060
50					0.400	0.134	0.540	0.092	0.510	0.079			0.450	0.051	0.380	0.034
200	0.590	0.102	0.440	0.126	0.610	0.042	0.480	0.231	0.460	0.147	0.480	0.048	0.500	0.033	0.340	0.046
800	0.700	0.044	0.490	0.210	0.620	0.041	0.390	0.046	0.470	0.036	0.500	0.054	0.550	0.097	0.420	0.060
3200	0.620	0.470	0.500	0.105	0.770	0.355	0.520	0.126	0.480	0.089	0.470	0.053	0.470	0.086	0.450	0.025
stem mass ratio (g/g)																
FU					0.350	0.045	0.260	0.044	0.320	0.101			0.300	0.076	0.320	0.044
50					0.470	0.104	0.250	0.046	0.270	0.091			0.300	0.079	0.330	0.080
200	0.180	0.079	0.220	0.116	0.270	0.026	0.290	0.120	0.320	0.091	0.350	0.062	0.270	0.036	0.330	0.047
800	0.170	0.076	0.160	0.040	0.160	0.018	0.140	0.021	0.340	0.052	0.310	0.054	0.240	0.054	0.240	0.094
3200	0.200	0.023	0.220	0.061	0.140	0.026	0.260	0.181	0.280	0.078	0.350	0.077	0.270	0.112	0.290	0.045
root mass ratio (g/g)																
FU					0.130	0.132	0.250	0.102	0.250	0.177			0.290	0.048	0.310	0.057
50					0.130	0.058	0.210	0.064	0.210	0.071			0.250	0.084	0.290	0.066
200	0.230	0.084	0.340	0.089	0.130	0.244	0.220	0.118	0.210	0.071	0.160	0.027	0.230	0.061	0.330	0.052
800	0.130	0.120	0.300	0.236	0.220	0.032	0.170	0.059	0.190	0.060	0.190	0.031	0.200	0.086	0.310	0.062
3200	0.180	0.045	0.280	0.075	0.090	0.044	0.210	0.074	0.240	0.064	0.150	0.024	0.240	0.075	0.230	0.065
specific leaf area (m^2 kg-1)																
FU					24.304	6.348	24.990	20.560	18.963	2.873			16.449	3.197	12.331	1.905
50					26.891	4.984	20.738	8.286	16.539	4.934			14.108	7.928	12.874	0.935
200	55.826	68.365	54.410	9.825	27.101	3.393	16.613	1.635	21.037	8.877	16.516	2.938	14.114	1.208	12.177	1.028
800	16.171	0.179	44.392	63.038	17.235	4.840	10.781	2.089	16.813	2.910	15.050	1.580	12.222	0.838	8.663	4.605
3200	14.641	1.121	34.558	4.337	17.832	3.127	9.395	0.733	16.213	5.919	13.112	1.091	11.219	4.056	9.837	1.509
leaf area ratio (m^2 kg-1)																
FU					12.979	4.576	12.702	2.617	8.342	2.490			6.263	1.675	4.683	0.987
50					11.145	3.417	11.678	2.190	8.337	3.460			7.060	3.399	5.079	0.675
200	42.978	93.805	22.900	6.753	15.858	2.609	8.273	3.945	9.858	3.117	8.329	2.157	7.100	0.739	4.150	0.611
800	11.407	1.282	22.505	2.027	11.521	2.829	4.183	0.854	8.004	0.871	7.399	1.428	6.720	1.271	4.153	2.268
3200	9.298	2.629	17.373	4.434	14.408	2.205	4.992	1.305	8.443	1.495	5.939	0.926	6.070	2.063	4.459	0.872

Appendix 2. Date and time of harvests. The number of seedlings harvested at each date is shown in brackets. Seedlings that were present at the first harvest but died at the second harvest are not included.

	Harvests		No. of days
	First	Second	
Cecropia			
FU	98/05/08	------	
50	98/05/08	------	
200	98/05/08	98/07/17	70
	98/05/08	98/08/28	112
800	98/05/08	98/07/17	70
3200	98/05/08	98/07/17	70
	98/05/08	98/08/21	105
Goupia			
FU	98/05/08	------	
50	98/05/08	------	
200	98/05/08	98/08/28	112
800	98/05/08	98/07/17	70
	98/05/08	98/08/21	105
3200	98/05/08	98/07/17	70
	98/05/08	98/09/11	126
Sclerolobium			
FU	98/10/08	99/03/08	152
50	98/10/08	99/03/08	152
200	98/10/08	99/03/08	152
800	99/08/06	00/01/17	133
3200	99/05/10	99/10/18	161
	99/05/25	99/10/26	154
Ormosia			
FU	97/10/21	98/03/31	161
	98/02/17	98/07/17	150
50	97/11/17	98/04/03	137
	98/02/17	98/07/17	150
200	97/11/17	98/04/17	151
	98/02/17	98/07/17	150
800	98/02/11	98/07/11	150
3200	98/02/11	98/07/11	150
	97/10/21	98/04/03	164
Hymenaea			
FU	97/08/15	98/02/17	186
50	97/08/15	98/02/17	186
200	97/08/15	98/02/17	186
Hymenaea			
800	98/10/07	99/03/09	153
3200	98/10/07	99/03/09	153
Carapa			
200	97/09/28	98/03/09	162
	97/11/17	98/03/09	112
800	97/08/27	98/02/11	185
	97/09/14	98/02/11	150
	97/09/28	98/03/09	162
3200	97/08/27	98/02/11	185
	97/09/14	98/02/11	150
Catostemma			
FU	97/12/05	98/05/05	151
	98/03/20	98/08/22	155
	98/01/14	98/06/17	152
50	97/12/05	98/03/20	105
	98/01/14	98/06/16	153
200	98/03/20	98/07/20	122
800	97/11/13	98/04/14	152
	97/12/08	98/05/08	154
	98/01/14	98/06/17	154
	98/03/20	98/08/21	154
3200	97/12/08	98/05/08	154
	98/01/14	98/06/17	154
	98/03/20	98/08/21	154
Mora			
FU	98/09/21	99/02/21	153
	98/10/01	99/03/28	178
	98/11/02	99/04/08	157
50	98/09/21	99/02/21	153
	98/10/01	99/03/28	178
200	98/09/12	99/02/12	153
	98/09/21	99/02/21	153
800	98/09/11	99/02/12	154
	98/09/21	99/02/21	153
3200	98/10/01	99/03/23	173
	98/09/11	99/02/12	154

"The best things about rain forests is that they never suffer from drought"

Dan Quale

CHAPTER 3

SURVIVAL AND GROWTH IN GAPS - A CASE STUDY FOR TREE SEEDLINGS OF EIGHT SPECIES IN THE GUYANESE TROPICAL RAIN FOREST

with Hans ter Steege & Marinus Werger

Abstract

Seedling survival and growth of eight rain forest tree species were compared in seven different gap sizes (50 - 3200 m^2). The results demonstrated no clear patterns of gap partitioning by species preferences to specific gap size ranges, but rather a shifting competitive hierarchy along the gap-size gradient. Seedling survival was only correlated with seed mass for seeds < 0.05 g and these species survived best in gaps ≥ 400 m^2 whilst larger seeded species had relatively high survival rates in all gaps. Seedling heights in small gaps were positively correlated with seed mass, however as seed mass increased this relationship was reversed. In the smallest gaps (< 200m^2), the species with the tallest seedlings at the beginning remained the tallest throughout the study period. The faster growing species (*Cecropia*, *Sclerolobium and Goupia*), that were relatively small at the beginning of the experiment, quickly overtook the other species, as early as approximately five months into the study and maintained this height advantage. The results of this study provide limited evidence for species preferences to a particular gap size. It does however indicate which gap sizes lead to the subsequent changes in the initial size hierarchy.

Keywords

Canopy openness, seed mass, seedling survival and growth, tropical rain forest

Introduction

The importance of gaps in the forest canopy, to the processes of seedling development and growth has been intensively studied throughout the century (Aubreville 1938, Richards 1952, Whitmore 1978, Brokaw 1985 and 1987, Hubbell and Foster 1986, Swaine and Whitmore 1988, Denslow *et al*. 1990, Brown and Jennings 1998, Webb 1998, Hubbell et. al. 1999). The debate in the recent past has focussed mainly on whether or not the size of the gap was the most important factor influencing seedling establishment, growth and survival (Orians 1982, Brandani et. al. 1988, Popma and Bongers 1991, Brown 1993, Brown and Jennings 1998).

The gap-size partitioning theory proposes that seedlings of different species partition canopy gaps because they are preferentially adapted to a particular gap-size class. This partitioning is possible either by a clear preference for a single gap-size or by a shifting competitive hierarchy, which causes a different species to dominate as changes in gap-size occur (Brokaw 1987, Raich & Gong 1990). A variety of gap-sizes would therefore favour the regeneration of a range of species, and a species would be competitively inferior outside of its' specific gap-size range.

However, evidence so far has indicated that most plant species show better growth as resources in a gap become increasingly abundant, rather than differing the level of resource they require for optimum growth (as proposed by the gap-size partitioning theory). These species will differ in the minimum amount of the resource they require to survive and in their maximum growth rate when resources are abundant. A shifting competitive hierarchy will therefore be established along a resource gradient. As resources become increasingly available, species not able to tolerate resource scarcity (usually the species with small seed masses) are able to grow faster than those that are tolerant of scarcity. Hence along a range of gap-sizes, where resources increase as the size of the gap increases, there may (will) be a shift or cross over in the size hierarchy with increasing gap-size. These mechanisms are tested in the present study by monitoring the survival and growth of seedlings of eight tree species common in the Guyanese tropical rain forests, in 20 artificial gaps of different sizes.

The first hypothesis to be tested is:

(1) *Tropical rainforest species show preferential adaptation to specific canopy gap-sizes.*

It has been argued that gap-size is the most important factor influencing the outcome of succession in gaps. This is because the size of a gap is the main determinant for the microclimatic processes in a gap (Whitmore 1996), which in turn influence the survival and growth of species and competition between the species. Others argue that the ability of seedlings to persist in the shaded understorey, and the size of these seedlings at the time of gap creation, is much more important in determining the future growth and development of gaps (Hubbell *et al*. 1999, Brown & Whitmore 1992). Two problems have frustrated the attempts of ecologists to assess the degree of gap partitioning among tropical rainforest seedlings.

The first is the difficulty in measuring and defining gap-size. Brown and Whitmore (1992) argue that when gaps are created plants respond to the change in microclimate and not gap-size per se and thus any measure of gap-size needs to reflect the magnitude of microclimate change rather than human perceptions of gap geometry. This measure of gap-size needs to take into account the radiation arriving from any direction, not solely from above. In this study, canopy openness derived from vertical hemispherical photographs is used to rank the gaps according to size.

The second difficulty that frustrates the attempts to test gap partitioning is that of the heterogeneity of natural seed and seedling banks. To investigate the relationship between gap size and seedling growth, ecologists need to test seedlings of several tree species in a range of different gap-sizes. To date there are remarkably few studies of interspecific differences between species in growth and survival under differing degrees of canopy openness. This is in no small part due to the difficulty of finding large seedling banks of different species growing simultaneously in a large number of canopy gaps of different sizes. Consequently, several studies have reported observations from very small numbers of gaps, or for very few species (but see Uhl *et al*. 1988, Kennedy and Swaine 1992, Brown and Whitmore 1992, Zagt 1997). Few studies have reported observations for species growing in gaps of different sizes for the same period. To eliminate this problem, artificial gaps have been created and replicated for this study. The gaps sizes used range from 50 m^2 to 3200m^2, a range that encompasses single tree fall to very large multiple tree fall gaps.

Seedlings of eight species have been planted into these gaps to ensure a sufficient number of individuals per species.

The second hypothesis to be tested in this study is

> *(2) Seed mass has a strong influence on the survival and growth responses of species in gaps of different sizes.*

Seed-mass is one of the most important characteristics that influences a species ability to germinate, establish and grow in gaps (Boot 1996). Shade tolerant (climax) species are usually characterised by seeds with large food reserves, which can be drawn upon in the establishment phase. Light demanding (pioneer) species on the other hand usually have small seeds with very little stored reserves. Species with large seeds are usually 'recalcitrant' species, whose seeds have short viability and cannot be stored for long period. They are usually able to germinate and survive in conditions of low light availability. Species with small seeds are usually referred to as 'orthodox' species, whose seeds have the capacity for extended dormancy and though able to germinate in understorey environments do not persist for very long as seedlings (Swaine *et al*. 1997, Kyereh *et al*. 1999). These species are better adapted to high light environments for their germination, growth and survival.

Dependence on canopy opening for germination and seedling establishment has been used to define the difference been large seeded shade tolerant and small seeded shade intolerant species (Swaine & Whitmore 1988), on the circumstantial evidence that the shade intolerant species are never found as young plants in forest shade. Boot (1996) argued that a strong relationship between seed mass and survival would only arise when plants differing in seed mass are grown in light conditions below their whole plant light compensation points. He further stated that the relationship would become weaker as the size of the gaps increased. His was one of the few studies that emphasised the importance of seed-size as a determinant for species partitioning of gaps of different sizes. However, he studied relatively large seeded species only in low light environments. The present study goes a step further in testing his hypothesis, by monitoring species that differ widely in their seed size and grown in and a wide range of gap-sizes.

Methods

Area description

The study was conducted from 1996 to 1999 in the Pibiri Research Area of the Tropenbos-Guyana Programme, located 49 km south of the Mabura Hill township (5°02'N and 58°38'W). Mean annual rainfall is about 2850 mm, with two distinct wet seasons lasting from May to August and December to February.

The soils in the area are generally classified as Acri-haplic and acri-xanthic ferralsols (FAO) or Kasarama sandy loans (Guyanese) (Khan *et. al*. 1980; van Kekem *et al*. 1996). These soils have a loamy sand top-soil and an increasing clay content with depth, but the texture in the subsoil is not heavier than sandy loam. Though well drained these soils are extremely nutrient poor, with the main constituent in the first 20 cm being SiO_2 (95%) (Brouwer 1996).

Vegetation in this region can be classified as mixed forest, with several tree species being dominant. *Chlorocardium rodiei*, *Eschweilera sagotiana*, *Lecythis confertiflora* are the dominant species with *Licania spp*., *Swartzia leiocalycina* and *Catostemma fragrans* occurring as co-dominants. *Mora gonggrijpii* is quite common in some areas, whilst *Carapa guianensis* and *Pentaclethra macroloba* occur in the more moist areas (van der Hout, 1999; Polak, 1992). *Paypayrola longifolia*, *Oxandra asbekii* and *Tapura guianensis* are the most common understorey species whilst *Peltogyne venosa* and *Hymenaea courbaril* are amongst the most common emergents. Average canopy height is 40 m and mean basal area about 34 m^2 ha^{-1}, with emergents attaining maximum heights of 50 m.

The Pibiri Gap Experiment

The Pibiri Gap Experiment was established in 1996 and is located in the West Pibiri Compartment of the Demerara Timbers Limited Mabura Hill Concession. It is a multidisciplinary study addressing the central issue of the definition of the maximum allowable gap-size for the regeneration of commercial species in the Guyanese forests (van Dam *et al*. 1999).

The growth and survival of the eight species were monitored in 20 gaps along a gradient of gap-sizes, ranging from single tree-fall to multiple tree-fall gaps. The gap-size range selected was derived from the relationship between photosynthetic photon flux density (PPFD) and gap-size. This relationship indicates that variation in PPFD occurs sigmoidally with a logarithmic change in gap-size (van Dam *et al.* 1999). This suggests that the greatest changes in PPFD should occur from 50m^2 to 5000m^2. The gap sizes chosen were 50, 100, 200, 400, 800, 1600, and 3200 m^2, and encompassed gap sizes likely to be found during both natural gap formation and logging operations. The latter six gap-sizes were replicated three times and the 50m^2 gap five times, to enable enough space for all the experimental work. Replication of exact gap-sizes proved quite difficult, however, the differences (in canopy openness) between the size classes were large enough for all replicates to be grouped (Table 1).

Table 1 *The gaps used in this experiment with the percentage of canopy closure. Canopy closure was calculated as the percentage difference between canopy openness at successive measurements.*

			Canopy closure (%) at each measurement					
Gap no.	**Aimed gap size**	**Canopy openness (%) at 37 days**	**167 days**	**308 days**	**479 days**	**621 days**	**754 days**	**884 days**
1	50	6.95	0.6	0.7	14.9	2.1	1.6	1.2
2	50	8.03	9.2	10.3	22.5	1.4	5.6	1.1
13	50	9.28	1.6	1.8	26.1	10.9	6.6	6.0
16	50	7.14	14.8	17.6	21.2	26.8	4.8	17.8
9	100	8.37	3.5	3.7	29.0	15.2	14.5	12.0
12	100	7.76	4.1	4.4	25.5	5.7	4.8	10.7
6	200	11.00	8.1	8.8	8.2	8.9	19.5	12.1
15	200	12.28	3.7	4.0	20.2	7.3	15.8	9.5
19	200	14.22	11.5	13.0	21.4	6.4	17.6	10.7
3	400	20.93	2.9	3.0	21.0	5.8	12.4	7.1
18	400	18.75	3.4	3.5	11.6	5.9	12.5	7.2
5	800	21.03	0.6	0.6	8.8	3.0	6.1	3.3
8	800	26.67	3.3	3.5	7.6	6.4	13.8	8.0
25	800	26.80	1.7	1.7	12.4	5.9	12.6	7.2
4	1600	31.09	1.0	1.0	5.2	9.2	1.6	1.6
14	1600	35.22	5.1	5.3	8.3	9.6	4.0	4.2
20	1600	28.38	2.5	2.6	13.2	8.1	3.4	3.6
22	3200	37.14	1.9	2.0	9.2	8.4	3.3	3.4
23	3200	41.88	0.7	0.7	10.1	7.3	2.8	3.0
24	3200	39.38	4.3	4.5	10.4	8.4	3.3	3.5

To eliminate the variability in growth conditions among gaps, all gaps were designed to be circular so that form and orientation would not be variables in the experiment. In addition to this, the experimental area within the gaps was cleared of all naturally occurring vegetation and debris leftover from the gap creation process. Gaps were created at least 120 m from each other to prevent gaps from influencing each other.

Species

Species (Table 2) were chosen on the basis of their seed-size, occurrence in the reduced impact logging plots (Chapter 3), and availability at the time of collections. Seeds were collected for *Ormosia*, *Pentaclethra* and *Sclerolobium*, whilst seedlings were collected for *Chlorocardium*, *Catostemma*, *Laetia*, *Goupia* and *Cecropia* (see Table 2 for full species names). All collections were made in the West-Pibiri Compartment (outside of the Pibiri Research Area), between February and August 1996. Seeds were collected from around the parent trees, and then placed in 1L black plastic bags (filled with loose brown sand) in nurseries for germination. Seedlings of 5 to 10 cm were collected, and since the plants were that small, the root system was not extensive. A 20-cm trench was made around each seedling at a radius of 25 cm and seedlings were collected with all soil. This was done to prevent excessive damage to the root system. Subsequently, non-rooted soil was discarded and seedlings were placed in 1L bags and put in the nurseries awaiting transferral to the gaps. Seed mass of the species was determined either from the literature (Hammond & Brown, 1995) or by weighing the seeds (only species collected as seeds).

Experimental set-up and measurements

Before transplantation, a grid was established within the gaps using cotton treads. Individual seedling implantation sites ranged in area from 0.25 m^2 in the 50m^2 gaps to 1m^2 in the 3200m^2 gaps. The spacing allocated was based on the projected opening of the canopy gap on the ground and the number of individuals to be introduced into the gap. In each gap, 80 individuals (8 species x 10 individuals each) were transferred from the nurseries and randomly assigned to the grid. Each individual was given a unique tag number for future measurements. During the first month after transplantation, plants were shaded with a layer of grey mosquito mesh, and were watered once daily to allow for acclimation to gap conditions. Dead or unhealthy individuals were replaced during this period.

The first measurements were done on the 25th and 26th November 1996 (5 weeks after transplantation), and thereafter repeated at quarterly intervals until March 1999; a total of 884 days. At each measurement, the stem length, number of leaves, leaflets and branches and the leaf lengths and widths were recorded. Height measurements were done with a graduated tape for individuals

Table 2 *Study species, seed mass, the number for parent trees from which seeds/seedlings were collected, and some related comments are also included. Unknown*[1, 2 & 3] *- collected in three, three and five different sites respectively, within the Pibiri Area, but exact number of parent trees not recorded.*

Scientific names	Vernacular names	Seed mass (g)	No of parent trees	Further comments
Cecropia obtusa Trecul.	Congo pump	0.00014	Unknown[3]	Most typical secondary species. Found in open areas and seeds can only germinate in light environments. Forms a dense stand in secondary forest.
Goupia glabra Aubl.	Kabukalli	0.00038	Unknown[1]	Dominant in seasonal forest and widely distributed. Usually forms a dense stand in secondary vegetation, mostly in open areas e.g. along roads and trails. Seeds germinate in large gaps and seedlings are found in ample numbers in these areas.
Laetia procera (Poeppig) Eichler	Warakaioro	0.005	Unknown[2]	Frequent in secondary forests, but also occurs in primary forest. Seeds germinate in open areas, but seedlings can survive in shaded areas.
Sclerolobium guianense Benth. Var	Kaditiri	0.348	9	Occasional to frequent in mixed forests. Seeds germinate in mature forest as well as in gaps. Seedlings found mostly in gaps.
Ormosia coccinea (Aubl.) Jackson	Barakaro	0.743	7	Frequent in secondary forests. Seeds have a very tough seed coat and germinate in both shade and light gaps.
Pentaclethra macroloba (Willd.) Kuntze	Trysil	6.494	13	Occurs in both primary and secondary forests. Found along swamps and river edges as well. Seeds germinate in light gaps and seedlings perform well in both shade and gaps.
Catostemma fragrans Benth.	Sand baromalli	44.596	9	Widely distributed in *Eperua* and evergreen seasonal forest. Seeds germinate in shade and seedlings are usually found below parent trees.
Chlorocardium rodiei (Schomb.) Rohwer	Greenheart	63.007	11	Reef forming species and dominant in Greenheart forest. Often growing mixed with *Mora gonggrijpii*. Seeds germinate in shade, usually near parents and seedlings survive in these shaded conditions.

up to 2 m and a measuring rod was used for taller individuals. For each individual, height was measured from the ground to the highest point of the plant.

From 26th November 1996 until 20th August 1997, hemispherical photographs were taken directly after enumerations to be used for estimating canopy openness. Photographs were taken with a Nikon/Fujix digital camera with Sigma 8-mm f2.8 fish-eye lens, set on a tripod at the centre of gaps. The top of the image was aligned to the true north. The film plane was kept at a standard height of 1 m above the ground. Photographs were usually made when the sun was low in the sky and unlikely to be opposite holes in a closed canopy - either before 08:00 hours or after 16:00 hours.

Naturally, occurring plants and re-sprouting stumps were cleared from between and around the experimental plants to prevent competition for resources. Plants were also protected against grazing by large animals and insect herbivory through the erection of a mesh fence and by spraying respectively. In all gap-size classes there was one gap used as a control, in which no pest and competition control treatments (weeding and spraying) were applied. Gaps didn't differ considerable in topography and soil chemistry. Two gaps were created on slopes but the slopes in these gaps are less than 5% (van Dam *et al*. 1999).

Data analysis

GAPS AND CANOPY OPENNESS

A few of the gaps were discarded from the analysis. One replicate from the 50, 100, 400, and 1600 m^2 gap sizes were not used. In the case of the 50 and 100 m^2 gaps, the numbers of replicates were reduced because more than 50% of the seedlings were damaged whilst the 400 m^2 replicate was eliminated because it had been created partly on the white sand ridge, which borders the south-eastern part of the research area. One of the replicate 1600 m^2 gaps was discarded from the analysis, because the excessively high mortality rates in this gap were due to attacks by Leafcutter ants (*Atta sp.*) on mainly two of the species (*Catostemma fragrans* and *Chlorocardium rodiei*).

For all photographs taken, the canopy openness (percentage unobstructed sky on the photograph) was calculated using the program Winphot 5.0 (ter Steege 1997). Images were processed using the program Paint Shop Pro 5.0. First, they were resized and then the colour channels split into red, blue and green. The image with the highest contrast (usually the blue channel) was used for further analysis. Contrasts were sometimes manually adjusted within this program by defining the high density of dark coloured pixels black and the high density light pixels white.

Differences in canopy openness at the plant level between replicate gaps were investigated using a one-way ANOVA. This was done for each gap size class separately. Differences between treated and non-treated gaps within particular gap size classes were not significant (Table 3). This implies that although there was an increase in stem density in the untreated gaps, this did not significantly reduce the canopy openness at the level of the target seedlings. Thus for the analysis all replicate gaps of any one size class are pooled.

Table 3 *Results of an ANOVA showing the differences in canopy openness between treated (weeded and sprayed) and untreated gaps. Canopy openness used was derived from hemispherical photographs made approximately half-way through the experiment. For the 200, 800 and 3200 m^2 gaps, n = 3, with 2 gaps of each size being treated. In the case of the 400 m^2, n = 2, with one of the gaps being treated and one untreated. The 50, 100, and 1600 m^2 gaps used, were all treated and thus p-values only indicate differences between replicate treated gaps. For these gaps sizes n = 4, 2 and 2 respectively.*

Gap-size	F-value	p-value
50 m^2	2.51	ns
100 m^2	1.85	ns
200 m^2	1.81	ns
400 m^2	0.83	ns
800 m^2	1.20	ns
1600 m^2	1.92	ns
3200 m^2	2.00	ns

EFFECT OF CANOPY OPENNESS AND SEED MASS ON SEEDLING SURVIVAL

To examine and compare the survival patterns between species over the experimental period, survival analysis (Goldstein 1994) was done. Life tables (Cox and Oakes 1984) were computed for all species in all gaps. The survivorship function (the cumulative proportion of individuals surviving to the respective measurement intervals) and the median survival times (the time at which the cumulative survival function is equal to 50%) were computed for all species and differences between species and gaps tested.

To assess the effect of seed-mass and gap size on species survival at the end of the experiment (884 days) a two way ANOVA was performed. Gap size and seed mass were used as the factors and mean seedling survival as the response variable. Results of the ANOVA were significant (see Results), hence, a Tukey test was done to identify which gaps and species (seed mass) differed significantly from each other.

THE EFFECT OF SEED MASS AND CANOPY OPENNESS ON SEEDLING HEIGHTS

The effect of canopy openness on seedling heights was tested with a multivariate ANOVA (Sokal and Rohlf 1995). The mean heights of all individuals of a species within a single gap were computed along with the mean of the gap canopy openness. This implies that for every gap, each species received a single height value that was representative of all living individuals at each measurement. Seed mass was used as the factor and canopy openness as the co-variable in this analysis. Results of the ANOVA were significant (see Results); hence, a Tukey test was done to assess the intra-specific variation within gaps.

Results

Canopy openness (rate of closure)

There was a minimal decrease in canopy openness of all gaps during the first year of the study (Figure 1), as compared with the final phase.

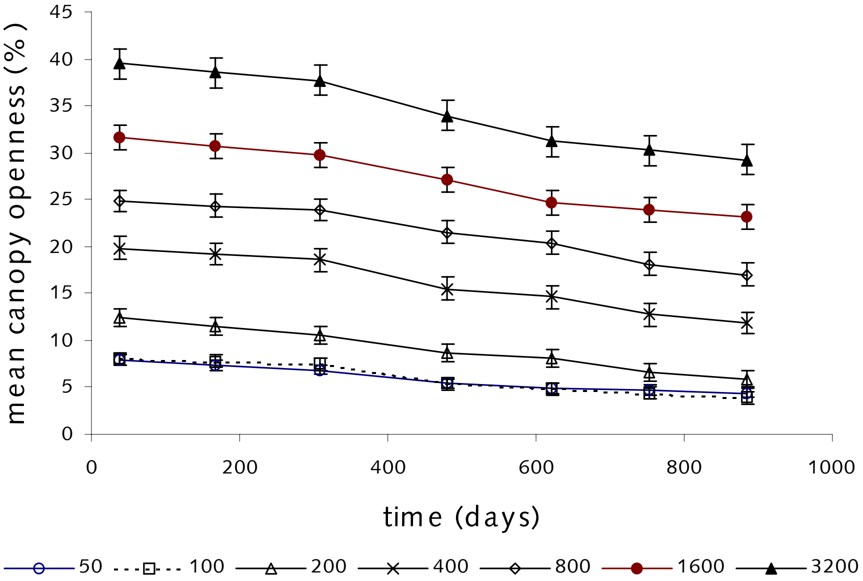


Figure 1. *The change in canopy openness (%) over the course of the experiment (884 days) for each gap size class with the standard error.*

The reduction in canopy openness was slightly higher for the smaller gaps when compared to large gaps. At the end of the measurement period, canopy openness in the two largest gaps had been reduced by 26% whilst in the gaps smaller than 400 m^2, more than 40% of the canopy openness had been reduced (Figure 1). Canopy closure rates between the three largest gap sizes were not significantly different from each other ($p < 0.01$), but the rate of closure of the other gap sizes were quite variable (see Table 1). The rate of closure was significantly different between measurement intervals for most of the gaps. The rate between 167 and 308 days was not significantly different for all gaps, but there was a marked increase in gap closure for all gaps between the 308 and 479 days (Table 1). In the smallest and the largest gaps, the rate was not significantly different at the last two measurement intervals, but for the intermediate gap sizes the rates of closure at the last three measurement intervals was quite variable.

Seedling survival

At the conclusion of the experiment 24% of the seedlings from a population of 1600 had died, with the highest mortality being experienced in the first half of the experiment ($t \leq 479$ days). In the two smallest gaps, sizes 36% had died and species having the lower seed masses (≤ 0.006g) were responsible for approximately 75% of this mortality.

Table 4 *Results of ANOVA showing the effects of gap size and seed mass on seedling survival. Gap size and seed mass were used as fixed factors and mean survival at the end of the experiment used as the response variable. In all cases p < 0.001.*

	df	**F-value**	**p-value**
Gap size	6	9.61	***
Seed mass	7	16.51	***
Gap size * seed mass	42	3.78	***

Both seed mass and gap size significantly influenced seedling survival (Table 4). Species showed significant differences in their survival responses to canopy openness as indicated by the significant interaction of seed mass and gap size (Table 4). These species differences were reflected in the median survival times of species derived from the survival analysis (Figure 2). *Cecropia, Goupia* and *Laetia* had considerably higher survival rates in larger gaps than small gaps with median survival times over 700 days in gap sizes 400 m^2. *Pentaclethra, Catostemma* and *Sclerolobium* all had median survival times greater than 800 days in all gap sizes whilst *Chlorocardium* and *Ormosia* both tended to have

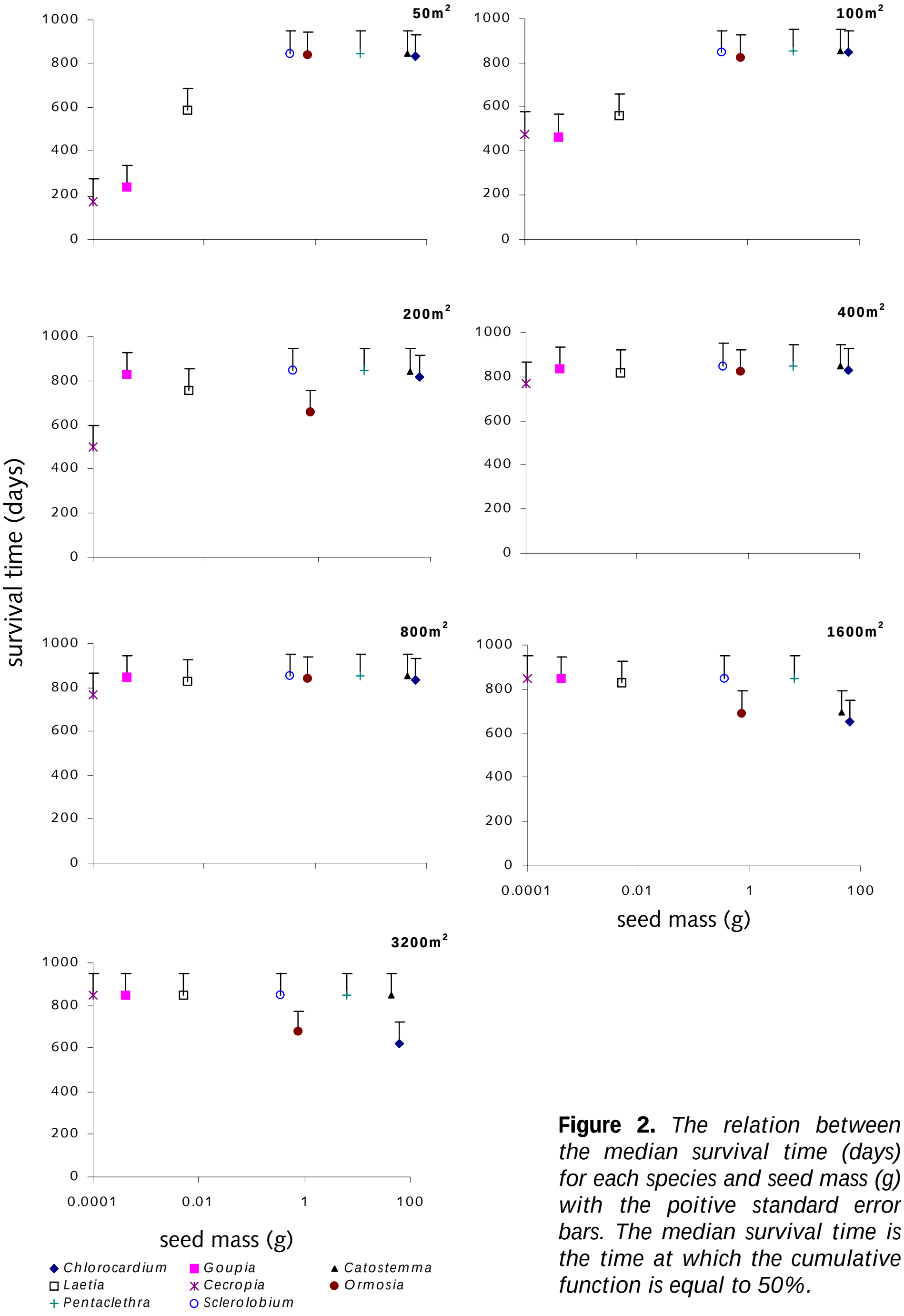


Figure 2. *The relation between the median survival time (days) for each species and seed mass (g) with the poitive standard error bars. The median survival time is the time at which the cumulative function is equal to 50%.*

slightly lower survival rates in the largest gaps. Significant correlations between seed mass and survival were only found for seed masses less than 0.05 (Table 5).

Table 5 *Results of Tukey HSD post hoc test showing the effect of gap size and seedmass on mean seedling survival at the end of the experiment. Gap sizes and species with the same letters are not significantly different (at the 0.05 level) from each other. Pearson correlation coefficients are shown for seed mass and gap size.*
*** Correlation is significant at the 0.01 level*

Species	Seed mass	Correlation coefficient	Gap size
Cecropia	0.00014^{a}	0.599**	50^{a}
Goupia	0.00038^{a}	0.549**	100^{a}
Laetia	0.005^{a}	0.346**	200^{a,b}
Chlorocardium	63.007^{b}	- 0.016	400^{b,c}
Ormosia	0.743^{b}	- 0.081	800^{b,c}
Catostemma	44.596^{c}	- 0.111	1600^{c}
Pentaclethra	6.494^{c}	0.072	3200^{c}
Sclerolobium	0.348^{c}	0.097	

These results clearly identify three groups of species (Figure 3, Table 5). The first group contains those species (*Catostemma*, *Pentaclethra* and *Sclerolobium*) that showed no significant differences in their survival with gap-size. The second group contains those species (*Cecropia*, *Goupia* and *Laetia*) whose survival increased with a corresponding increase in gap-size, and the third group (*Chlorocardium*, *Ormosia*) are the species that had a concurrent decrease in their survival rates with an increase in gap-size. Correlations with seed mass were found only for species in the second group (Table 5).

Seedling height growth

Gap size and seed mass both significantly influenced seedling heights (Table 6). Seedling heights were significantly different between measurement intervals and interactions between all the above-mentioned factors were significant (Table 6). In the small gaps there was an increase in seedling height as seed mass increased, however as gap size increased there was a negative relation between seedling height and seed mass (Figure 4). Species heights increased as gap size increased (Figure 5) although the significance of this increase was quite variable (Table 7).

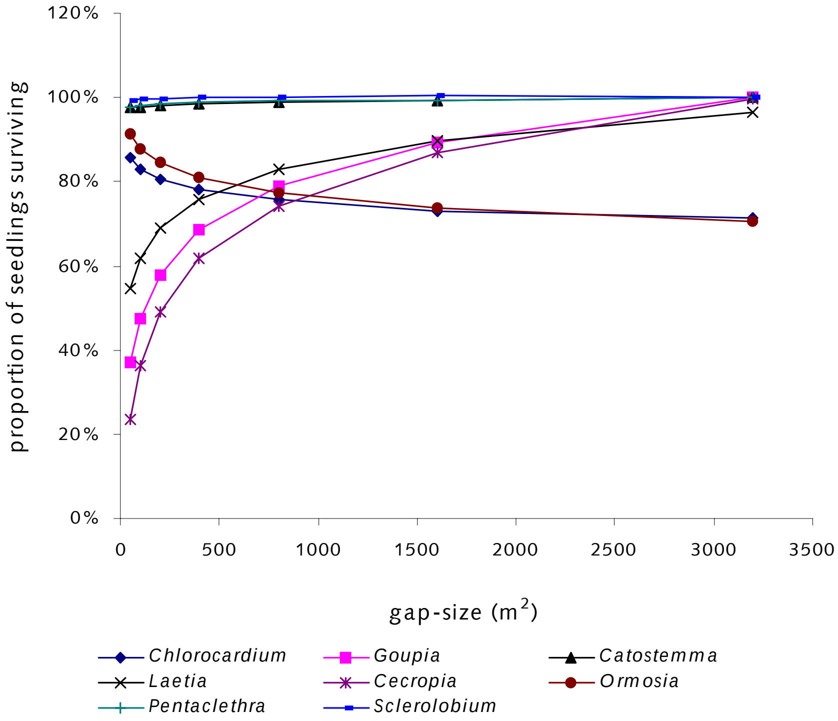


Figure 3. *The survival curves for the eight study species as a function of gap-szie. The survival function is derived from the cumulative proportion of seedlings per spcies that survives at each measurement. Since the probabilities of a seedling surviving are assumed to independent across the measurement intervals, the survivorship is computed by multiplying out the probabilities of survival across all previous intervals.*

In the smallest gaps (< 200m^2), the species with the tallest seedlings at the beginning remained the tallest throughout the study period (Figure 5). The faster growing species (*Cecropia*, *Sclerolobium and Goupia*), that were relatively small at the beginning of the experiment, quickly overtook the other species, as early as approximately five months into the study. These species maintained very high height growth rates and were the tallest plants at the end of the experiment. Height growth in the first year of the experiment was generally relatively slow, especially in the smaller gaps with none of the leading species greater than 3 m tall at the end of the first year. Clearly, the larger gaps (> 800 m^2) contained the taller seedlings of all species. *Sclerolobium*, *Cecropia* and *Laetia* experienced a six fold increase in height from the beginning to the end of the experiment in the large gaps than in the small gaps while *Chlorocardium* and *Ormosia* showed approximately an increase of 1.5 times in height.

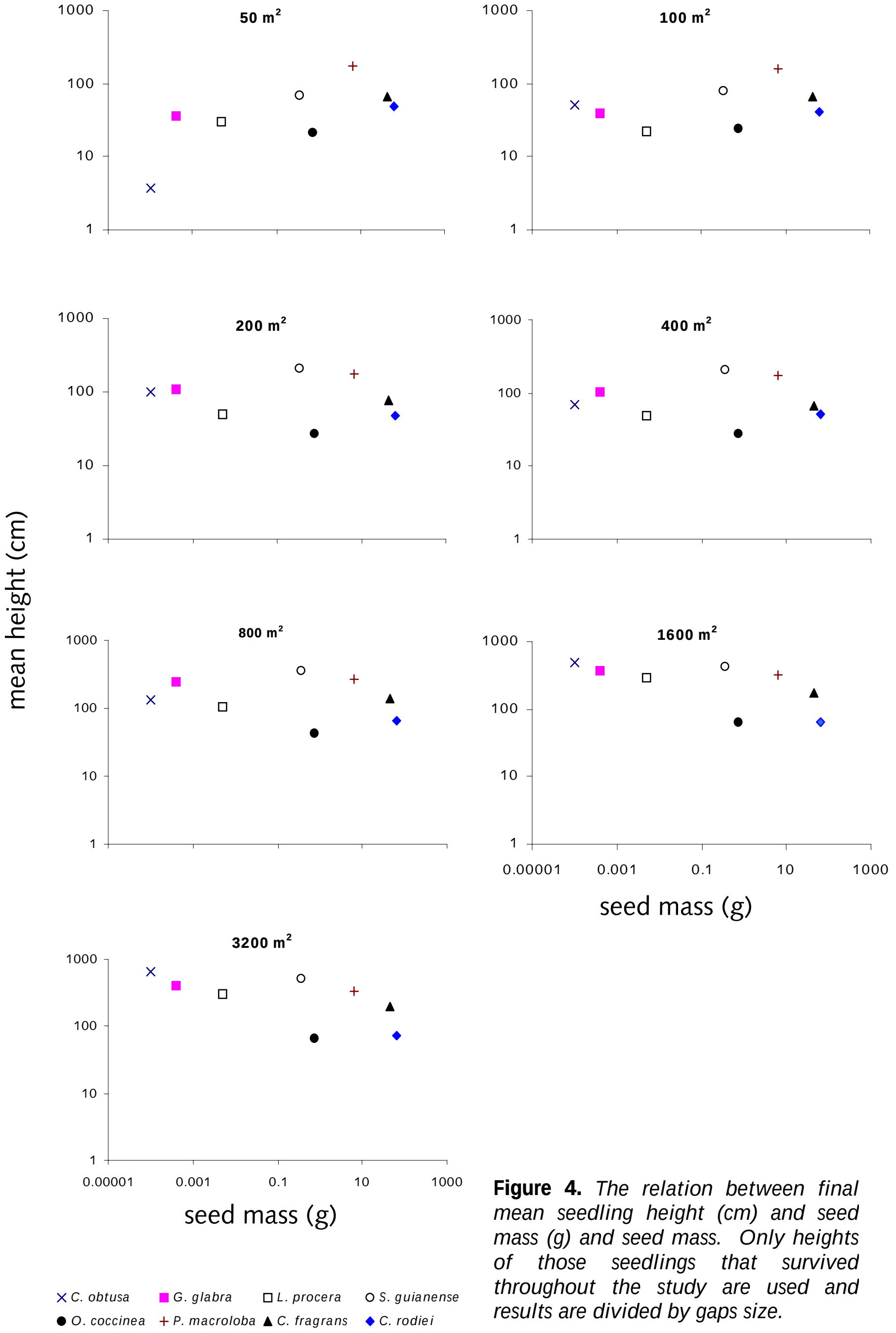


Figure 4. *The relation between final mean seedling height (cm) and seed mass (g) and seed mass. Only heights of those seedlings that survived throughout the study are used and results are divided by gaps size.*

Table 6 *Results of the multivariate ANOVA showing the effects of seed mass, gap-size, time and their interactions on seedling heights amongst the 8 study species. The F-values and significance levels (p-values) are shown. In all cases p < 0.001.*

Effects	df	F-value	p-value
Seed mass	7	65.61	***
Gap-size	6	8.54	***
Time	6	42.26	***
Seed mass * gap-size	42	12.86	***
Seed mass * time	42	46.81	***
Gap-size * time	36	48.70	***
Seed mass * gap-size * time	252	11.00	***

Discussion

This study had two major objectives: (i) to examine whether the eight tropical rain forest species chosen showed survival and growth preferences for a particular gap-size range and (ii) to determine the influence of seed size on the species preferences shown in gaps of different sizes. The results demonstrated no clear patterns of gap partitioning by species preferences to specific gap sizes. Some evidence was found for a seed size influence on seedling survival and growth in gaps.

Hubbell and Foster (1986) proposed that the vast majority of tropical rain forest species are in fact generalists, with the extremes being those species showing very high and low tolerances to shade. This implies that most tropical rain forest species are capable of surviving and growing in a wide range of gap sizes, although their occurrence in a gap may be limited to specific zones within that gap. Grubb (1996) reviewed studies done between 1942 and 1994 on the role of seed mass on seedling regeneration. For most of the studies reviewed, very wide and overlapping ranges of seed mass values were found for species considered shade tolerant and strongly light demanding. The results of the present study do indicate a negative relation between small gaps and the survival of the three species with the lowest seed masses, but most of the five other species survived equally well in the entire gap size range. These five species range in seed mass from 0.35g to 63.01g, and have been classified as either long-lived pioneers or shade tolerant species. Foster and Janson (1985) monitoring 203 species, demonstrated a positive relationship between seedling survival of large seeded species and small gaps, a finding supported by

Table 7 *Results of Scheffé showing the intraspecific variation in species height responses within gaps. Heights were ln transformed before the analysis and were not significantly different between gaps with the same letters for each species.*

	50	100	200	400	800	1600	3200
Cecropia	*a*	*a*	*b*	*b*	*b*	*c*	*c*
Goupia	*a*	*b*	*ab*	*ab*	*c*	*cd*	*d*
Laetia	*a*	*a*	*c*	*b*	*c*	*d*	*e*
Chlorocardium	*b*	*a*	*ab*	*ab*	*c*	*cd*	*d*
Ormosia	*a*	*a*	*ab*	*a*	*c*	*c*	*bc*
Catostemma	*a*	*a*	*a*	*a*	*b*	*b*	*c*
Pentaclethra	*a*	*b*	*b*	*b*	*c*	*d*	*d*
Sclerolobium	*a*	*a*	*b*	*c*	*d*	*d*	*e*

Boot (1996). Both studies suggest that the extra resources in cotyledons of large seeds increased the survivorship of these species in small gaps. However, *Sclerolobium* and *Ormosia*, two relatively small seeded species, had over 90% seedling survival in small gaps. *Catostemma* and *Chlorocardium*, the species with the largest seed mass exhibited similar survival rates.

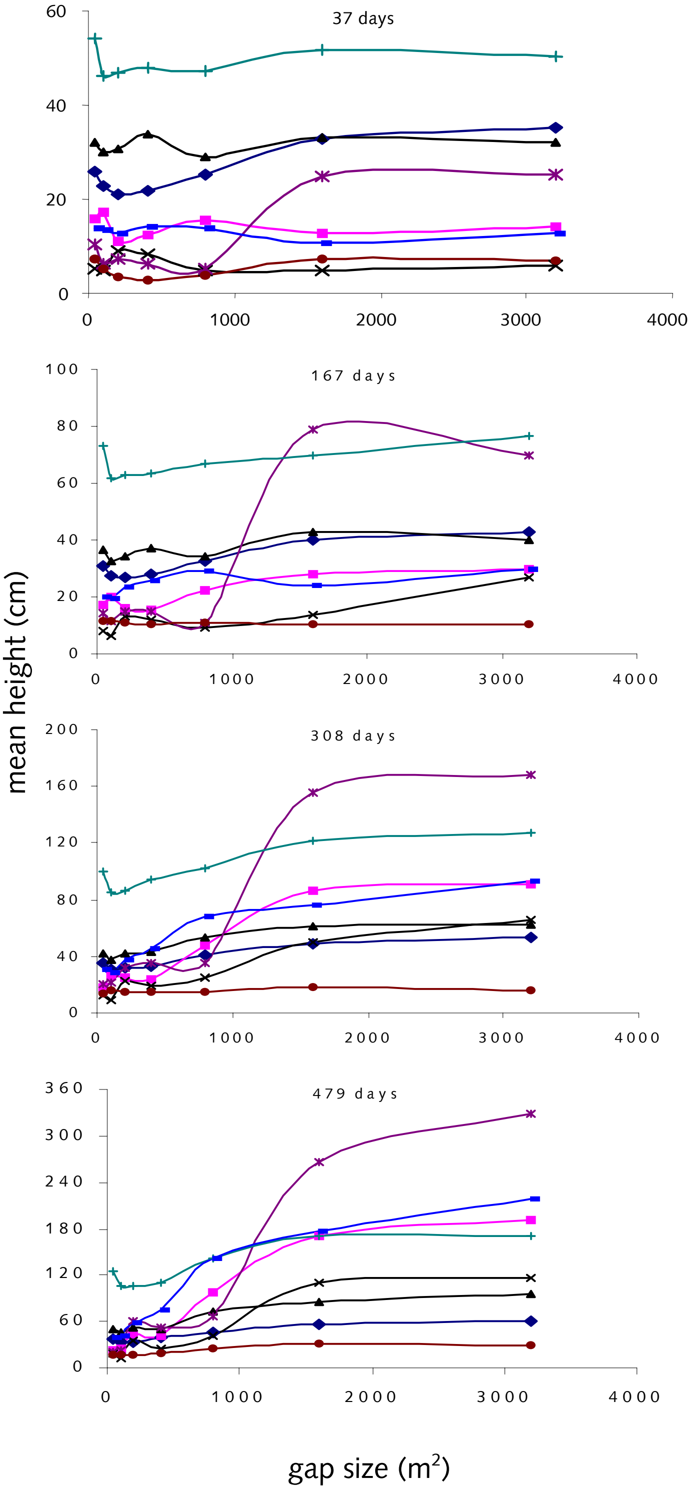
Furthermore, Brown and Whitmore (1992) found varied survival responses of three dipterocarp species to a range of gap size, although these were naturally established seedling populations. In the present study *Chlorocardium* and *Ormosia*, two species considered shade tolerant, exhibited relatively high mortality rates in the largest gaps. This was quite surprising since in those gaps, the light demanding species such as *Cecropia* and *Goupia* grew quite fast and soon shaded the slower growing *Chlorocardium* and *Ormosia* seedlings. As a result, the latter species did not experience full sunlight in these gaps, for a prolonged period. However, Kennedy and Swaine (1992) and Poorter (1998), found that mortality of shade tolerant species was low in large gaps, even under competition by other seedlings. Thus, so far, no clear-cut pattern has emerged in the relationship between seed size and seedling survival over a gap size range.

Height growth of all eight species was enhanced by an increase in gap-size. Although there were species differences in growth in some gaps, there was little evidence of species specialisation on a narrow gap size range. All seedlings in the present study grew faster in the largest gaps. *Cecropia*, *Sclerolobium*, *Goupia* or *Pentaclethra* always occupied the top height positions in all gaps. Five months after transplantation into the gaps *Cecropia*, which was initially one of the smallest seedling, had grown taller than all the other species, and maintained that height advantage for the duration of the study. The smaller gaps were generally dominated (in height) by *Pentaclethra*. This species initially produced the largest seedling in all cases and in the small gaps quickly amplified this advantage. In the large gaps however, the initial height advantage was quickly lost to the faster growing species, but it maintained its fast height growth rate. The obvious conclusion is that more light leads to increased height growth.

Gap partitioning

While controlled studies indicate that tropical rain forest tree species perform differently along a gap size gradient (Bazzaz & Wayne 1994, Sipe & Bazzaz 1995, Burslem 1996, Poorter 1999), hardly any evidence of gap-size preference has been reported from observational studies of species distributions in natural forest. Most of these studies in natural forest report no correlation between species composition and gap size (Raich & Gong 1990, Brown & Whitmore 1992, Oberbauer *et al*. 1993, Lieberman *et al*. 1995, Chapter 3). For example, Lieberman *et al*. (1995) found that 86.5% of all tree species ≥ 10 cm dbh in an 11-ha plot of the La Selva forest, Costa Rica, were randomly distributed with respect to levels of canopy openness. They concluded from the evidence that none of the species studies was restricted in its distribution to specific levels of canopy openness.

One possible reason why gap partitioning is rarely observed in natural forest may be that these gaps mostly contain advanced regeneration. Advance regeneration refers to the juveniles of shade tolerant species present in the understorey before gap creation. Regrowth in gaps is often dominated simply by the tallest advance regenerators at that time (Brown & Jennings 1998, Chapter 4). The tallest plants intercept the most light irrespective of whether or not it is able to respond with rapid growth. Plant size is an integration of its total growth history. It does not depend on whether conditions are currently optimum for growth nor on whether the plant has the highest rate of growth of those in competition for light. This is evident from direct observations and from the fact that overall gap composition changes little during regrowth (Brokaw & Scheiner 1989, Runkle 1998, Hubbell *et al*. 1999, Chapter 3). Thus, pre-gap patterns in the understorey, not post-gap partitioning, largely determine gap composition and the size hierarchy at the time of gap creation (Brokaw & Scheiner 1989). These processes may therefore be more important than the relative difference between species growth rates in gaps in determining the outcome of competitive interactions after gap formation.


37 days
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308 days
200
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120
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mean height (cm)
gap size (m²)

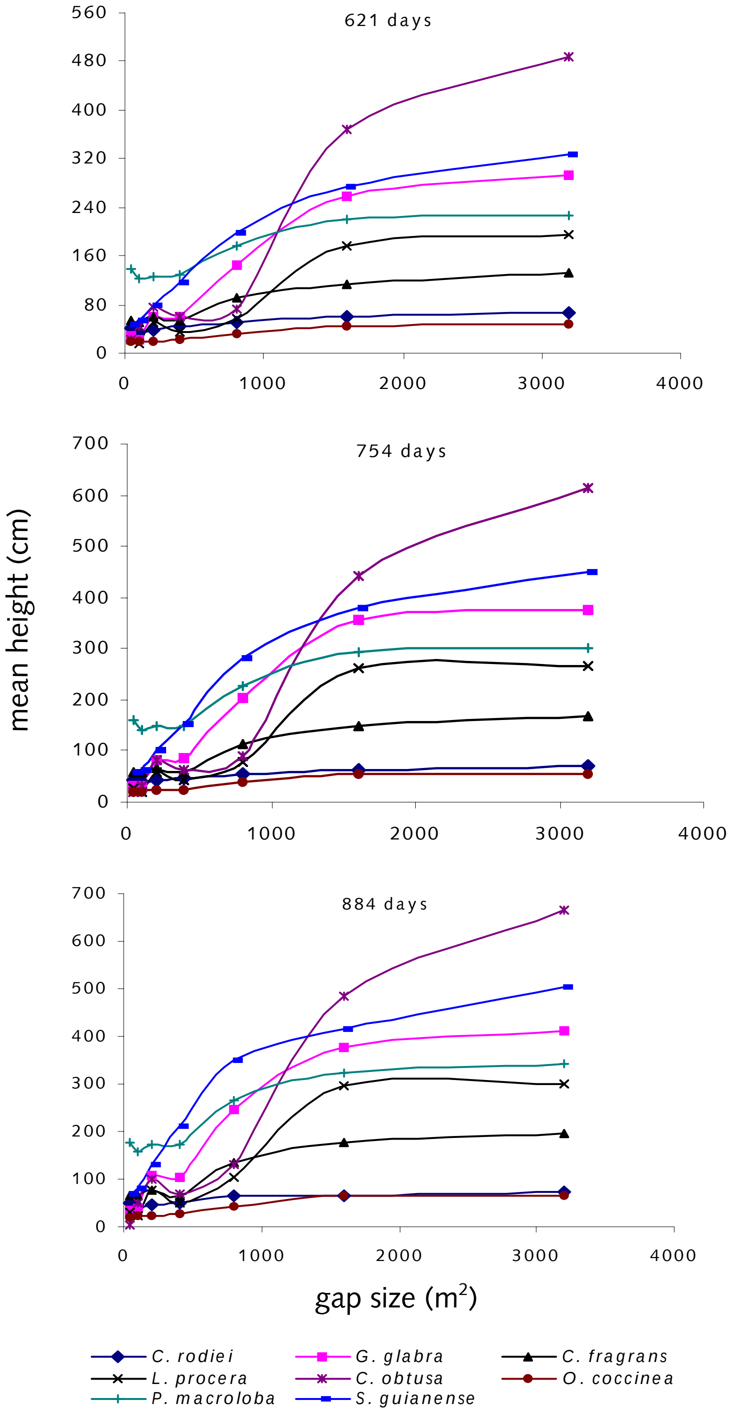

Figure 5. *The mean height (cm) of surviving seedlings at successive remeasurements throught the 884 day study as a function of gap size.*

Tilman (1982) first suggested that a trade off exists between the maximum rate at which a seedling may exploit an abundance of light (and other resources) and it's tolerance to reduced levels of light. Rather than differing in the level of light, they require for fast growth (as proposed in the gap-size partitioning theory), most seedlings will show better growth as light becomes increasingly abundant. A shifting competitive hierarchy will therefore be established along a light gradient (Keddy 1989). As light becomes increasingly available, species not able to tolerate low light levels are able to grow faster than those that are tolerant to scarcity. The pattern of growth of seedlings in this study appears to confirm this model. All showed improved growth in larger gaps, but differed in their maximum heights attained during the study period. Brown and Whitmore (1992) and Brown (1996) also found similar patterns of seedling growth.

Another important point to note is that although some species, which show preferences for smaller gaps, may not be able to withstand high light levels and survive and grow in the centre of large gaps, they may occur at the edges of these gaps. This would imply that species distribution in a range of gap sizes might ultimately be limited only by their dispersal into those gap zones for which they are best adapted.

The results of this study provide limited evidence for species preferences to a particular gap size. It does however indicate which gap sizes lead to the subsequent changes in the initial size hierarchy and shows how seedlings grown in sub optimal light conditions beneath taller individuals are able to compete for a superior position in the size hierarchy. This points towards a shifting competitive hierarchy instead of preference along a gap-size gradient.

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CHAPTER 4

LEAF LIFE SPANS OF SEEDLINGS OF EIGHT SPECIES IN THE GUYANESE TROPICAL RAIN FOREST

with Marinus Werger

Abstract

Leaf life spans of tropical rain forest species were studied in gaps over a period of 22 months. Seedlings of eight species were grown in seven different gaps sizes and the relationship between leaf survival, gap size and shade tolerance was examined. There was a negative relation between leaf survival and gap size for most species whilst leaf production was enhanced by gap size. Leaf loss decreased and leaf survival percentages increased with increasing shade tolerance of species, indicating a slower leaf turnover for more shade tolerant species.

Keywords

Leaf life spans, gap size, tree seedlings, tropical rain forest

Introduction

Tropical rain forest species can be divided roughly into two groups, gap-dependent and shade tolerant species. 'Gap-dependent' species are shade intolerant, germinate and grow rapidly in tree fall gaps, and usually have high mortality rates in the understorey (Swaine et *al*. 1997, Poorter 1998). 'Shade tolerant' species on the other hand, germinate, grow and have high survivorship in the forest understorey. This differentiation between species is most pronounced during the early stages in their life cycle (Chapter 2 & 3).

The ability of a plant to respond to the formation of a gap in the canopy may have important fitness consequences. Responses to increased light can occur at the leaf level and involve acclimation of the photosynthetic apparatus, or at the whole plant level because of changes in the growth or allocation patterns (Chapter 2). A plant's growth and morphology may be modulated through the regulation of its leaf production and abscission (Bongers & Popma 1988, Kursar & Coley 1999). The growth of plant stems depends on the production of internodes, and each internode is produced in association with a new leaf.

Leaf life span is therefore an important life history trait of plants with respect to their growth and response to light (Reich et *al*. 1991, Coley 1988, Kikuzawa & Ackerly 1999). Shade tolerant rain forest species are thought to have longer leaf life spans than shade intolerant species (Bongers & Popma 1988). In a simple theory, leaf life span is related to a balance between costs and benefits. Specifically, when the costs of maintaining a leaf through unfavourable periods exceeds the profits leaves will be discarded (Chabot & Hicks 1982). As a leaf becomes more expensive to make, its life span will have to be increased to pay back the costs (Johnson & Tieszen 1976, Poorter & Villar 1997). Such leaves are usually well protected against herbivores to ensure their longevity. This again increases the costs. Hence, long lived leaves of rain forest species tend to have higher dry weight (or cost) per leaf area (King 1994; Reich et al. 1997), lower light-saturated photosynthetic rates (Reich et al. 1992; Mulkey et al. 1993; Ackerly 1996), less damage from photoinhibition (Lovelock et al. 1998), and greater defences against herbivores (Coley 1998).

These differences associated with life span suggest that it would be costly for a species with long-lived leaves to shed them prematurely (Reich et *al*. 1991). In contrast, shade intolerant species often have leaves that are short-lived and can be more readily discarded if the environment changes or when self-shading occurs due to further height growth of the plant. Hence, extended leaf life span may be hypothesised as an adaptive strategy employed by species for survival in the shade (Harrington et. *al* 1989), and short leaf life span may be considered an adaptation for rapid growth rate (Coley 1988).

Based on these considerations two hypotheses can be put forward concerning the effects gaps may have on the leaf dynamics of seedlings:

(1) Leaf life span of all species is influenced by gap-size and decreases with increasing gap size.

An increase in gap size corresponds with an increase in light availability. This increase in light results in faster plant height growth for all species. At the shoot and whole-plant level, one of the consequences of height growth is self shading among leaves as new leaves are produced in upper canopy positions and older leaves occupy successively and less illuminated positions (Ackerly & Bazzaz 1995a). Self shading and the consequent reduction in light levels results in lower photosynthetic rates mean that the cost of maintaining the leaves are too much for the plant and hence the leaf is shed.

(2) Shade tolerant species have longer leaf life-spans than pioneer or long lived pioneer species

Shade tolerant species have relatively slower growth rates and consequently produce limited amounts of carbohydrates. They can therefore not produce many leaves and must retain their few leaves for a longer period. The slow leaf production limits the incidences of self-shading (Ackerly 1999). Investments into protecting leaves against herbivory also increases the cost per unit leaf area and hence makes a slow leaf turnover beneficial.

To test these hypotheses, plants were grown in the centre of seven gaps ranging in sizes from 50 to 3200 m^2. New leaves on fully acclimated seedlings were followed for 22 months.

Materials and methods

Study species, growth conditions and measurements

The study was carried out in the Pibiri Research Area of the Tropenbos-Guyana Programme, located 49 km south of the Mabura Hill township (5°02'N and 58°38'W between June 1997 and April 1999).

Species were chosen based on known life history traits and availability at the time of collections. Seeds were collected for *Ormosia coccinea, Pentaclethra macroloba* and *Sclerolobium guianensis*, whilst newly germinated seedlings (5 - 10 cm) were collected for *Chlorocardium rodiei, Catostemma fragrans, Laetia procera, Goupia glabra* and *Cecropia obtusa.* All collections were made in the West-Pibiri Compartment (outside of the Pibiri Research Area), between February and August 1996.

In each gap, 80 individuals (8 species x 10 individuals each) were randomly assigned to predetermined sites at the gap-centre of the seven gaps (50, 100, 200, 400, 800, 1600, 3200 m^2). Each individual was given a unique tag number for future identification. During the first month after transplantation, plants were shaded with a layer of grey mosquito mesh, and were watered once daily to allow acclimation to gap conditions. Dead or unhealthy individuals were replaced during this period (see Chapter 3 for full experimental set-up).

In order to determine leaf life spans, new leaves produced were marked with *'white out'* from June 1997 (eight months after transplantation) until December 1998. After this period, no new leaves were marked. Leaves were monitored weekly and followed for a total of 22 months. In the case of *Goupia*, *Laetia* and *Sclerolobium* only a subset of the new leaves were marked in the large gaps. This was done because these species rapidly produced new leaves and following all new leaves proved quite time consuming. The number of leaves marked is therefore an underestimation of leaf production of these species. The absence of each leaf was noted and dated on a subsequent survey, with leaf lifetime estimated as the time interval between the two dates.

Data analysis

Data were analysed using analysis of variance, and Kaplan Meier's survival analysis (SPSS 8.0 for Windows (SPSS Inc 1997)). A two way ANOVA was used to test for differences in leaf survival times between species and between gap sizes. Since significant differences were observed, an Scheffé test was performed to determine in which gap sizes and between which species leaf survival times were significantly different.

Kaplan Meier's survival analysis was used to compare the survival curves of the leaves of different species in the seven gap sizes. Median leaf life spans for each species was estimated from the data in this analysis. Median leaf life span was used because especially for species with long lived leaves many leaves (<50%) were still alive when the monitoring period ended and thus mean life span could not be determined. For those species that lost all leaves during the monitoring period, the values for the mean and median leaf life span were similar.

Results

Effect of gap-size on species leaf loss patterns

The number of leaves marked for most species was highest in the intermediate gap sizes (400 – 800 m^2) and lowest in the smallest gaps (Table 1). The highest number of marked leaves was recorded for *Goupia* and *Laetia*.

Table 1 *The number of leaves marked for all species during the first 18 months of the study period. In brackets, the percentage of leaves abscised is shown.*

	50 m^2	100 m^2	200 m^2	400 m^2	800 m^2	1600 m^2	3200 m^2
Cecropia	8 *(100)*		11 *(100)*	13 *(100)*	14 *(100)*	16 *(100)*	10 *(100)*
Goupia			17 *(100)*	30 *(100)*	30 *(100)*	38 *(100)*	36 *(100)*
Laetia	3 *(100)*	8 *(100)*	13 *(100)*	16 *(100)*	20 *(100)*	27 *(100)*	28 *(100)*
Sclerolobium	21 *(100)*	29 *(100)*	22 *(75)*	34 *(82)*	17 *(83)*	16 *(7)*	16 *(12)*
Catostemma	13 *(38)*	17 *(87)*	18 *(71)*	21 *(48)*	19 *(100)*	17 *(100)*	17 *(92)*
Chlorocardium	3 *(100)*	9 *(100)*	6 *(67)*	17 *(36)*	10 *(100)*	14 *(100)*	14 *(100)*
Ormosia	9 *(48)*	10 *(90)*	8 *(50)*	15 *(70)*	18 *(100)*	19 *(100)*	14 *(100)*
Pentaclethra	21 *(88)*	29 *(76)*	22 *(65)*	24 *(31)*	17 *(8)*	16 *(26)*	16 *(40)*

Leaf turnover patterns were significantly different between gaps ($F_{6,866}$ = 5.28; P = ***), and between species ($F_{7,866}$ = 36.94; P = ***). A higher percentage of leaves were lost in the largest gaps as compared the small and intermediate gap sizes. Six of the species experienced more than 90% leaf turnover in the three largest gap sizes, while only three species experienced more than 90% leaf turnover in the 200 and 400 m^2 gaps. *Laetia*, *Goupia* and *Cecropia* experienced 100% leaf turnover (marked leaves) in all gaps whilst *Pentaclethra* was the only species that never lost all marked leaves in any of the gaps (Table 1).

Leaf survival

The differences in leaf turnover rates suggest that for most species, leaves survived longer in the intermediate gap sizes. Figure 1 shows the survival percentages for all species in the gaps. From these survival curves, species can be placed into three groups. The first group consists of *Cecropia*, *Goupia* and *Laetia*, species with steep curves and median survival times of less that half a year (in most cases) (Table 2).

Table 2 *Median survival times (days) with standard error of species in all gaps. Gaps (species) followed by the same letters are not significantly different from each other (Scheffe's test).*

	50^{b}	100^{c}	200^{c}	400^{bc}	800^{ab}	1600^{a}	3200^{a}
Catostemma^{cd}	499 ± 49	626 ± 167	402 ± 59	497 ± 54	633 ± 302	423 ± 20	364 ± 2
Cecropia^{a}	87 ± 51		187 ± 36	253 ± 56	126 ± 51	130 ± 0.72	126 ± 21
Chlorocardium^{bc}	392 ± 103	367 ± 78	561 ± 91	505 ± 54	423 ± 85	354 ± 23	337 ± 39
Goupia^{a}			156 ± 0.68	281 ± 55	211 ± 28	160 ± 57	126 ± 4
Laetia^{ab}	126 ± 90	303 ± 70	341 ± 56	388 ± 10	292 ± 22	322 ± 23	262 ± 22
Ormosia^{bc}	455 ± 88	343 ± 61	392 ± 58	364 ± 114	292 ± 30	294 ± 78	249 ± 35
Pentaclethra^{cd}	375 ± 120	392 ± 23	392 ± 27	549 ± 52	609 ± 40	519 ± 49	561 ± 50
Sclerolobium^{d}	409 ± 81	426 ± 6	409 ± 33	495 ± 75	419 ± 42	635 ± 17	615 ± 25

In most gaps, the leaves of these species experienced 0% survival after a bit more than 1 year. *Ormosia*, *Catostemma*, *Chlorocardium* and *Sclerolobium* make up the second group. These species experienced low leaf survival in the largest gaps (three species) and/or the smallest gaps (Table 1).

Sclerolobium had its highest leaf survival in the two largest gaps whilst the other three had their highest leaf survival between the 50 and 400 m^2 gaps. Median survival times for leaves of these species ranged from more than 1 year to over 2 years (Table 2). *Pentaclethra*, the only species with some marked leaves remaining in all gaps, comprised the last group. At the end of the monitoring period, this species had more than 20% of marked leaves remaining in the smallest gaps, and more than 60% remaining in the largest gaps.

For all species, survival percentages of early leaf cohorts were lower than those of later ones, indicating that mostly the oldest leaves were shed first. There were no significant differences in leaf survival times of old or young cohorts.

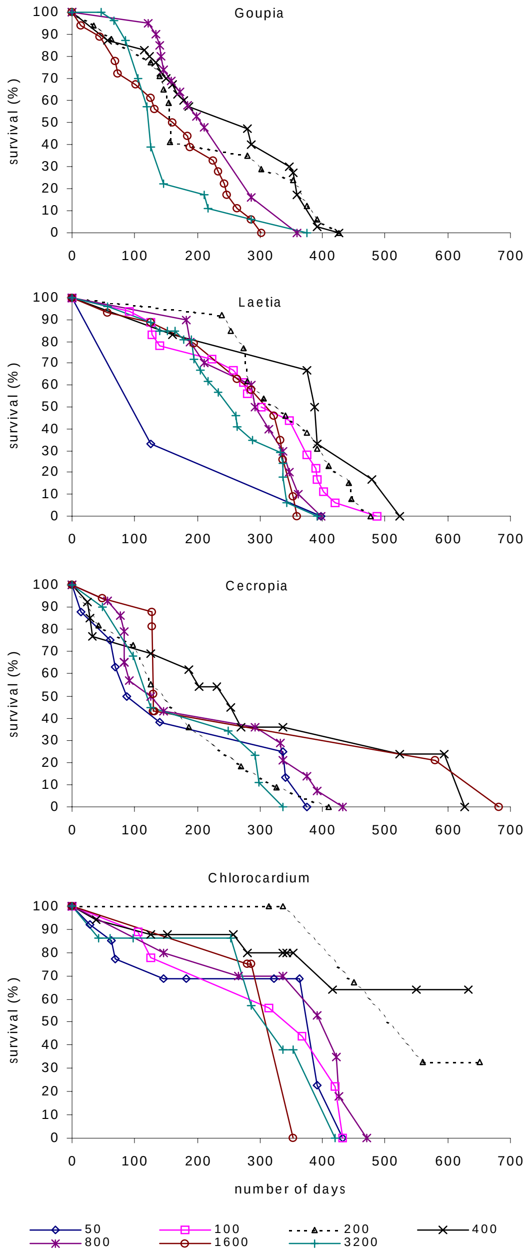

Figure 1 *Leaf survival percentages of the differentspecies over the study period. Each plot is indicative of a species and each line a different gap size.*

Discussion

The effect of gap size on leaf life spans and leaf turnover

Are leaf life spans influenced by gap size? In all species, the production rate of leaves was higher in large gaps than in small gaps. Median survival times indicate that life spans were longest in the intermediate gap sizes for most species. The increased leaf production and leaf loss rates resulted in a higher leaf turnover in the large gaps when compared to small gaps.

These results are in agreement with those of Langenheim et *al*. (1984) who showed that seedlings of three Amazonian and two Australian tropical rain forest species had higher leaf production in the sun than in the shade.

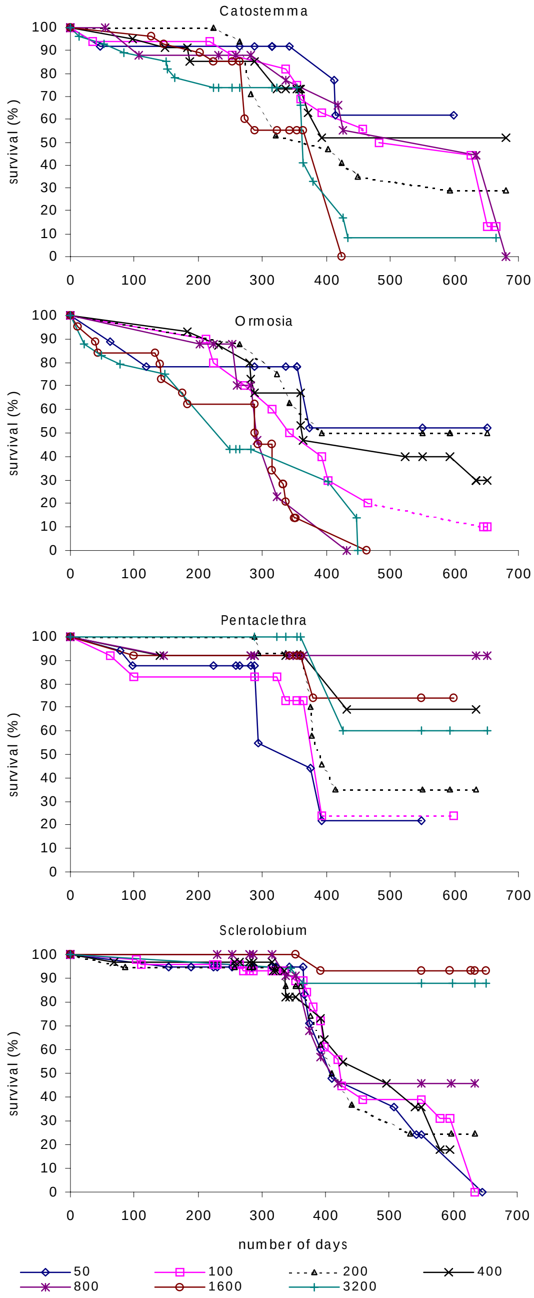

Figure 1 cont'd
Leaf survival percentages of the different species over the study period. Each plot is indicative of a species and each line a different gap size.

Bongers & Popma (1988) working with seedlings in the Mexican rain forest found higher leaf life spans in the forest understorey and in small gaps when compared to large gaps. Leaves produced in the large gaps tend to have high specific leaf weights (SLW) (Chapter 2). The fact that these high SLW leaves had lower survival percentages in large gaps compared to in small gaps, indicates that in large gaps more costly leaves are shed earlier in comparison to small gaps.

Leaf life spans and shade tolerance

Do shade tolerant species have longer leaf life spans than shade intolerant species? The results indicate that the more shade tolerant species (*Chlorocardium*, *Catostemma*, *and Ormosia*) had higher leaf survival than the less tolerant species (*Cecropia*, *Goupia*, *and Laetia*). *Sclerolobium*, a long-lived pioneer had low survival percentages in all but the two largest gaps while leaves of *Pentaclethra*, a species which survives equally well in large and small gaps, had relatively high survival rates in all gaps.

Shade tolerant species produce fewer leaves and at a slower rate whilst the fast growing species do just the opposite. The amount of resources that shade tolerant species invest in one leaf is therefore relatively much higher than that of one leaf of a shade intolerant species. Hence, the consequences of discarding shade tolerant leaves are much more severe than is the case for shade intolerant leaves. Furthermore, the production of many leaves by shade intolerant species results in reduced illumination of older leaves that will be lower on the stem. The costs of maintaining these older leaves outweighs the benefits since these leaves will have lower photosynthetic rates than younger leaves at the top of the stem which are exposed to higher levels of radiation. This results in the shedding of these leaves as new leaves are rapidly produced.

Ecological considerations

Plants with a high leaf turnover are likely to have an advantage over plants with a slow leaf turnover when subject to environmental changes: when necessary (and when sufficient resources are available) these plants are able to rapidly change their morphology and architecture (Bongers & Popma 1988). *Cecropia*, *Laetia* and *Goupia*, the three light demanding species, all had high leaf turnover rates irrespective of gap size. This may mean that the leaf life span of these species is not very flexible but these species are mostly growing under high light conditions with sufficient assimilates to produce new leaves. Under continuously varying environmental conditions, physiological flexibility is probably more important than morphological flexibility for shade tolerant species. This may be reflected in a wider range of light availability in which an existing leaf can function properly.

In conclusion, the results of this study suggest that there are strong correlations between gap size, shade tolerance and leaf life spans. It also raises the possibility that species (such as *Pentaclethra*), with great plasticity in modifying their leaf life spans, may be able to grow well in a wide range of gap sizes where the resource availability is also quite variable. On the other hand, species without plasticity in this regard will occupy only a narrower range of gap sizes or have rapid leaf turn over rates.

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"Tropical rain forests are both the fearsome jungle of our fantasy and the fertile Eden of our myth"

Phillip Stott 1999

CHAPTER 5

RECRUITMENT, MORTALITY AND SPECIES COMPOSITION OF NATURALLY ESTABLISHED SEEDLING POPULATIONS IN SELECTIVELY LOGGED TROPICAL RAIN FOREST IN GUYANA

Abstract

Recruitment, mortality and the species composition of naturally established tree seedlings were investigated in logged (1994) forests in Guyana between 1996 and 1999. In two hundred and forty nine 2 x 2 m plots, tree seedling responses to canopy openness (1 - 37%) were monitored.

There was a positive relationship between recruitment and canopy openness until the largest canopy openness class, where recruitment declined. Mortality of newly recruited seedlings was more than double that of old seedlings. As canopy openness increased mortality of old seedlings also increased and decreased only in the largest class, but no clear pattern emerged for the young seedlings.

Species were classified into shade tolerant, intermediate and pioneer guilds and the composition of these guilds in the plots was examined. Species composition was influenced by canopy openness but the change over time was not significant. Pioneer species densities were low in all canopy openness classes while the shade tolerant species represented more than 50% of all stems in all canopy openness classes and in all years. With an increase in canopy openness, the density of the shade tolerant species also increased but no clear pattern emerged for the pioneers.

Keywords

Canopy openness, recruitment, mortality, shade tolerance, intermediate and pioneer species, seedling density, species composition, tropical rain forest, Guyana

Introduction

The most common method of logging in tropical rain forest is to exploit the important timber species, without much concern for the residual forest stand (Uhl & Viera 1989, Poore 1989, Macedo & Anderson 1993, Webb 1998, de Graaf *et al.* 1999). This results in forests that have very low commercial value and are often ecologically degraded. In several countries where timber resources have been depleted or where high extraction rates are problematic, methods for sustainable timber extraction have been investigated (De Graaf 1986, Jonkers 1987, Caldecott 1988, Sips 1993, Pinard & Putz 1996, van der Hout 1999).

Yet, there is concern about the impact of logging on the species composition and diversity (Whitmore and Sayer 1992), even where sustainable timber management is the objective (de Graaf & Poels 1990). Reduced impact logging is proposed as a technique to extract timber while minimising damage to forest structure, diversity and regeneration potential (Hendrison 1990, van der Hout 1999). In this paper the early effects of reduced impact harvesting on tree seedlings species composition, regeneration and diversity is examined.

To maintain near-natural forests, logging should aim at producing a disturbance pattern similar to the natural pattern found in that habitat. In tropical forests, natural tree fall gaps are a common form of disturbance (Lawton & Putz 1988, Yavitt *et al.* 1995, van der Meer & Bongers 1996). Gaps are known to be important for the successful regeneration of many tree species (Clark & Clark 1992, Denslow & Hartshorn 1994), and contribute to the maintenance of forest diversity (Orians 1982, Pickett 1983, Brandani *et al.* 1988, Enright *et al.* 1993). Gaps have therefore been the focus of many publications (Denslow 1980, Brokaw, 1980, 1985, 1987, Swaine & Whitmore 1988, De Steven, 1989, Brown 1993, Brown & Jennings 1998).

The size of a canopy gap is the main determinant for the microenvironment within a gap (e.g. soil moisture, nutrient status, light quantity and quality - Chazdon & Fetcher 1984, Ashton 1992). Richards (1952) discussed the importance of gap size in favouring species of different ecology.

Many studies have shown that the difference in gap size promotes differentiation of seedling recruitment and mortality among species (Bazzaz 1984, Brokaw 1985, Denslow 1980, Raich & Gong 1990, Turner 1990). It is assumed that no one species is able to be competitively superior across a wide range of different gap sizes and that niche specialisation is therefore an advantage (Sipe & Bazzaz 1995). Denslow (1980) has argued that a species may regenerate preferentially beneath a specific size of canopy gap that creates optimum conditions for its recruitment and survival.

Juveniles of the more shade-tolerant species, which have persisted in the shade before gap creation, are usually the dominant regenerative group. Larger gap sizes, which are typical of logged over forests, promote the germination and growth of the fast growing pioneer species, (which may have been present in the soil seed bank or later dispersed into the gap), and may prove unfavourable for other species (which may have been present as seedlings or are restricted by the prolific regeneration of the pioneers) (Lawton & Putz 1988). On the other hand, Hubbell *et al.* (1999) found that species did not always germinate all sites where they were favoured due to recruitment limitation. In cases where this occurs, the sites are usually won by 'default species' that may not be the best competitors for that particular site.

These differences among species are of considerable importance in ecology and forestry. Defining functional groups or response groups of species effectively increases sample size when generalizing about how species differ and how forest composition is affected by disturbance. In forestry, the degree of canopy openness made during exploitation has marked effects on the composition of the trees regenerating and thus on the future timber crop in rain forest (Hendrison 1990, Webb 1998, d'Oliveira 2000).

Many of the studies on seedling regeneration have been carried out in controlled shade house experiments. In contrast, only a small proportion of ‘canopy-gap seedling’ studies were performed in situ, i.e. investigating the effect of gaps on actual rates of recruitment and survival rates of naturally occurring seedlings (but see Clark & Clark 1987, Lieberman & Lieberman 1987, Nunez-Farfan & Dirzo 1988, Turner 1990 & 1991, Li 1991). Further, even fewer studies have looked at seedling regeneration in logging gaps. An examination of logging gap regeneration will provide insight into the potential impacts of logging on the species composition of the forest and the processes, which influence this composition. This study attempts to examine the recruitment and mortality of naturally established seedling popoulatoins in logging gaps.

This study addresses three questions about gap-phase regeneration in selectively logged mixed forest in the tropical rainforest in Guyana. First, are the patterns of seedling recruitment and mortality influenced by canopy openness? Second, what is the effect of canopy openness on the species composition and distribution patterns and is there a shift in species composition of the plots over time? Finally, to what extent is the species composition controlled by the composition of the surrounding vegetation?

Methodology

Area description

The study was conducted from 1996 to 1999 in an area covering approximately 1000 ha and designated the Pibiri Research Area within the Tropenbos-Guyana Programme. The area is located about 40 km south of the Mabura Hill Township, and approximately 250 km south of the capital, Georgetown, between 5° 05' and 5 °10' N and 58 °25' and 58 °35' W. Soils in this area belong to the Berbice formation, consisting mainly of Ferraalsols and Ferralic arenosols (van Kekem *et al.* 1996, Khan *et al.*1994).

Canopy height of the forest is estimated between 30 - 40 m, with emergents reaching up to 50 m. The vegetation is dominated *Chlorocardium rodiei* interspersed with *Lecythis confertiflora*, *Licania spp*., and *Catostemma fragrans* as co-dominant species (van der Hout, 1999). Species composition is variable, and is influenced by site factors such as soil texture, topography, water availability and differences in successional phase in forest dynamics (Ek 1997, van der Hout 1999).

Experimental set-up

This study was conducted within an area that was harvested using reduced impact logging techniques (van der Hout 1999). Within 100 ha blocks, fifteen 2 ha plots were established. Each plot was further subdivided into 20 x 20 m recording units (49 per plot). The plots were subjected to three different logging intensities and one control (replicated three times), in mid 1994. The experiment is described in detail in van der Hout 1999.

Plot selection for the current study began 14 months after logging. Plots were selected based on canopy openness. For this a horizontoscope was used to examine the canopy opening at the centre of each of the 20 x 20 m units of 12 of the study plots. This image was compared with sample images for which canopy openness was already known and an estimate was then made of canopy openness for the horizontoscope image. Estimated canopy openness for all sites was classified into five logarithmic classes ranging from 1 - 2 through to 16 - 32 % canopy openness. From each of the first four classes, fifty sites were randomly chosen. In the last class, only 49 sites were available and this resulted in a total of 249 sample sites in total. Plots measuring 2 x 2 m were then established at the chosen sample sites. Each plot was demarcated by four steel rods all connected with fishing line.

Measurements

Censuses were taken between February and April 1996 and at one-year intervals thereafter until 1999. For each census, the month when most of the field data was collected is considered the month of the census.

Individuals (seedlings to adults) of all tree species occurring within the plots were labelled with an individually numbered aluminium tag. With the assistance of a tree-spotter, all individuals were identified in the field by their vernacular names and then later assigned their scientific names. In a few cases, some individuals remained unknown. The identification process was later completed up to the species level, but where the vernacular names represented more than one botanically related species, it remained at the genus level.

Germination of new seedlings and survival of all other individuals was followed over this four-year period. No record could be made of seedlings that germinated after a census but died before the next census was taken. Therefore, mortality and recruitment are likely to be higher than reported.

By definition, new seedlings are considered to belong to the same cohort of the year in which they were first encountered. Seedlings of the first census are of mixed ages, and they are not considered a cohort. Plants that were damaged and re-sprouted were not considered dead.

All adult trees within a 20m radius of the plots were identified and their co-ordinates with respect to the plots were measured during the first census. Adults were taken as individuals with a dbh of 20 cm and above. This may have resulted in a few understorey species that attain reproductive maturity at smaller sizes being overlooked.

Canopy openness was measured in each plot immediately following the censuses, using hemispherical photography. A standard Nikon 35mm camera with 8 mm Sigma Fish-eye lens was used in 1996 and in subsequent years a Fujix DS505^{TM} 35 mm digital camera with similar Sigma Fish-eye lens was used. The camera was mounted and levelled on a tripod and oriented towards the true north. Pictures were usually taken close to either dawn or dusk and were always taken in the same location (centre of the plot) at 1 m above the ground.

Data analysis

Statistical analysis was carried out with SPSS 8.0 (SPSS Inc., Chicago IL 1997).

CANOPY OPENNESS

The hemispherical photographs were pre-processed using Paint Shop Pro 5 (vs. 5.01 Jasc. Software Inc. 1991-1998). This included resizing the image and then splitting the channels into red, blue and green. The analysis continued with the blue channel, which was then analysed for canopy openness in Winphot (ter Steege 1997). Repeated measures ANOVA was used to test for differences in canopy openness between years over the four-year measurement period. Plots were then divided into five equal canopy openness classes ranging from 0-5% to > 25%.

The distribution of plots into canopy openness classes was quite variable and significant (one-way ANOVA - $F_{5,15} = 9.9$; $P < 0.001$) between years. In 1996 the two smallest classes accounted for 57% of the plots and in 1999 66% as compared with 8 % and 1% in 1996 and 1999 for the 2 largest classes respectively. The direction of the rates of canopy closure differed significantly ($F_{5,10} = 5.9$; $p < 0.01$) between classes. Some classes showed an increase in the rate of closure in the last two years whilst the majority showed the highest closure rates in the first year of the experiment (Figure 1). Temporal differences were significant only in the two largest classes ($F_{2,5} = 9.7$; $p > 0.05$). These classes also recorded the highest canopy closure rate, which implies that the larger gaps were closing at a faster rate than the small gaps.

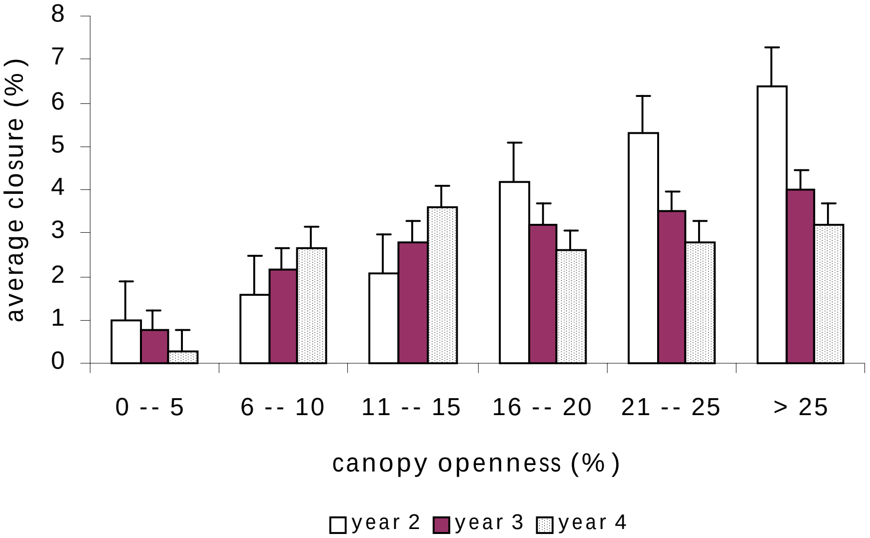

Figure 1 *The mean canopy closure of each class per year. The number of plots per year is the same (distribution of plots in 1996 is used) and error bars are indicative of standard errors of the mean.*

SEEDLINGS

Only seedlings (defined as individuals with heights not exceeding 150 cm) were used in the following analysis. Saplings and adults were eliminated from the data set because the most dynamic responses/changes occurred at the level of the seedlings. Canopy openness of 1996 is used throughout the remainder of the analysis.

Density

To assess the effect of canopy openness on seedling densities a one-way ANOVA was performed using canopy openness (class) as the independent variable. The total (sum of all four years) seedling density recorded in each class was used as the response variable.

Recruitment

To assess the effect of canopy openness on the recruitment of new seedlings into the plots a one-way ANOVA was performed using canopy openness (class) as the independent variable. The total number of new seedlings recruited into the plots (sum of all four years) in each class was used as the response variable.

Mortality

The number of deaths relative to the number of live individuals was calculated for each canopy class (all years together). This was done separately for newly recruited and old seedlings and the effect of canopy openness tested for with a two-way ANOVA. Age and canopy openness class were used as the independent variables in the ANOVA.

SPECIES COMPOSITION AND DISTRIBUTION

The number of species per m^2 was calculated for each class and year. To assess the effect of canopy openness and time on species density a two-way ANOVA was performed on these data.

Species composition

Species were classified into three regeneration niche guilds: light demanding, shade tolerant and intermediate species. Classification was based on data available in the literature and the observed distribution of these species in the field. The number of species, number of stems, species per stem, density of stems and the percentage of all stems were calculated for all guilds. This was done separately for each canopy openness class and for each year. Data were tested with multivariate ANOVA, using canopy openness, year and guild as independent variables.

Species distribution

The distribution of species with canopy openness was analysed for the 20 most abundant species. These species comprised over 72% of the total seedling population and as such, their distribution patterns are indicative of the general trends found in the population.

The Poisson distribution was used to describe the pattern of species distribution with canopy openness (log expected frequency = $ß_0$ + $ß_1$ canopy openness - $ß_1$ canopy openness^2 + error), where $ß_0$ is a constant and $ß_1$ is the coefficient of canopy openness. The Poisson distribution was used to model the distribution of the species because the sample size (number of individuals per species) was not fixed and the number of individuals within a plot was independent of the number of individuals within another plot. The number of adult trees surrounding the plots was corrected for by including them in the model, and testing the distribution patterns when adults were equal to zero. The goodness of fit of this distribution was tested with Student's t-test and Chi-square.

EFFECT OF SURROUNDING VEGETATION

Adults population

The number of adults per canopy openness class was calculated and differences between classes tested with a one-way ANOVA. The effect of adult densities on the seedling (of the adult species) densities in the canopy openness classes was tested with a two-way ANOVA.

Results

General population structure

From February 1996 through March 1999, 11,419 seedlings were recorded in the 249 plots. Among these, 5770 (51%) were already present at the time of the first census in February 1996 (Table 1).

Table 1 *Vegetation characteristics of the 249 plots in the Pibiri Reserve, Guyana. Data refer to all seedlings of tree species measured between 1996 and 1999. The total plot area is 996 m^2.*

	1996	1997	1998	1999
Total number of seedlings (density (N/m^2))	**5770** (5.79)	**6706** (6.73)	**8538** (8.57)	**7769** (7.8)
Total number of species (density (N/m^2))	**121** (0.12)	**134** (0.14)	**140** (0.14)	**139** (0.14)
No. of unidentified seedlings (%)	4.0	5.2	4.4	4.2
Shannon's diversity index (H')	1.6	1.7	2.0	2.0
Mortality (# of ind.)		857	1121	1672
Recruitment (# of ind.)		1793	2953	903
Ave. canopy closure (%)		3.4	2.7	2.5

The remainder were newly germinated seedlings recorded in the subsequent three years. During this period 3650 seedlings died, of which 51% were seedlings that were present at the first census. This implies that although there was quite some recruitment of new seedlings into these plots, the population was dominated by plants present at the first census.

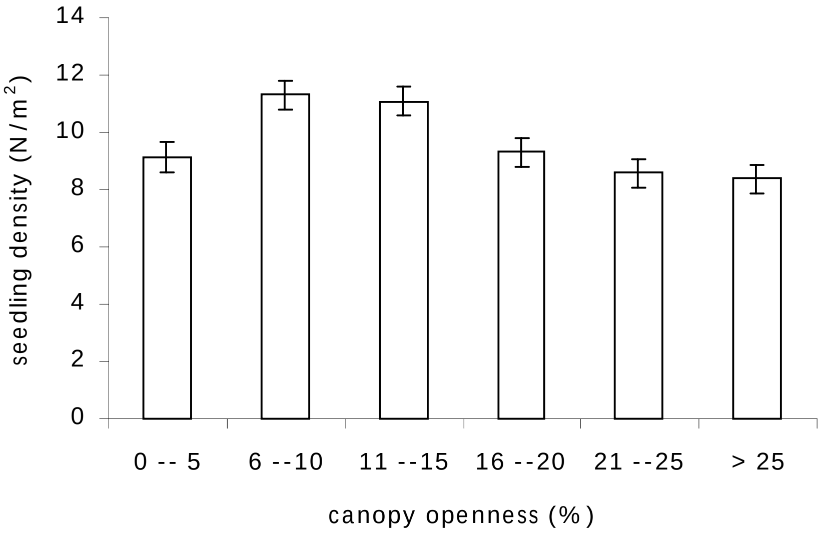

Figure 2 *The distribution of all seedlings (per m^2) recorded between 1996 through 1999 in the canopy openness classes. Standard error bars are shown and bars with the same letters are not significantly different from each other.*

Ninety-six percent of all seedlings were identified as belonging to 147 taxa. The remaining 484 seedlings could not be identified. The total number of species was highest in 1998, but although significantly different from 1996 and 1997, it was not significantly different to the number of species in 1999. Thirty-seven families were present, and Leguminosae was the most abundant with 19 genera and 25 species. Only three families had more than 10 species, Lauraceae (16), Chrysobalanaceae (11), and Annonaceae (11). The most abundant species were *Lecythis confertiflora* (Lecythidaceae), *Chlorocardium rodiei* (Lauraceae), and *Catostemma fragrans* (Bombacaceae).

Effect of canopy openness

SEEDLING DENSITY

Canopy openness significantly influenced seedling densities (F = 51.94; $p < 0.001$). Densities increased between the first two classes, remained more or less constant and then decreased with further increases in canopy openness (Figure 2). Densities between the high-density canopy openness classes (6 – 10 and 11 – 15%) were significantly different from the other classes.

RECRUITMENT

As with seedling density, there was a significant relation (F = 29.70; $p < 0.01$) between recruitment and canopy openness (Figure 3). As canopy openness increased, the number of new seedlings coming into the plots also increased, decreasing only at the largest canopy openness class. Recruitment was highest in the 21 - 25% canopy openness class and lowest and > 25% canopy openness classes.

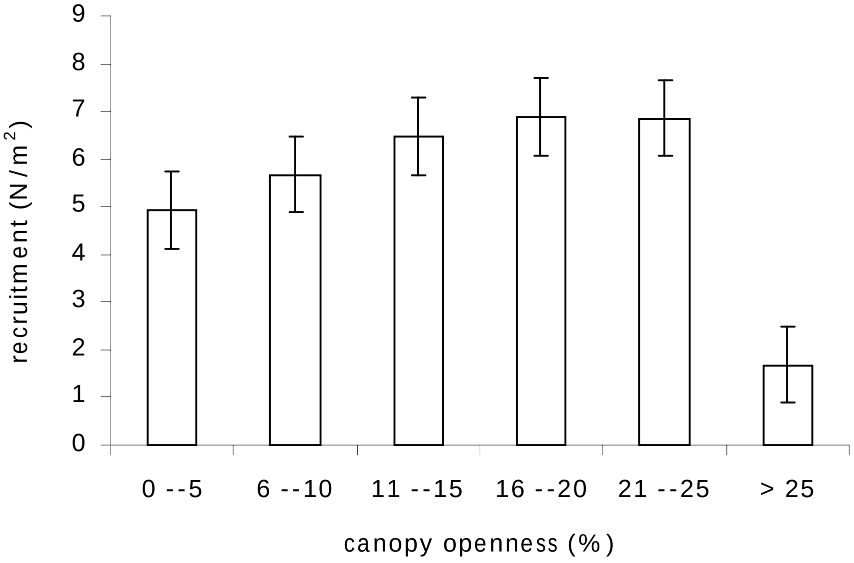

Figure 3 *The distribution of all new seedlings (per m^2) recruited into the canopy openness classes between 1997 through 1999. Standard error bars are shown and bars with the same letters are not significantly different from each other.*

MORTALITY

The pattern of seedling mortality with canopy openness was different between old and newly recruited seedlings (Figure 4). Mortality of young seedlings was significantly higher than old seedlings in all canopy openness classes (F = 62.52; p < 0.001). For old seedlings, mortality increased with increasing canopy openness up to the 16 - 20% canopy openness class, and then decreased slightly in the larger canopy openness classes (Figure 4). Young seedlings suffered their highest mortality in the smallest and the second largest canopy openness class, but no clear pattern with canopy openness emerged.

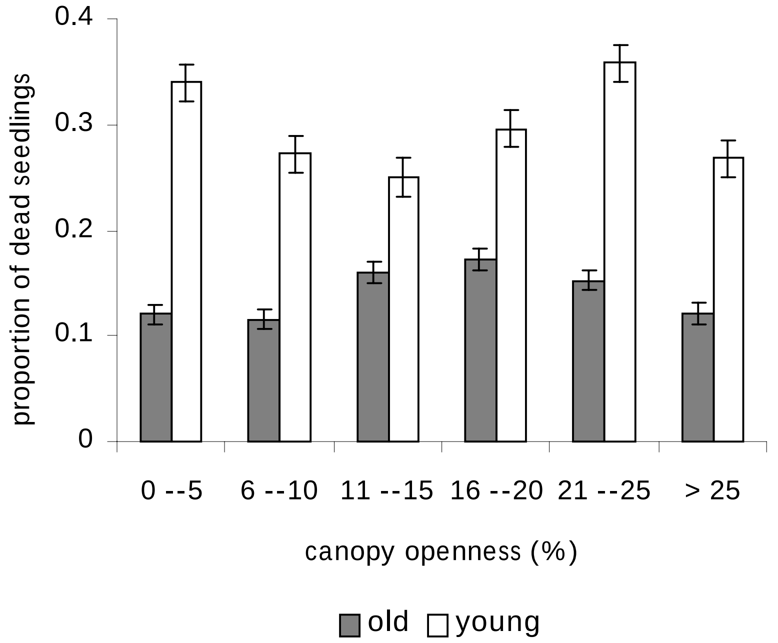

Figure 4 *The effect of canopy openness on seedling mortality of old and young seedlings. Mortality is represented as the number of dead individuals relative to the number of live individuals. Standard error bars are shown and bars with the same letters are not significantly different from each other.*

Species composition and distribution patterns - canopy openness and temporal effects

GENERAL PATTERNS

Species distributions were significantly influenced by canopy openness ($F_{5,24}$ = 6.27, p = 0.002) (Figure 5). As canopy openness increased the number of species per m^2 also increased, with the largest/highest canopy openness class having double the number of species as the other classes (data not shown). Scheffé tests showed that differences between the first four classes were not significant, however species density in the two largest classes were significantly different from the others and each other.

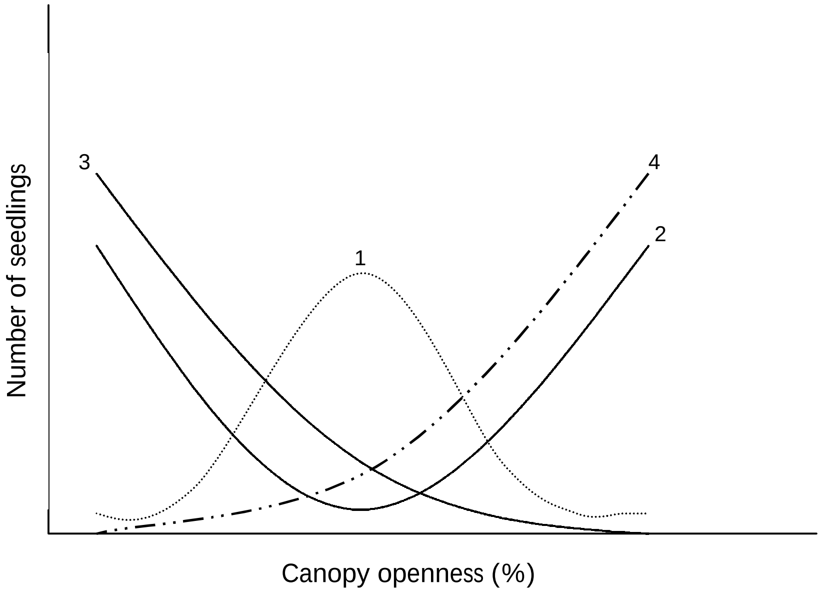

Figure 5 *The four main patterns of species responses to canopy openness as indicated by the Poisson distribution of the 20 most abundant species.*

Table 2 The guild composition of the plots during the study period in the six canopy openness classes.

	# of species present				**# of stems present**			
	1996	1997	1998	1999	1996	1997	1998	1999
shade tolerant species (n = 54)								
0 -- 5	27	31	34	33	789	1299	1230	1000
6 -- 10	40	44	45	45	1532	1727	2138	1962
11 -- 15	31	34	32	35	654	535	905	1015
16 -- 20	28	26	31	30	436	467	731	589
21 -- 25	15	21	22	23	89	146	257	222
> 25	16	16	16	17	104	100	96	76
intermediate species (n = 66)								
0 -- 5	43	47	45	41	331	428	419	343
6 -- 10	44	44	51	51	600	635	848	781
11 -- 15	36	37	44	49	338	317	438	501
16 -- 20	30	34	36	36	226	211	416	329
21 -- 25	17	28	32	29	38	72	129	102
> 25	21	20	20	18	33	30	36	31
pioneer species (n = 27)								
0 -- 5	12	12	15	13	33	56	75	60
6 -- 10	20	19	21	21	161	168	177	181
11 -- 15	17	17	18	19	77	68	101	106
16 -- 20	13	13	15	15	64	64	114	94
21 -- 25	8	12	14	12	25	27	47	48
> 25	4	4	4	4	7	7	8	5

SPECIES COMPOSITION

Fifty-four species were classified as shade-tolerant, sixty-six as intermediates and twenty-seven as light demanding (Table 2). Canopy openness and species guild significantly influenced the species composition of the plots (Table 3). These differences were not significant over time. The stem density of light demanding species was high for all but the lowest canopy openness class.

Table 2 continued. Stem data represent the 147 species recorded at the 4 censuses that were classified unto pioneer, intermediate and shade tolerant guilds.

Species per stem				**Density of stems (N/m^2)**				**% of all stems**			
1996	1997	1998	1999	1996	1997	1998	1999	1996	1997	1998	1999
0.03	0.02	0.03	0.03	3.34	5.50	5.21	4.24	68.43	72.85	71.35	71.28
0.03	0.03	0.02	0.02	4.61	5.20	6.44	5.91	66.81	68.26	67.59	67.10
0.05	0.06	0.04	0.03	3.34	2.73	4.62	5.18	61.18	58.15	62.67	62.58
0.06	0.06	0.04	0.05	2.87	3.07	4.81	3.88	60.06	62.94	57.97	58.20
0.17	0.14	0.09	0.10	1.39	2.28	4.02	3.47	58.55	59.59	59.35	59.68
0.15	0.16	0.17	0.22	6.50	6.25	6.00	4.75	72.22	72.99	68.57	67.86
0.13	0.11	0.11	0.12	1.40	1.81	1.78	1.45	28.71	24.00	24.30	24.45
0.07	0.07	0.06	0.07	1.81	1.91	2.55	2.35	26.17	25.10	26.81	26.71
0.11	0.12	0.10	0.10	1.72	1.62	2.23	2.56	31.62	34.46	30.33	30.89
0.13	0.16	0.09	0.11	1.49	1.39	2.74	2.16	31.13	28.44	32.99	32.51
0.45	0.39	0.25	0.28	0.59	1.13	2.02	1.59	25.00	29.39	29.79	27.42
0.64	0.67	0.56	0.58	2.06	1.88	2.25	1.94	22.92	21.90	25.71	27.68
0.36	0.21	0.20	0.22	0.14	0.24	0.32	0.25	2.86	3.14	4.35	4.28
0.12	0.11	0.12	0.12	0.48	0.51	0.53	0.55	7.02	6.64	5.60	6.19
0.22	0.25	0.18	0.18	0.39	0.35	0.52	0.54	7.20	7.39	6.99	6.54
0.20	0.20	0.13	0.16	0.42	0.42	0.75	0.62	8.82	8.63	9.04	9.29
0.32	0.44	0.30	0.25	0.39	0.42	0.73	0.75	16.45	11.02	10.85	12.90
0.57	0.57	0.50	0.80	0.44	0.44	0.50	0.31	4.86	5.11	5.71	4.46

Similarly, the percentage of seedlings of these light demanding species increased nearly eight times from 2.9% in the smallest canopy openness class to 16.5% in the 20-25% class in 1996 and then decreased (Table 2). Despite these changes, abundance per stem and the number of species per class did not follow this trend of increasing as canopy openness increased.

The density of the shade tolerant species remained relatively constant over the first five classes but increased in the largest canopy openness class (Table 2). The density of these species collectively was approximately 6 times higher than that of the light demanding species in the largest canopy openness class. The shade tolerant species represented more than 50% of all stems in all classes and years (Table 2). Intermediate species as expected were intermediate in their gap occupancy rates.

Table 3 *Multivariate ANOVA table, showing the results of the main effects and the only significant interaction.*

	Canopy openness		**Guild**		**Year**		**Canopy openness * guild**	
			F	**P**	**F**	**P**		
No. of species	65.29	< 0.001	232.77	< 0.001	4.81	0.005	5.76	< 0.001
No. of stems	17.15	< 0.001	41.31	< 0.001	1.09	0.36	28.83	< 0.001
Species per stem	41.30	< 0.001	42.75	< 0.001	1.38	0.26	10.38	< 0.001
Density of stems	4.92	0.001	188.23	< 0.001	4.43	0.007	4.46	< 0.001

DISTRIBUTION PATTERNS FOR THE MOST ABUNDANT SPECIES

The Poisson analysis of the 20 most abundant species indicated four patterns of species distribution with canopy openness (Figure 5). Species typified by the most common distribution (observed in 12 species) exhibited low seedling densities at the highest and lowest extremes of the canopy openness range (pattern 1 in Figure 5; Appendix 1). A few species showed the reverse trend (seedling densities being highest at the extremes but lowest in the intermediate range - pattern 2, Figure 5). Other patterns of distribution observed were a positive and negative relation between seedling abundance and canopy openness (Figure 5). No distinctions could be made in the type of species showing these different distribution patterns since most of the species were shade tolerant canopy or sub canopy species with a few being shade tolerant understorey species.

For most species the distribution patterns over the four years remained essentially constant. Exceptions were:

- Those species for which distributions in the first two years were different to the distribution patterns in the last two years over the canopy openness range (e.g. *Quiina guianensis;* $p < 0.001$). In the first two years the number of seedlings decreased gradually with canopy openness: with the highest number of seedlings being recorded at the lowest canopy openness values. In the last two years, the number of seedlings increased slightly before decreasing again at the highest canopy openness levels.

- Those species for which distributions in the final year were different to the other years (e.g. *Calycolpus goetheanus;* $p < 0.05$). In the first three years seedling numbers were highest at the lowest and/or highest canopy openness levels for these species respectively, however in the final year the pattern was reversed.

- Those species for which the distribution in the second year was different from the other three years (e.g. *Lecythis confertiflora;* $p < 0.001$). Seedling distribution patterns in the second year showed the highest seedling number at the lowest and the highest canopy openness classes whilst for the other three years this pattern was reversed.

EFFECT OF SURROUNDING VEGETATION

It is expected that the distribution of adults in the surrounding plot areas will contribute to the likelihood of finding seedlings within the plots. Within the 20-m radius of the plots, 56 adult species were mapped of which 21 had more than five individuals occurring (Appendix 2). Adult abundances were lower around plots in large gaps as compared with plots in smaller gaps. The three most abundant adult species: *Lecythis confertiflora, Chlorocardium rodiei*, and *Catostemma fragrans,* were also the most abundant seedlings species within the plots. However, for ten of the twenty most abundant adult species (*Swartzia leiocalycina*, *Eschweilera coriacea*, *Pentaclethra macroloba*, *Aspidosperma excelsum*, *Swartzia schomburgkii*, *Peltogyne venosa*, *Chaetocarpus schomburgkianus*, *Goupia glabra*, *Carapa guianensis*, *Eperua falcata*), few seedlings were encountered within the plots. Of these ten species, eight were light demanding or intermediate species (Appendix 2).

Similarly, no adults were found for three of the most abundant seedling species (*Paypayrola longifolia*, *Quiina indigofera*, *Sandwithia guyanensis*). These were understorey species, for which the adults may have been overlooked (see methods). The seedling populations of plots in the smaller canopy openness levels were usually a good reflection of the adult population (Figure 6). However, for some species, this correlation of seedling and adults diminished with increasing canopy openness.

Discussion

Effect of canopy openness on recruitment and mortality

Recruitment was significantly affected by canopy openness and seemed low especially in the > 25% canopy openness class. Two reasons for this may be first the lack of a supply of seeds or potentially unfavourable conditions for germination and survival in these large gaps. This may be part of the reason why Peña-Claros (2000) found that germination percentages were much lower in large gaps when compared to small gaps in Bolivia. As shown in this data, adult populations surrounding plots in the largest canopy openness class were much lower than in the other plots. The lower probability of seeds reaching plots in high canopy openness classes (because of the greater distance between these plots and parent trees), may be the primary reason for the low recruitment of seedlings in these classes. There are indications however, that higher canopy openness promote higher establishment success up to a certain level. This is contrary to what has been found before in several studies where recruitment levels were highest in the understorey or small gaps (Li 1991, Uhl *et al*. 1988).

Mortality was also significantly affected by canopy openness. The patterns were different for old and young seedlings. The well-established older seedlings had much lower mortality rates than the newly recruited seedlings. In the canopy openness classes where recruitment was highest (Figure 3), mortality of old seedlings was highest. This may indicate that these two processes are related or even complementary. It also suggests that newly recruited seedlings are especially vulnerable to the extremes of low and high canopy openness levels.

These results confirm those of Sizer (1992) but are contrary to those of Uhl *et al*. (1988). Working with natural seedling populations in San Carlos Venezuela Uhl *et al*. found that the size of the canopy opening did not influence seedling density, recruitment and mortality. They attributed this to the predominance of seedlings established before gap creation.

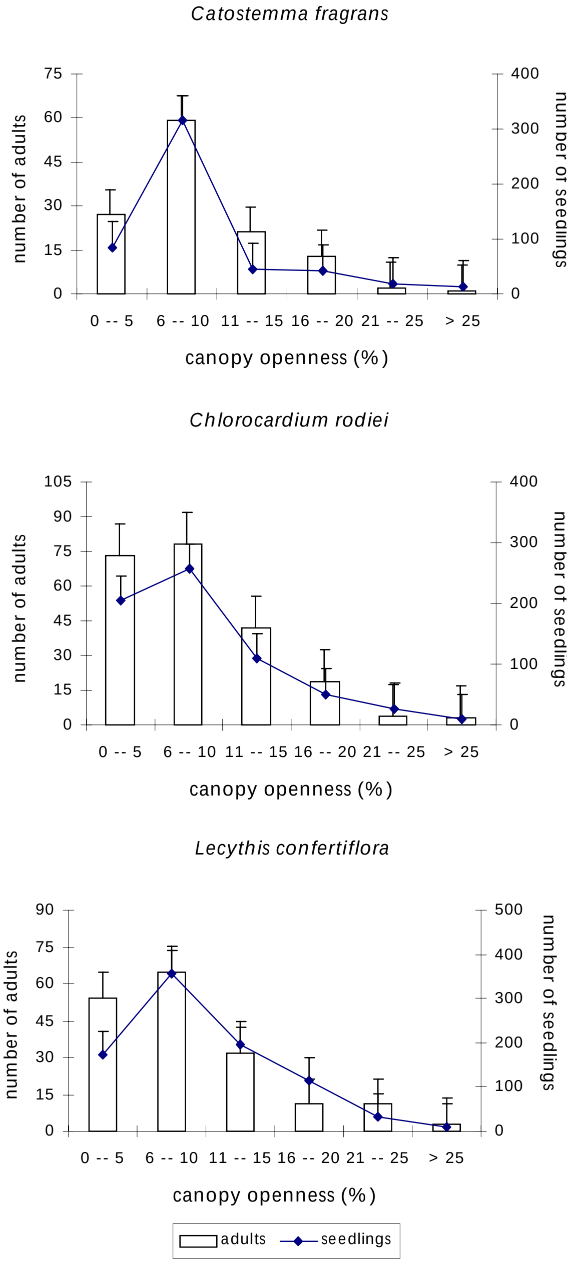

Figure 6 *The relationship between the number of adults and the number of seedlings with canopy openness. Error bars are indicative of the standard error.*

These forests are also relatively undisturbed (Uhl & Murphy 1981) and one reason for the difference in results may be the difference in sample sizes. They used six natural gaps ranging from single tree fall (5 gaps) to multiple tree fall (1 gap), and sampled 786 plants whereas in this study, plots were placed in 249 different gap sizes and over 10,000 individuals were sampled.

Species composition

This study indicates that local species compositions were established before or very early after logging since there were no significant temporal effects on the species composition. The plots (and all canopy openness classes) were dominated by the shade tolerant species. This is the reverse of what would be expected especially in the large gaps in which the high light conditions are usually expected to favour the light demanding pioneer species. Pioneer species were at a numerical disadvantage in all canopy openness classes especially at the lower canopy openness levels when compared to the shade tolerant and intermediate species. This may be the reason for the rarity of pioneer species in these forests that are characterised by small gaps except in the areas where selective logging is practised (ter Steege & Hammond accepted). However, that these pioneers did manage to achieve high densities in plots in the higher canopy openness levels is strong evidence not only of their higher dispersal and colonising abilities (Swaine *et al*. 1997).

The species composition of the plots seemed to be controlled more by the composition of the adult population surrounding the plots and not chance. This implies that adults produced good samples of seed and hence seedlings in their vicinity, although this was not the case for all species. Li (1991) studying the seedling populations at La Selva also found significant correlations between adult and seedling species abundances. There were cases where seedlings of some species were found although no adults were in the vicinity and vice versa. It should be noted that whilst species presence may be informative, species absence does not necessarily indicate unsuitability or recruitment limitation. Adult species distributions have been shaped by environmental factors, for long periods of time and the inference may be made that adults are excluded from locations where edaphic or other conditions render an area unsuitable. In contrast, seeds might germinate and grow for short periods in relatively unlikely sites (see for example the distribution of *Catostemma fragrans*). Therefore, it is likely that seedlings should be more widely distributed than adults of the same species.

Species distribution

While there were no significant changes in the pattern of species distribution between 1996 and 1999, canopy openness did influence the distribution patterns. Distributions seemed to be very species specific, with species conforming to four general patterns (Figure 7). However, attempts to develop and improve categorizations of species based on their distribution patterns over the canopy openness gradient proved difficult. This was because there were overlaps in responses of understorey, sub canopy, canopy, and shade tolerant species.

This study has shown that the species composition of these gaps were dominated with seedlings that were present prior to logging or just after logging. The contribution of new recruits was minimal even in large gaps.

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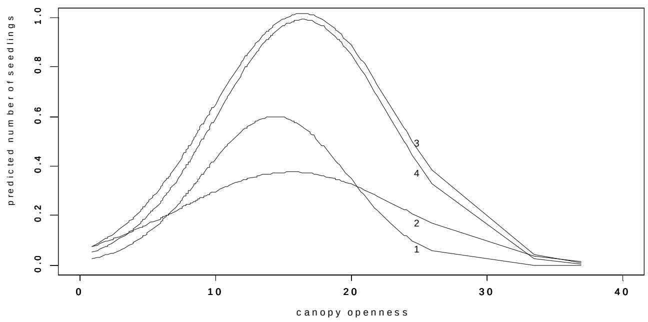
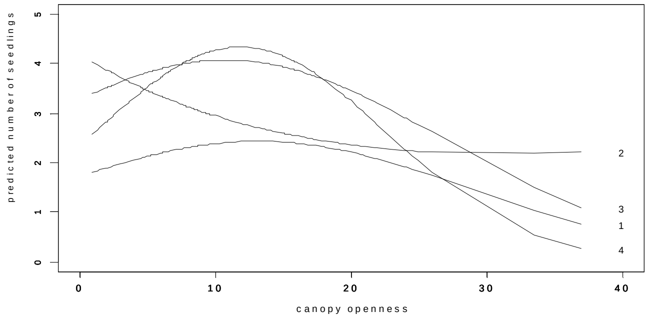
Appendix 1

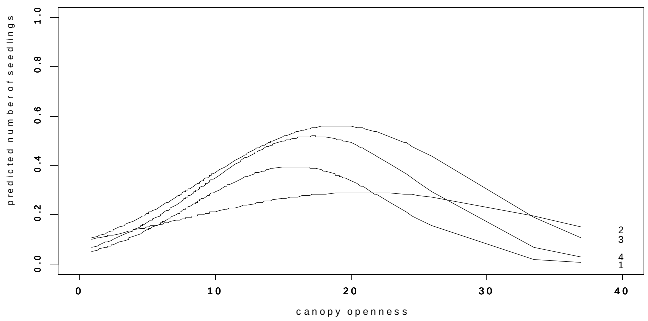
The Poisson distribution plots for the 20 most abundant species between 1996 and 1999. The years are represented by the number 1 - 4, with 1 being the first year (1996) and 4 the last year (1999) of the experiment. The distribution pattern (as shown in Figure 5) and the difference between years are also indicated.



Eschweilera wachenheimii
- pattern 1 (p > 0.05)

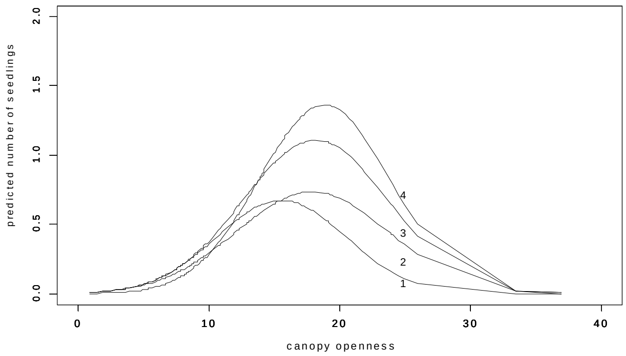


Lecythis confertiflora
- pattern 1 (p < 0.001)

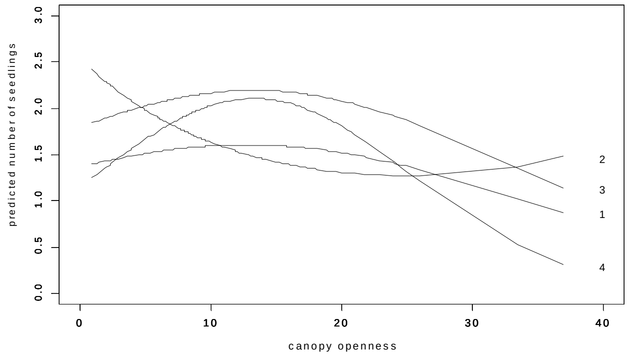


Licania densiflora
- pattern 1 (p > 0.05)

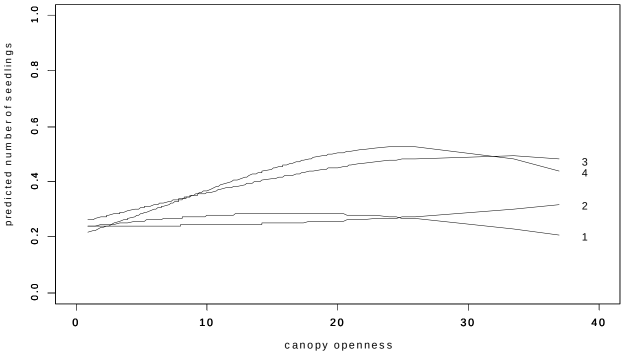
Appendix 1 continued



Mora gongrijpii
- pattern 1 ($p > 0.05$)



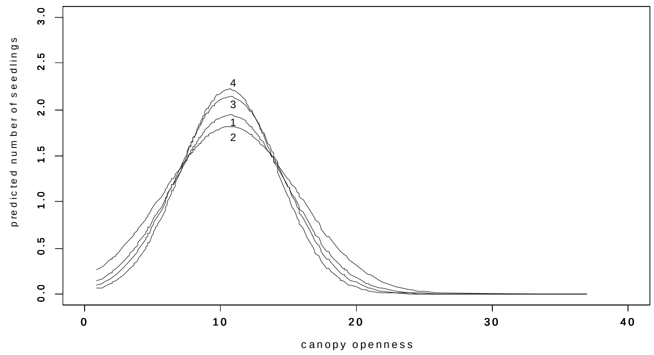
Oxandra asbeckii
-pattern 1 ($p < 0.05$)



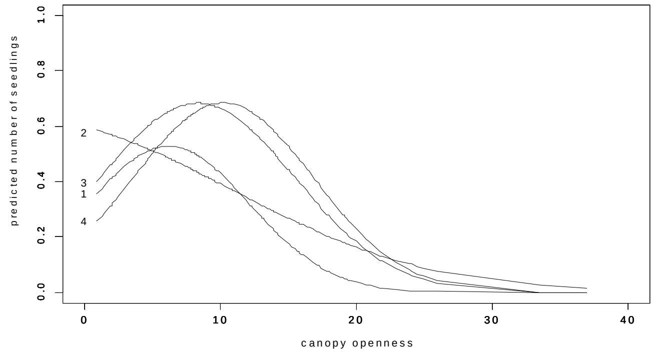
Parinari campestris
-pattern 1 ($p > 0.05$)

Appendix 1 continued

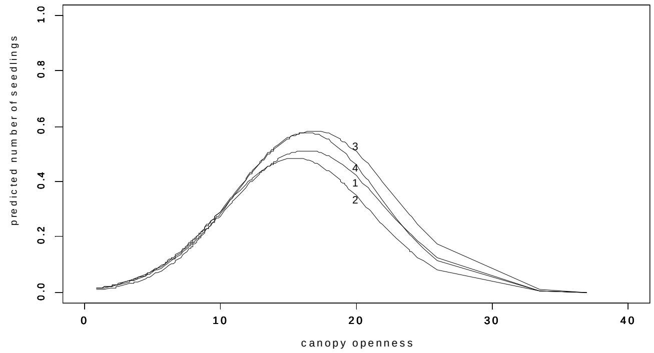
Ocotea spp.
- pattern 1 (p > 0.05)



Sandwithia guianensis
- pattern 1 (p > 0.05)

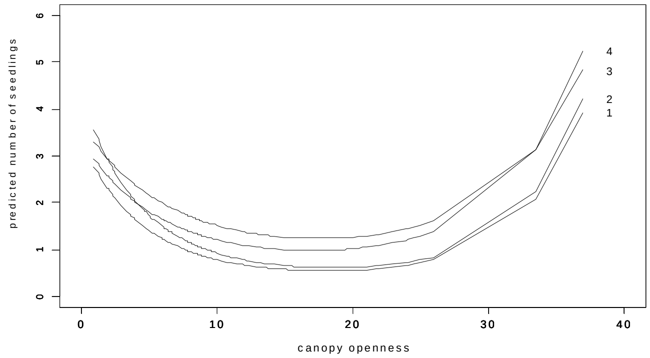


Vouacapoua macropetala
- pattern 1 (p > 0.05)

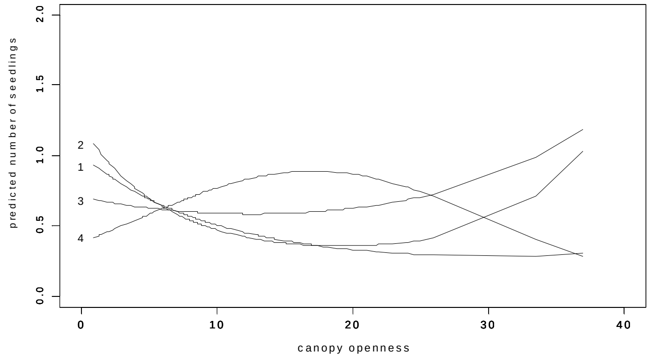


Appendix 1 continued

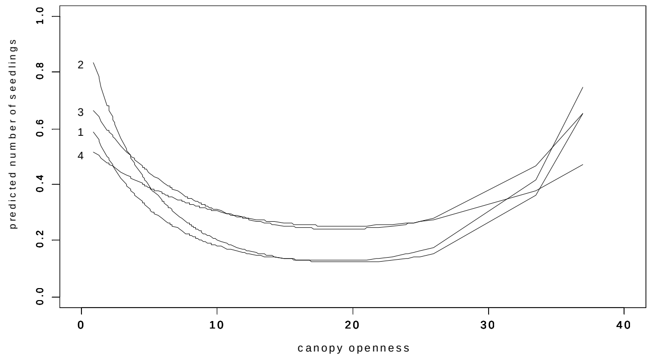
Catostemma fragrans
- pattern 2 (p > 0.05)



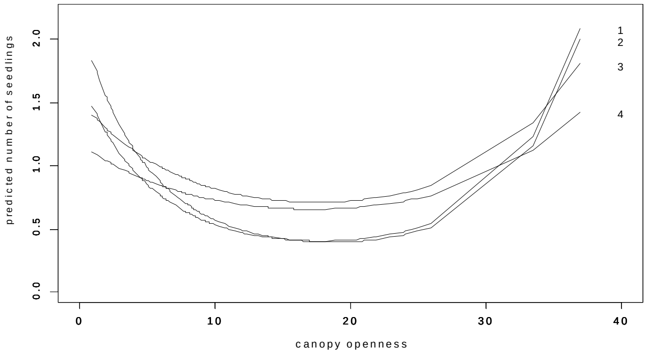
Calyocolpus goetheanus
-pattern 2 (p < 0.05)



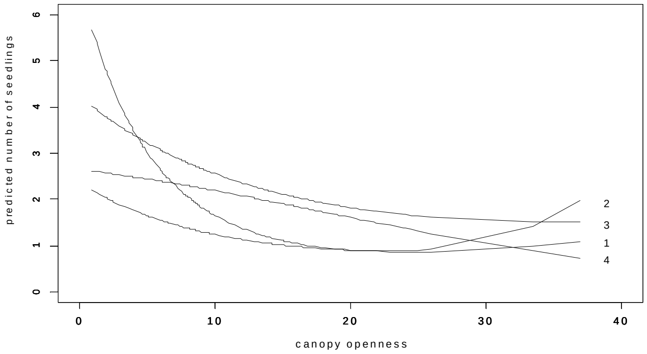
Licania alba
- pattern 2 (p > 0.05)



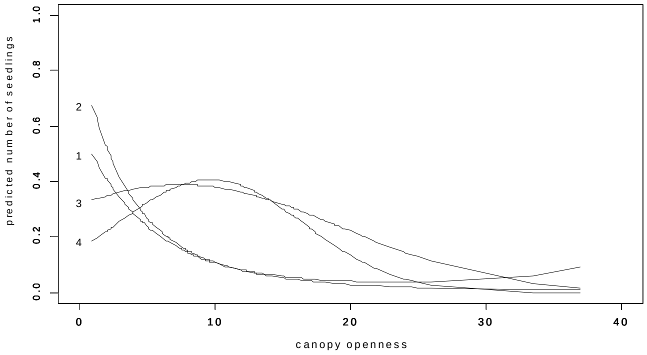
Appendix 1 continued



Tapura guianensis
- pattern 2 (p > 0.05)

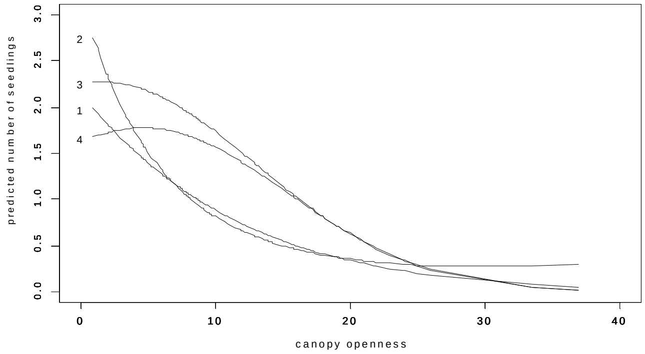


Chlorocardium rodiei
- pattern 3 (p > 0.05)

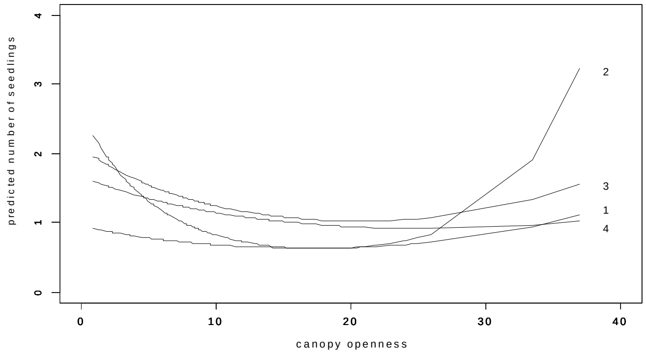


Eschweilera sagotiana
-pattern 3 (p < 0.05)

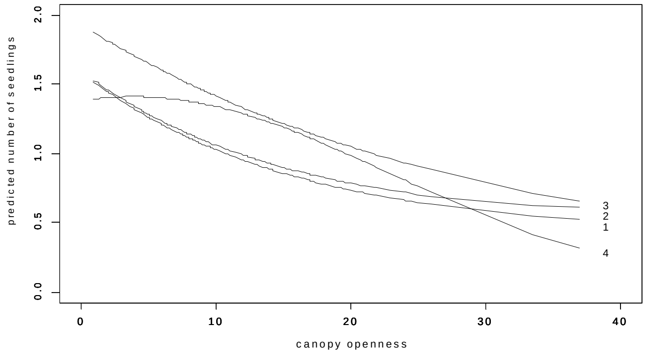
Appendix 1 continued



Inga spp.
- pattern 3 (p > 0.05)

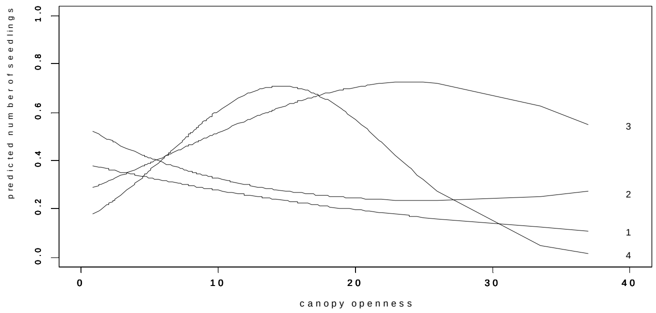


Licania heteromorpha
- pattern (p > 0.05)

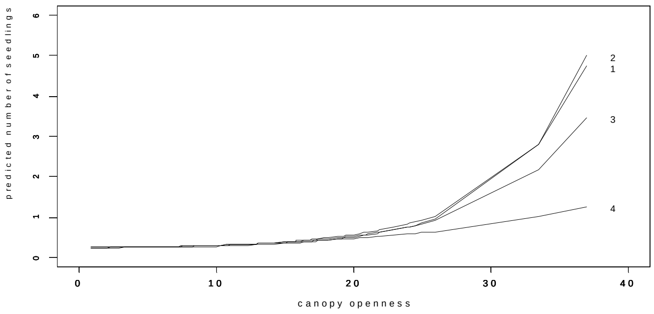


Paypayrola longifolia
- pattern 3 (p > 0.05)

Appendix 1 continued



Quiina guianensis
- pattern 3 (p < 0.001)



Bocageopsis multiflora
- pattern 4 (p > 0.05)

Appendix 2

List of species encountered in all 249 research plots in the Pibiri reserve between 1996 through 1999. The guilds are defined as S - shade tolerant; I - intermediate; P - pioneers.

VERNACULAR	SPECIES	FAMILY	GUILD	Adults in 20 m radius
ADEBERO	*Paypayrola longifolia*	Violaceae	S	0
AIOMORAKUSHI	*Pouteria cladantha*	Sapotaceae	I	...
ARARA, Broad leaf	*Unonopsis glaucopetala*	Annonaceae	S	...
ARARA, Fine Leaf	*Bocageopsis multiflora*	Annonaceae	S	10
ARARA, Smooth Skin	*Guatteria atra*	Annonaceae	S	...
AROMATA	*Clathrotropis brachypetala var. brachypetala*	Leguminosae/Papil.	S	...
ARUADAN	*Sloanea spp. (2)*	Elaeocarpaceae	I	8
ARURUDAN	*Slonea spp.*	Elaeocarpaceae	I	...
ASASHI	*Rheedia benthamiana*	Guttiferae	I	...
ASEPOKO	*Pouteria guianensis*	Sapotaceae	I	7
ASEPOKOBALLI, Broad Leaf	*Pouteria jenmanni*	Sapotaceae	I	9
ASEPOKOBALLI, Fine Leaf	*Pouteria caimito*	Sapotaceae	I	...
AWASOKULE	*Tovomita spp.(2)*	Guttiferae	I	...
BARAKARO	*Ormosia coccinea*	Leguminosae/Papil.	S	8
BAROMALLI, Sand	*Catostemma fragrans*	Bombacaceae	S	129
BAROMALLI, Swamp	*Catostemma commune*	Bombacaceae	S	10
BLACKHEART	*Acosmium praeclara*	Leguminosae	S	...
BLOODWOOD	*Vismia guianensis*	Guttiferae	P	...
BOKOTOKON	*Licania sp.2*	Chrysobalanaceae	I	7
BURADA	*Parinari campestris*	Chrysobalanaceae	I	10
BURADIYE	*Nectandra grandis*	Lauraceae	S	...
BURUBURULI	*Licania heteromorpha var. heteromorpha*	Chrysobalanaceae	S	...
CONGO PUMP, Common	*Cecropia obtusa*	Moraceae	P	...
CONGO PUMP, High bush	*Cecropia spp.*	Moraceae	P	...
CONGO PUMP, Long leaf	*Cecropia sciadophylla*	Moraceae	P	...
CORKWOOD, Hill	*Pterocarpus spp.*	Leguminosae	I	...
CRABWOOD	*Carapa guianensis*	Meliaceae	I	45

Appendix 2 continued

VERNACULAR	SPECIES	FAMILY	GUILD	Adults in 20 m radius
FUKADI	*Terminalia amazonica*	Combretaceae	I	...
FUTUI	*Jacaranda copaia subsp. copaia*	Bignoniaceae	P	8
GALE, Almond	*Aniba citrifolia*	Lauraceae	S	...
GALE, Ginger	*Aniba kappleri*	Lauraceae	S	...
GALE, Greenheart	*Aniba excelsa*	Lauraceae	S	...
GREENHEART	*Chlorocardium rodiei*	Lauraceae	S	219
HACHIBALLI	*Simaba multiflora*	Simaroubaceae	P	...
HAIAWA	*Protium guianense var. guianense*	Burseraceae	I	...
HAIAWABALLI	*Protium tenuifolium*	Burseraceae	I	...
HAUDAN	*Lecythis holcogyne*	Lecythidaceae	S	7
HICHU	*Eugenia patrisii*	Myrtaceae	S	...
HIKURIBIANDA	*Simaba cedron*	Simaroubaceae	P	...
HISHIRUDAN	*Dulacia guianensis*	Olacaceae	S	...
HIWARADAN	*Chaunochiton kappleri*	Olacaceae	I	...
HURUEREROKO	*Cordia nodosa*	Boraginaceae	P	...
IMORO	*Palicourea guianensis*	Rubiaceae	P	...
ITIKIBOROBALLI	*Swartzia sprucei var. tessellata*	Leguminosae/Papil.	I	...
ITURI-ISHI-LOKODO	*Helicostylis tomentosa*	Moraceae	S	...
KABUKALLI	*Goupia glabra*	Celastraceae	P	12
KADITIRI	*Sclerolobium guianense var. guianense*	Leguminosae	P	10
KAIARIMA	*Maytenus myrsinoides*	Celastraceae	S	7
KAIRIBALLI	*Licania heteromorpha var. perplexans*	Chrysobalanaceae	S	13
KAKARALLI, Black	*Eschweilera sagotiana*	Lecythidaceae	S	29
KAKARALLI, Wirimiri	*Lecythis confertiflora*	Lecythidaceae	S	176
KAMAHORA	*Pouteria venosa subsp. amazonica*	Sapotaceae	I	7
KANOABALLI	*Byrsonima stipulacea*	Malpighiaceae	P	...
KARAMPAI	*Annona spp.*	Annonaceae	P	...
KARISHIRI	*Oxandra asbeckii*	Annonaceae	S	8
KAUTA	*Licania laxiflora*	Chrysobalanaceae	I	...

Appendix 2 continued

VERNACULAR	**SPECIES**	**FAMILY**	**GUILD**	**Adults in 20 m radius**
KAUTABALLI	*Licania alba*	Chrysobalanaceae	I	65
KAUTABALLI, Fine Leaf	*Licania majuscula*	Chrysobalanaceae	S	...
KIRIKAUA	*Iryanthera spp.*	Myristicaceae	S	...
KOKORITIBALLI	*Pouteria reticulata subsp surinamensis*	Sapotaceae	I	7
KOMARAMARA	*Duroia eriophila var. eriophila*	Rubiaceae	I	...
KOMARAMARABALLI	*Amaioua guianensis var. guianensis*	Rubiaceae	I	...
KONOKO	*Licania cuprea*	Chrysobalanaceae	I	...
KORAROBALLI	*Hymenolobium sp.*	Leguminosae/Papil.	I	...
KOYECHI	*Rollinia exsucca*	Annonaceae	S	...
KUDIBIUSHI	*Micropholis venulosa*	Sapotaceae	I	...
KULISHIRI, Black	*Cupania spp (2)*	Sapindaceae	P	...
KULISHIRI, Common	*Matayba sp1*	Sapindaceae	P	...
KULISHIRI, White	*Matayba sp2*	Sapindaceae	P	...
KURIHIKOYOKO	*Anaxagorea dolichocarpa*	Annonaceae	S	...
KUROKAI	*Protium decandrum*	Burseraceae	I	7
KUYAMA, Red	*Xylopia pulcherrima*	Annonaceae	I	...
KUYAMA, White	*Xylopia nitida*	Annonaceae	I	...
KWAKO	*Marlierea montana*	Myrtaceae	S	...
LANABALLI	*Gustavia hexapetala*	Lecythidaceae	S	...
LOCUST	*Hymenaea courbaril var. courbaril*	Leguminosae	I	9
MAHO, Rough Leaf	*Sterculia regosa*	Sterculiaceae	I	7
MAHO, Smooth Leaf	*Sterculia pruriens var. glabrescens*	Sterculiaceae	I	7
MAMURIBALLI	*Mouriri sp.*	Melastomataceae	P	...
MANARIBALLI , Like	*Pseudopiptadenia suavolens*	Leguminosae	I	...
MANYOKINABALLI	*Geissospermum sericeum*	Apocynaceae	I	...
MARISHIBALLI	*Licania densiflora*	Chrysobalanaceae	I	36
MARISHIBALLI, High Bush	*Licania sp.1*	Chrysobalanaceae	I	...
MORA	*Mora excelsa*	Leguminosae	S	...
MORABALLI	*Pouteria coriacea*	Sapotaceae	I	...

Appendix 2 continued

VERNACULAR	SPECIES	FAMILY	GUILD	Adults in 20 m radius
MORABUKEA	*Mora gongrijpii*	Leguminosae	S	50
MOROBALLI	*Talisia squarrosa*	Sapindaceae	S	...
MUNIRIDAN	*Siparuna sp.*	Monimiaceae	S	...
OKOKONSHI, BROAD LEAF	*Quiina indigofera*	Quiinaceae	I	0
OKOKONSHI, FINE LEAF	*Quiina guianensis*	Quiinaceae	I	...
PARAKUSAN	*Swartzia schomburgkii var. jenmanii*	Leguminosae	I	15
PASTURE TREE	*Trymatococcus paraensis Ducke*	Moraceae	S	...
PERO-ISHI-LOKODO	*Tabernaemontana spp.*	Apocynaceae	P	...
POOR KERETI	*Ocotea spp.*	Lauraceae	S	...
PURPLEHEART	*Peltogyne venosa var. densiflora*	Leguminosae	I	14
ROKOROKO	*Macoubea guianensis*	Apocynaceae	S	...
RURI	*Chaetocarpus schomburgkianus*	Euphorbiaceae	P	13
SADA	*Zanthoxylum apiculata*	Rutaceae	I	...
SAREBEBEBALLI	*Vouacapoua macropetala*	Leguminosae	I	31
SEREBEDAN	*Swartzia oblanceolata*	Leguminosae	I	...
SHIBADAN, smooth leaf	*Aspidosperma album*	Apocynaceae	P	...
SHIBALLIDAN	*Hebapetalum humiriifolium*	Linaceae	I	...
SHIRADA	*Inga laterifolia*	Leguminosae	I	...
SHIRUA	*Nectandra cuspidata*	Lauraceae	I	...
SILVERBALLI, Brown	*Licaria cannella*	Lauraceae	S	...
SILVERBALLI, Kereti	*Ocotea spp. (2)*	Lauraceae	I	8
SILVERBALLI, Kurahara	*Ocotea glomerata*	Lauraceae	I	...
SILVERBALLI, White	*Ocotea canaliculata*	Lauraceae	S	...
SILVERBALLI, Yellow	*Aniba hypoglauca*	Lauraceae	S	...
SIMARUPA	*Simarouba amara*	Simaroubaceae	P	...
SUYA	*Pouteria speciosa*	Sapotaceae	I	10
SWIZZLESTICK	*Mabea spp.*	Euphorbiaceae	S	...
TABLE TREE	*Cordia exaltata*	Boraginaceae	P	...

Appendix 2 continued

VERNACULAR	SPECIES	FAMILY	GUILD	Adults in 20 m radius
TATABU	*Diplotropis purpurea*	Leguminosae/Papil.	I	9
TRYSIL	*Pentaclethra macroloba*	Leguminosae/Mimos.	P	27
TURELI	*Zygia racemosa*	Leguminosae/Mimos.	I	...
ULU	*Trattinickia spp.(2)*	Burseraceae	I	...
UNIKIAKIA	*Licania hypoleuca*	Chrysobalanaceae	I	...
UNKNOWN "A"	*Sandwithia guyanensis*	Euphorbiaceae	S	0
UNKNOWN "C"	*Eugenia sp.*	Myrtaceae	S	...
WABAIMA	*Licaria cayennensis*	Lauraceae	I	...
WAIABALLI	*Tapura guianensis*	Dichapetalaceae	S	8
WALLABA, Ituri	*Eperua grandiflora*	Leguminosae	I	...
WALLABA, Soft	*Eperua falcata*	Leguminosae/Caesal.	S	35
WAMARA	*Swartzia leiocalycina*	Leguminosae/Caesal.	I	51
WARAIA	*Miconia gratissima*	Melastomataceae	P	...
WARAKAIORO	*Laetia procera*	Flacourtiaceae	P	...
WARAKOSA	*Inga spp.*	Leguminosae/Mimos.	I	12
WILD GUAVA	*Calycolpus goetheanus*	Myrtaceae	S	7
YARI YARI	*Duguetia negelecta*	Annonaceae	S	...
YARURU	*Aspidosperma exselsum*	Apocynaceae	P	23
YAWAREDAN	*Tachigali rusbyi*	Leguminosae/Caesal.	I	...
YEKORO	*Licaria vernicosa*	Lauraceae	S	...
YESHIDAN	*Duguetia sp.*	Annonaceae	S	...

"Numbers are like people; torture them long enough and they'll tell you anything"
Anonymous

CHAPTER 6

HEIGHT GROWTH RESPONSES OF NATURALLY ESTABLISHED TREE SEEDLINGS IN THE TROPICAL RAIN FOREST IN GUYANA

Abstract

This study presents an analysis of the first four years of growth after selective logging in 249 2 x 2 m plots in the Guyanese tropical rainforest. Seedling heights responses were significantly influenced by stem density and seedling age but not by canopy openness, seed mass or species guilds. There were significant differences between the mean heights of old seedlings (established before the first census) and young seedlings (established after the first census). The tallest individuals at the beginning of the experiment remained amongst the tallest seedlings at the end. Results of this study contradict those of many controlled experiments (including chapter 3), where seedlings show clear patterns of seedling height growth with canopy openness.

Keywords

Height growth, seedlings, plant density, seed mass, canopy openness, tropical rain forest, Guyana.

Introduction

Many tropical rainforest tree species depend on, or benefit from, canopy gaps for successful regeneration (Brokaw 1987; Denslow & Hartshorn 1994; Kennedy & Swaine 1992; Popma & Bongers 1988; Fraver *et al*. 1998). Whitmore (1975) describes the tropical forest growth cycle as consisting of three phases: gap, building and mature. Similarly, Oldeman (1978) describes 'chablis' (tree-fall) and 'sylvigenesis' (forest development) in the tropics. Both models postulate a dynamic initial gap-phase of rapid colonisation and growth after gap formation. During the gap-phase, plants usually display rapid growth by the elongation of their stems (Burton & Mueller-Dombois 1984, Denslow *et al*. 1990, Popma & Bongers 1988, Turner 1990). However, for how long after gap creation is this rapid growth maintained?

Several experimental studies have emphasised the growth response of tropical seedlings to variation in light availability (Popma & Bongers 1988, Osunkoya *et al*. 1993) and interspecific differences in these responses (Ashton 1995, Boot 1996, Poorter 1998). Together with the practical experience of foresters, the experimental approach has fostered a view that tree species segregate over a gradient of shade tolerance. The contrast pioneer-climax species is quite well known (Swaine & Whitmore 1988). Shade tolerant (climax) species tend to survive well and grow slowly in the shaded understorey, but show a low response to conditions of improved illumination. Shade intolerant (pioneer) species tend to have a lower survival in the understorey, but respond strongly to increased light (Kitajima 1994, Kobe *et al*. 1995). According to the aforementioned view, the competitive hierarchy between species depends on the prevalent light climate and may in principle, show reversals in species ranking over the course of succession (Grubb 1996, Whitmore 1996). The great value of this is that it offers a general framework for understanding gap succession at a community level over a long period.

The species composition of the stand that eventually fills the gap is determined exclusively by the growth and survival of the plants in the vegetation. Probabilities of growth and survival are influenced by the variation in the plant height (size) (Brown & Whitmore 1992), the density of each species (Condit *et al*. 1996), and the intrinsic growth rates of species (Poorter 1998, Kobe 1999) in addition to other factors such as herbivory and disease (Clark & Clark 1991).

Survival in a gap is related to the size of a seedling; in general, taller seedlings should be favoured over smaller ones (Brown & Whitmore 1992, Boot 1996, Zagt 1997). Hence, seedlings that were present before the creation of the gap should have a size advantage over seedlings recruiting into the gap, but this depends on the amount of damage sustained in the gap-forming event (Kennedy & Swaine 1992) and the ability to adapt to the new conditions. A high growth rate can prove much more advantageous than a large initial seedling size (Chapter 2), and usually result in fast growing recruits out-competing the more shade tolerant species at were present before the gap was formed (Kennedy & Swaine 1992, Boot 1996). This is only possible in large gaps since in small gaps light levels are too low for the survival and growth of these fast growing species (Poorter, 1998, Peña 2000, Chapter 2 & 3). Experimental studies have demonstrated this by manipulating light environments in greenhouses and examining the growth rates of species differing in shade tolerance. These studies are carried out with even aged and even sized seedlings with an absence of competition from neighbours (but see Poorter 1998 & Chapter 2). In the field however, seedlings are rarely growing in homogeneous stands and there is always competition among seedlings.

A disappointingly small number of studies have examined growth in the natural un-manipulated seedling populations, which are needed to provide a field test of the experimentally obtained results (Welden *et al*. 1991, Brown & Whitmore 1992, Denslow 1995, Lieberman *et al*. 1995, Whitmore & Brown 1996, Zagt 1997, Hubbell *et al*. 1999). The main questions addressed in these studies were - 'How do seedlings in a natural forest environment respond in terms of their height growth to the degree of canopy opening in gaps?' 'Are species height growth responses in gaps of different sizes influenced by inherent characteristics?' 'Do species show differential height growth in gaps of different and does this result in shade tolerant species dominating the small gaps and the understorey and shade intolerant species dominating the large gaps?'

The answers to these questions will go a long way in enabling ecologists and foresters to understand species co-existence in the rain forest. The issue of predictability of seedling growth and competition at patch level is relevant for silvicultural aspects of forest management. Silvicultural management aims at the manipulation of the forest in pursuit of an economically or ecologically favourable species composition (Lamprecht 1989). The main management tool is the manipulation of the forest canopy. This allows control over the gap size frequency and the light environment of the forest or of desired species, and thus species composition (Brown & Whitmore 1992, ter Steege *et al*. 1996).

In this paper, seedling height growth responses to canopy openness are addressed. To accomplish this, multi-aged seedling populations occurring in a range of gap sizes were monitored for four years after selective logging. By studying naturally established seedling populations, this study proposed to determine whether the processes and factors that were previously shown to be significant in experimental situations are also meaningful under field conditions, where many factors simultaneously act and interact on seedlings.

The following associated hypotheses are proposed:

- There is a positive relation between seedling height growth and canopy openness

- Species differ in their height growth patterns in relation to canopy openness, seed mass and stem densities

Methodology

Seedling growth was measured in plots that were located over a light gradient in twelve 1 ha permanent sample plots that had been harvested using 3 levels of reduced impact logging in 1993.

Plot selection

The plots are located 49 km south of the Mabura Hill Township, and 250 km south of the capital Georgetown on two brown sand ridges and adjacent slopes separated by a white sand ridge in the study area. The forests in this area are evergreen and are classified as *Chlorocardium rodiei* forest interspersed by other forest types e.g. *Eperua* forest on white sand, *Mora* forest along creeks, mixed forest lacking *Chlorocardium* and liana forest. The climate, topography, forest composition and plot layout have been described in detail by Ek (1997) and van der Hout (1999). Each plot was further subdivided into 20 x 20 m recording units (49 per plot). These plots were subjected to four different logging intensities (replicated three times) in mid 1994. The experiment is described in detail in van der Hout (1999).

Plot selection for the current study began 14 months after logging. A horizontoscope was used to examine the image at the centre of each of the 20 x 20 m units in the 12 study plots. This image was compared with sample images for which canopy openness was already known and an estimate was then made of canopy openness for the horizontoscope image. Estimated canopy openness for all sites was classified into five logarithmic classes ranging from 1 - 2 through to 16 - 32 % canopy openness. From each of the first four classes, fifty sites were randomly chosen. In the last class, only 49 sites were available and this resulted in a total of 249 sample sites in total. Plots measuring 2 x 2 m were then established at the chosen sample sites. Each plot was demarcated by four steel rods all connected with fishing line.

Seedling measurements

For the purpose of analysing general trends on seedling growth in gaps, the first measurement was carried out between February - April 1996 and thereafter annually until 1999. Within each plot all seedlings of tree species (≤ 150 cm) were tagged and their height recorded. Height measurements were done with a graduated tape for individuals to the nearest centimetre. The presence of liana infestation, crown and stem damage (due to the logging exercise or herbivory) was recorded. Most individuals were identified by their vernacular names in the field with help from an experienced tree-spotter and later by their species names. Where the vernacular names represented more than one botanically related species, the name of the genus was used. In a few cases, some individuals remained unknown. These individuals were excluded from the analysis.

Canopy openness

Hemispherical photographs were taken immediately following a census using a digital Nikon F 35mm camera with Sigma fish-eye lens levelled on a tripod. Since the photos gave a much more accurate and less subjective estimation of light than the horizontoscope, the canopy openness derived from the photographs were used in the data analysis. Photographs were usually taken close to either dawn or dusk and were always taken in the same position (centre of plot) and at a height of 1 m above the ground.

The digital image was first processed in Paint Shop Pro 5 (vs. 5.01 Jasc Software Inc.1991-1998). First, it was resized and then the colour channels split into red, blue and green. The image with the highest contrast (usually the blue channel) was used for further analysis. Contrasts were sometimes manually adjusted within this program by defining the high density of dark coloured pixels black and the high-density light pixels white. Hemiphots were then analysed using Winphot 5 software (ter Steege 1997) for canopy openness. The canopy openness as calculated by the pictures is a measure of the canopy openness at the level of the seedlings since it includes sapling canopies as well.

Data analysis

SEEDLING DISTRIBUTION OVER HEIGHT CLASSES

Seedlings (all species) were divided in 10 equal height classes. Old seedlings were distinguished from young ones. Old seedlings were those that were present at the first census and young seedlings, those that germinated during the study period. Seedlings were defined as individuals ≤150 cm. The frequency distribution of seedlings over years and height classes was tested with a multivariate ANOVA. An Scheffé (post-hoc) test was subsequently performed to identify in which classes were seedling numbers significantly different.

SEEDLING HEIGHT GROWTH RESPONSES

The distribution of seedling height in relation to canopy openness was demonstrated by calculating the average heights of all seedlings in six equal canopy openness classes. Canopy openness classes ranged from 0 - 5% through to > 25% and the number of plots within the classes varied from 96 in the second class to 16 in the largest class. Canopy openness used here is that as measured in 1996.

To assess the effect of canopy openness, species guild, plant density and seed mass on annual plant height growth responses, a repeated measures analysis of variance was performed. Seed mass, species guild and age were used as fixed factors and annual canopy openness and annual plant density (number of live individuals) as covariates. Plants were divided into 8 logarithmic seed mass classes starting with

0.00001 - 0.0001g until $\geq$100 g (Table 1). The majority of seedlings in the study plots fell into the larger seed-size classes with 41% of the population occurring in the 0.1 - <1 g class. The seed mass data was adapted from Hammond & Brown (1995) and ter Steege (2000) and the majority of seedlings in the study plots fell into the larger seed-size classes with 40% of the species occurring in the 0.1 - <1 g class. Species were grouped as shade tolerant, intermediate and pioneer species guilds. This analysis was done separately for 'old' and 'new' seedlings. Excluded from this analysis were seedlings that had re-sprouted after damage.

Table 1 *The distribution of species recorded in thestudy area into seed mass groups. Seed mass data taken from Hammond & Brown (1995) and ter Steege & Hammond (accepted).*

Seed mass class	Range (g)	% of species
1	0.0001 - 0.00001	0.81
2	0.001 - 0.0001	2.42
3	0.01 - 0.001	4.84
4	0.1 - 0.01	14.52
5	1 - 0.1	40.32
6	10 - 1	20.97
7	100 - 10	14.52
8	> 100	1.61

Results

The seedling population

A total of 10321 seedlings were measured in the 249 four m^2 plots. Of these 45 % were already present at the first census. The best year for recruits was 1998 with 2939 new seedlings being recorded in that year (Chapter 5). Among these seedlings were those that had re-sprouted, due to damage either during the logging process or due to herbivory or some mechanical stress thereafter. More than 1600 seedlings had produced sprouts with 74% of these being seedlings present at the first census.

Table 2 *Results of the multivariate ANOVA showing the effect of the height classes and time on the seedling distribution patterns of both old (established before the first census) and new (established after the first census) seedlings.*

	Old seedlings		New seedlings	
	F	p	F	p
Height classes	35.94	< 0.001	11.41	< 0.001
Time	5.79	> 0.05	2.89	< 0.01

Seedling distribution over height classes

The number of seedlings decreased as the size of the classes increased for both old and young seedlings (Table 2). The number of seedlings in the three smallest height classes were almost double that of the other classes. Scheffé test results indicated that for old seedlings the number of seedlings in the three smallest height classes were significantly, different to the others (31 - 150 cm) (Figure 1).

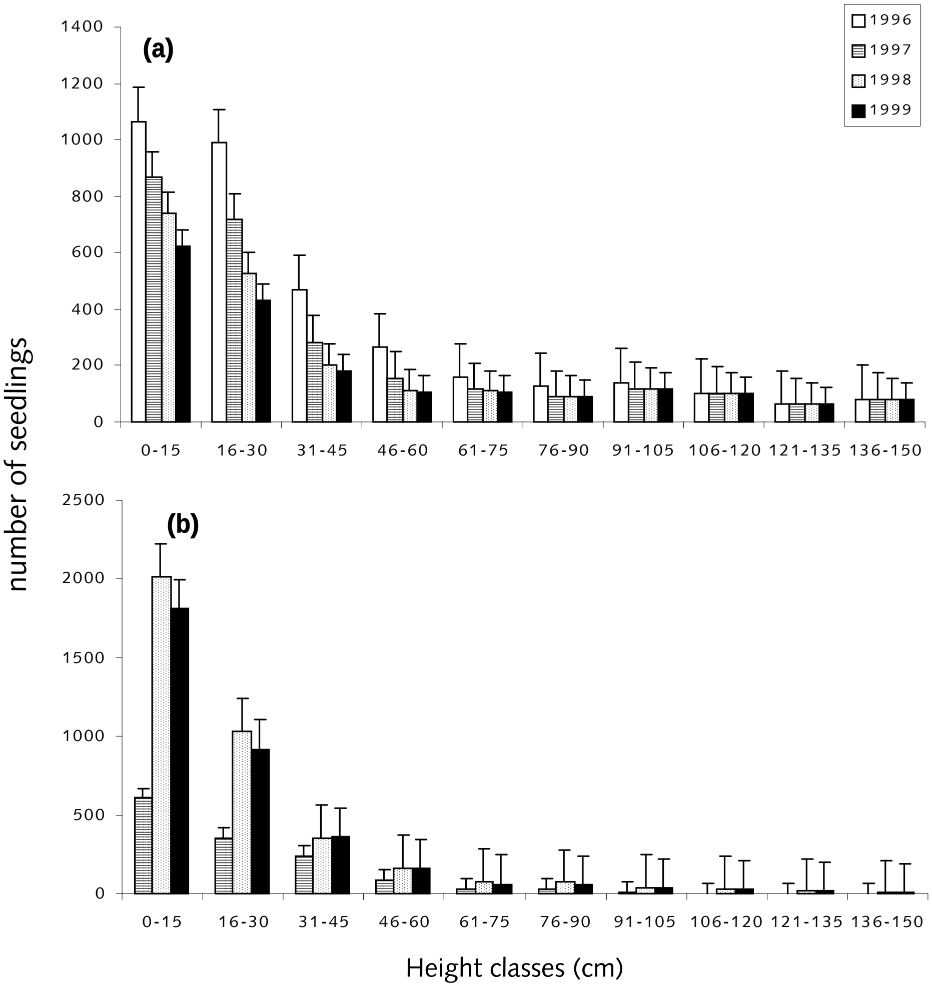


Figure 1 *Stem distributions into height classes for (a) old and (b) new seedlings. Each bar represents a different year and error bars are indicative of the standard error of the mean.*

Seedling distributions between years were significant only in the case of the old seedlings (Table 2). Seedling numbers in 1996 and 1997 were usually higher than those in 1998 and 1999 (in the first 3 height classes). The number of new seedlings, in the 0 -15 cm and 16 - 30 cm classes were significantly higher than the other classes and the number of seedlings in 1997 was significantly less than in 1998 and 1999 (Figure 1).

Seedling height growth responses

The repeated measures ANOVA indicated that seedlings heights were significantly affected by stem density, and seedling age, but not by canopy openness, species guild or seed mass (Table 3).

Table 3 *Results of repeated measures ANOVA showing the effects of canopy openness, density and seed mass on the heights of old and new seedlings. Seed mass was used as a fixed factor and canopy openness, and density as covariates.*
*(p < 0.001:***, p < 0.01:**, p < 0.05:*, p > 0.05:ns)*

	Old seedlings		**New seedlings**	
	F	p	F	p
Canopy openness 96	2.073	0.15		
Canopy openness 97	0.005	0.94	0.226	0.635
Canopy openness 98	0.006	0.94	0.278	0.598
Canopy openness 99	0.006	0.94	0.001	0.981
Density 96	2.23	0.135		
Density 97	37.84	<0.001	0.015	0.904
Density 98	1.65	0.2	0.913	0.34
Density 99	13.2	<0.001	15.372	<0.001
Seedmass	2.09	0.061	1.402	0.202
Species guild	3.75	0.164	0.326	0.563

Figure 2 indicates that the heights of old seedlings increased with canopy openness then decreased again at the highest canopy openness levels. This pattern was significantly different in the last two years with plants in the 11 - 15% canopy openness class being shorter than those in the 6 - 10% class (Figure 2). Seedling heights differed significantly between years ($F = 650.93$, $p < 0.001$), with Scheffé tests showing seedling numbers in the first two years significantly lower than the last two. Newly recruited seedlings showed quite similar height growth patterns as the old seedlings. Seedlings in the largest canopy openness class (> 25%) tended to be slightly taller than those in the other classes. New seedlings were recorded in these plots only during the third year of the experiment (Figure 2). The shortest seedlings were recorded in the three classes spanning 11 - 25 % canopy openness. Seedling heights increased over time (Figure 2), but this was not significant. The heights of old seedlings were influenced by stem density in two out of the four years (1997 & 1999) whilst the heights of the new seedlings were only affected by density in the last year (1999).

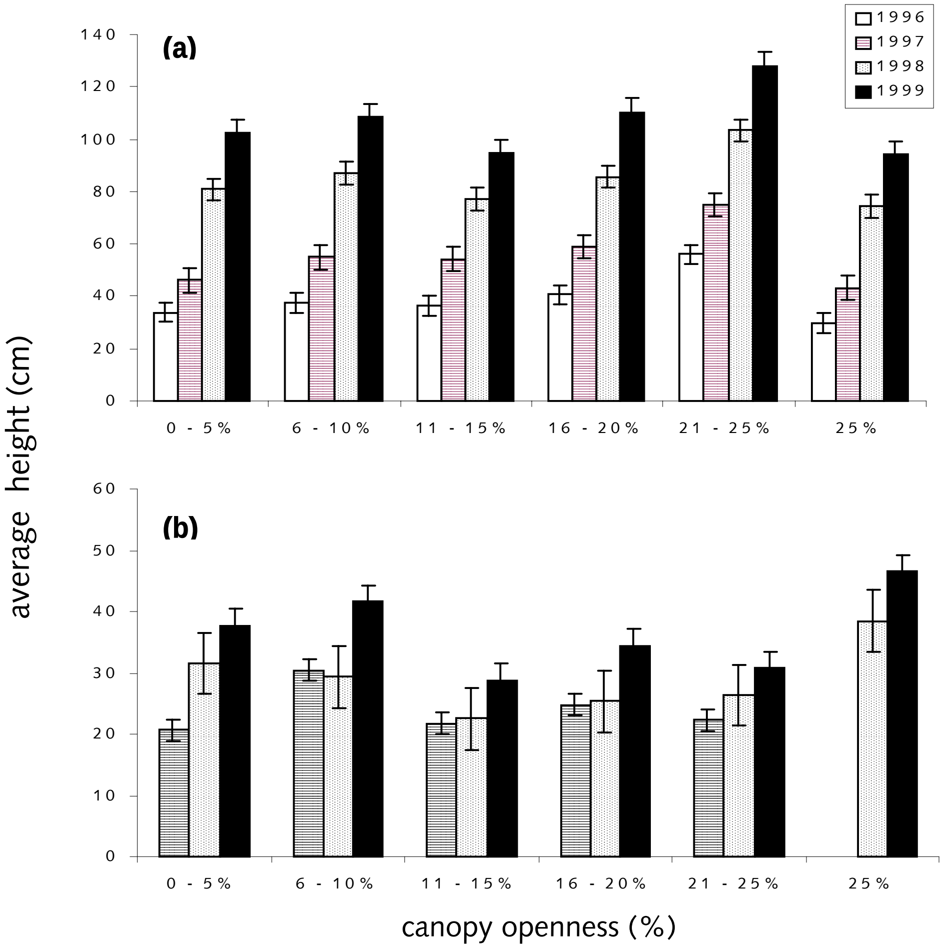


Figure 2 *Mean height of surviving (a) old and (b) new seedlings as a function of canopy openness. Each bar represents a different year and error bars are indicative of the standard error of the mean.*

Pearson correlations indicate that stem density and seedling age were all significantly correlated with seedling heights in the last three years of the experiment (Table 4). Seedling heights (old and new collectively) were positively correlated with seed mass, species guilds and canopy openness (in 1996 & 1997), and negatively correlated with canopy openness in 1998 & 1999. However, none of these correlations was significant (Table 4).

Table 4 *Pearson correlations between seedling heights, canopy openness, density, seedling age, species guild and seed mass. Significant correlations are indicated in italic ($p < 0.05$).*

		Canopy openness (%)	**Density**	**Age**	**Species**	**Seed mass**
Height	*1996*	0.030	-0.003	0.031	0.111	0.001
	1997	0.081	*0.050*	*0.042*	0.156	0.032
	1998	-0.054	*0.118*	*0.379*	0.213	0.049
	1999	-0.078	*0.308*	*0.451*	0.187	0.087

Differences in species height growth rates

Seedling height growth rates exhibited a pattern of a sharp increase between the first and second canopy openness class followed by a gradual decrease until the highest canopy openness class (Figure 3). Most species did not occur in all six canopy openness classes and as a result clear patterns of individual species height growth responses between the canopy openness classes were not observed (Appendix 1).

The eight species used in the Pibiri Gap Experiment (Chapter 2) showed significant differences in their height growth responses to canopy openness. *Ormosia* and *Laetia* were not included in the analysis because too few individuals of these species occurred in the plots. With the exception of *Goupia* - Catostemma, *Cecropia*, *Chlorocardium*, *Sclerolobium*, and *Pentaclethra*, all showed their highest height growth rates in the 6 - 10 % canopy openness class (Appendix 1). There were no clear patterns of height growth responses of these species to canopy openness.

Figure 4 shows the seedling heights of the 20 tallest seedlings in 1996 and 1999 compared with the heights of the tallest seedlings in the final year in rank order.

There was remarkably little difference in the tallest seedlings in 1999 and the heights of those seedlings that were the tallest in 1996. In most cases, the tallest seedlings at the beginning of the experiment remained the tallest seedlings at the end of the experiment.

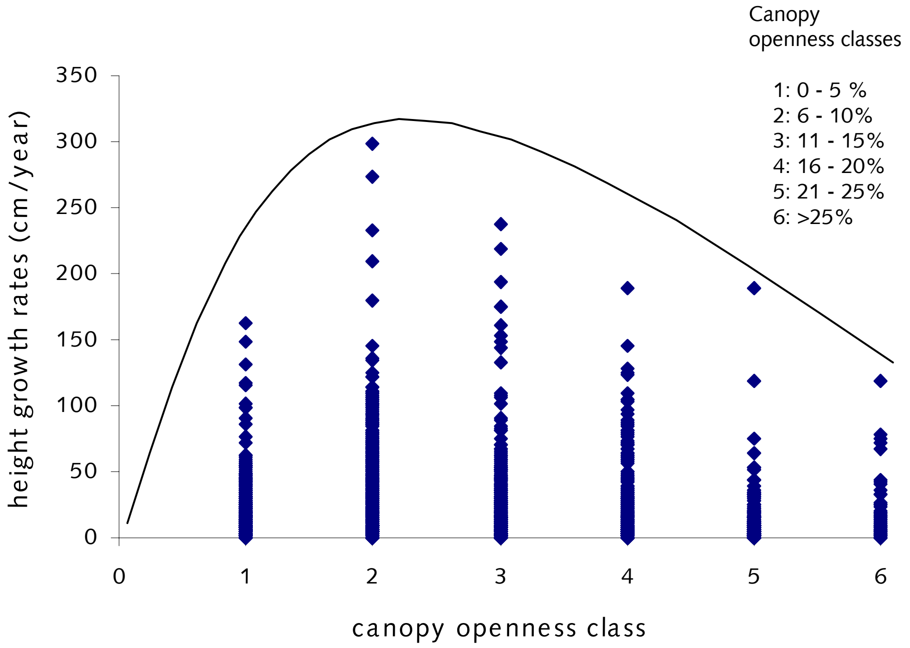


Figure 3 *The relationship between canopy openness and mean seedling height growth rate. Height growth rates of all seedlings are included in this plot except those that died after one census, or those germinating after the third census. Seedlings that respouted or exhibited inconsistent growth are also excluded.*

Discussion

Canopy openness and seedling heights

In an undisturbed tropical forest, the majority of the seedlings occur in low light and their dynamics is a consequence of this light environment (see Denslow 1987). In this study, the use of gaps of different sizes with varying canopy densities, made it possible to look at seedling height growth responses across a range of natural light levels.

The evidence from this study indicates no clear and furthermore significant relation between seedling heights and canopy openness or seed mass. This is contrary to the findings of experimental studies of seedling growth in manipulated light environments (e.g. Bongers & Popma 1988, Osunkoya *et al*. 1993, Veenendaal *et al*. 1996, Chapter 3) and in the field (De Steven & Putz 1984, Howe 1990, but see Clark & Clark 1992, Clark *et al*. 1993, Zagt 1997). Seedlings in these experiments invariably show a strong response of height growth to light availability, although the response may be complex (Ashton 1995). By design, experiments use seedlings of similar initial size and keep most other conditions constant; therefore, differences in growth performance between species are regulated only by their morphological and physiological behaviour. While the heights of the naturally established seedlings in this experiment were enhanced by canopy openness, the relationship was certainly not clear.

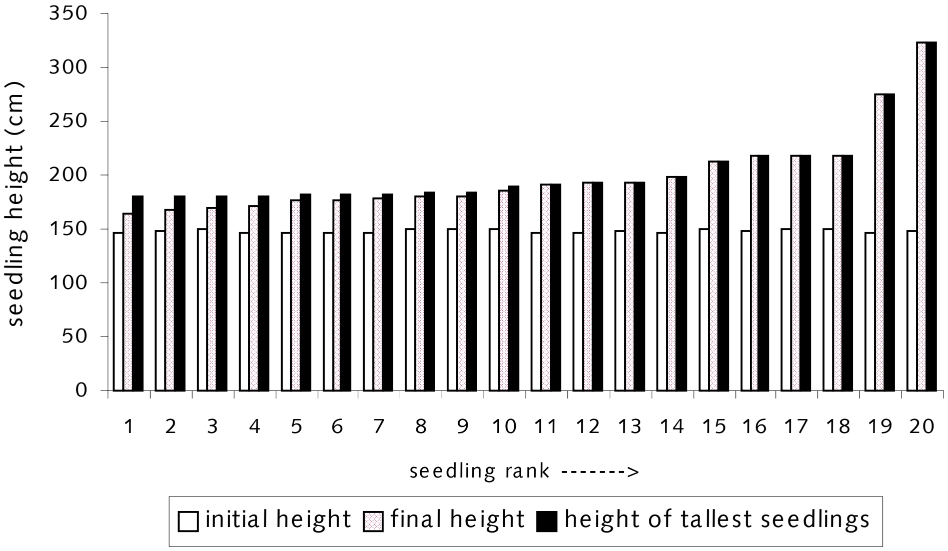


Figure 4 *The relation of the heights in 1999 of the 20 tallest seedlings at the beginning (1996) of experiment with the heights of the 20 tallest seedlings at the end of the experiment (1999).*

Seedling heights were influenced by stem density and seedling age. The old seedlings represented in this case the advanced regeneration in the gaps and dominated the plots in all canopy openness classes. This resulted in the overall gap composition in terms of the tallest individuals changing very little over the four-year period. The effects of the initial size differences between seedlings on their eventual heights at the end of the experiment were quite clear. Whitmore & Brown (1996) found however, that after approximately six and a half years, the initial size difference conferred on seedlings due to the age difference had disappeared. The faster growing *Shorea johrensis* was able to overtake the more shade tolerant *Hopea nervosa* in most of their gaps. Hence, the advantage conferred by a large initial size may only be a short-term benefit that can be maintained with fast growth rates.

Height growth rates - canopy openness and species effects

The optimum curve for seedling height growth rates indicated that growth rates were highest between 6 - 10% canopy openness classes, and lowest at the highest canopy openness class. This pattern suggests that the notion of 'more light more growth' as has been documented in several studies (e.g. Bongers *et al*. 1988 Popma & Bongers 1988, Denslow *et al*. 1990, Chapter 3), does not apply in the case of these naturally established seedlings (but see Whitmore & Brown 1996). In fact, most species had higher growth rates in the smaller canopy openness classes. This is quite similar to what has been described for some dipterocarp seedlings (Sasaki & Mori 1981) and for some shade tolerant rain forest species (Chazdon 1986).

There may be several reasons why the height growth rates were lower in the largest gaps as compared to the small gaps. The first of these is competition, which may be in the form of lianas and/or grasses. The presence of these may have had severe consequences for the height growth rates. In the largest gaps, the grasses had a stifling effect on seedlings, quickly overtopping seedlings and forming a very dense canopy. Lianas may have been less effective in restricting seedling growth, as they were less vigorous in their growth than the grasses. The presence of these two life forms and the abundance of newly recruited seedlings into the plots in the large gaps resulted in these plots having much higher stem densities than the plots in the smaller canopy openness classes (Chapter 5). This results in increased competition for resources (especially light).

Another important reason why this pattern of height growth rates with canopy openness was found may be due to the difference in the canopy openness measured and the canopy openness experienced by the seedlings. Canopy openness was measured at 1 m height above the ground and in some cases is a reflection of sapling canopy openness. Seedlings that are under the shade of these saplings will therefore experience much lower levels of canopy openness and not those as recorded. On the other hand, the results imply that there is a group of species that are not only able to survive (Chapter 5) but also to grow fast in the relatively low light gaps. This is contrary to most of the findings reported for studies of this nature (cf. Zagt 1997) which have show either low survival in low light environments and fast growth in high light or vice versa (Kitajima 1994, Kobe *et al*. 1995, Boot 1996).

Most of the species followed in this study showed a maximum rather than a linear response to increased canopy openness. Height growth increased until a certain canopy openness level, and thereafter declined or remained relatively constant. Perhaps for naturally established seedlings, once canopy openness levels are increased, other factors directly related to this increase (e.g. nutrients) become limiting producing this threshold effect.

On closer examination of a subset of species having a range of life history traits (see Chapter 2), clear differences in growth rates were observed. Growth rates exhibited here were much lower than those observed in a controlled experiment, but the pioneers still maintained the highest growth rates (Appendix 1). However, these pioneer species were found in relatively low numbers and exhibited their highest growth rates at much lower canopy openness levels than was the case in the controlled experiment. One reason for these observed low abundances of the pioneers in the experimental plots may be the relatively undisturbed nature of these forests (ter Steege & Hammond accepted). This implies that these pioneers may not be present in large numbers as adults and hence seedling abundances will inevitably be low. Secondly, although the range of 6 -10 % canopy openness may be relatively dark (compared to the light levels where these pioneers are usually observed) and seemingly favourable for the more shade tolerant species, there is enough light available for the rapid growth of these light demanding species. The result may be that these species are able to grow quickly to out-compete the juvenile canopy made up of shade tolerant species that were present prior to logging. However, the faster height growth rates in the large gaps may have been at the cost of mechanical stability in some cases, leading to snapping of the tops of stems, and hence re-sprouting. This was also more prevalent in plots experiencing high canopy openness levels and for pioneer species (*pers obs*). In fact, the three species most prone to sprouting (all individuals re-sprouted from the top) were all pioneers. It is quite well documented that damage (due to herbivory) is much more prevalent in larger gaps (Dalling *et al.* 1997), and that species damaged at the seedling stage have a very slim chance of ever recovering.

With regard to their regeneration responses, forest tree species are often grouped into two or three classes based on their establishment, survival and growth patterns. However, this categorisation is most times not based on species responses in natural condition but in manipulated experiments that many of the factors that affect a species performance in field are controlled. In this study using abroad range of canopy openness' and 147 naturally occurring species, it was difficult to see clear patterns of responses to canopy openness.

Conclusion

Canopy openness was not a good predictor of seedling height growth responses, but rather significant correlations were found with seedling age and stem density. Initial plant size also proved important in determining the height rank of seedlings after four years. Results of this study contradict the findings of several controlled experiments (including chapter 3), where clear patterns of seedling height growth with canopy openness are observed. This indicates that the results of field experiments are not easily translated into field behaviour.

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Appendix 1

Species height growth with canopy openness. *The mean and standard deviation of the height growth rate (cm/month) per species is shown for each canopy openness class. Height growth rates were calculated for all individuals of species that were recorded for more than one census and had not sprouted or shown abnormal growth. Blank spaces are indicative of cases where there were too few individuals to calculate the species height growth rate.*

VERNACULAR	**SPECIES**	**FAMILY**	**SEED MASS[1] CLASS**
ADEBERO	*Paypayrola longifolia*	Violaceae	4
ARARA, Broad leaf	*Unonopsis glaucopetala*	Annonaceae	5
ARARA, Fine Leaf	*Bocageopsis multiflora*	Annonaceae	5
ARARA, Smooth Skin	*Guatteria atra*	Annonaceae	5
AROMATA	*Clathrotropis brachypetala*	Leguminosae/Papil.	7
ARUADAN	*Sloanea spp. (2)*	Eleocarpaceae	6
ASASHI	*Rheedia benthamiana*	Clusiaceae	4
ASEPOKO	*Pouteria guianensis*	Sapotaceae	6
ASEPOKOBALLI, Broad Leaf	*Pouteria jenmanni*	Sapotaceae	6
ASEPOKOBALLI, Fine Leaf	*Pouteria caimito*	Sapotaceae	6
AWASOKULE	*Tovomita spp.(2)*	Clusiaceae	6
BARAKARO	*Ormosia coccinea*	Leguminosae/Papil.	6
BAROMALLI, Sand	*Catostemma fragrans*	Bombacaceae	7
BAROMALLI, Swamp	*Catostemma commune*	Bombacaceae	7
BLACKHEART	*Acosmium praeclara*	Leguminosae	5
BLOODWOOD	*Vismia guianensis*	Guttiferae	3
BOKOTOKON	*Licania sp.2*	Chrysobalanaceae	5
BURADA	*Parinari campestris*	Chrysobalanaceae	7
BURADIYE	*Nectandra grandis*	Lauraceae	7
CONGO PUMP, Common	*Cecropia obtusa*	Moraceae	2
CONGO PUMP, High bush	*Cecropia spp.*	Moraceae	2
CORKWOOD, Hill	*Pterocarpus spp.*	Leguminosae	6
CRABWOOD	*Carapa guianensis*	Meliaceae	7
DALLI, Hill	*Virola sebifera*	Myristicaceae	6
DEVILDOOR TREE	*Glycydendron amazonicum*	Euphorbiaceae	5
DUKA	*Tapirira obtusa*	Anacardiaceae	5
FERN TREE	*Touroulia guianensis*	Quiinaceae	5
FIRE TREE	*Ind.1*		4

Appendix 1 continued

[1]*Seed-mass classes:* **1***: >100g;* **2***: 100 - 10g;* **3***: 10 - 1g;* **4***: 1 - 0.1g;* **5***: 0.1 - 0.01g;* **6***: 0.01 - 0.001g;* **7***: 0.001 - 0.0001g;* **8***: 0.0001 - 0.00001g*

[2]*Canopy openness classes: Class1:0-5%, Class 2: 5.1-10.1%, Class 3:10.2-15.2%, Class 4:15.3-20.3%, Class 5:20.4-25.4%, Class 5:20.4-25. 4%, Class 6:>25.4%*

Class 1[2]		**Class 2**		**Class 3**		**Class 4**		**Class 5**		**Class 6**	
Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
16.42	15.74	15.55	15.91	11.10	9.87	9.37	8.19	10.49	13.21	78.43	---
---	---	34.68	43.95	---	---	---	---	---	---	---	---
---	---	27.98	29.10	13.52	15.76	29.18	36.64	10.40	---	21.96	12.23
---	---	21.13	29.88	6.89	5.47	13.33	2.78	6.55	9.12	---	---
---	---	11.85	1.48	---	---	15.01	---	---	---	---	---
---	---	21.29	15.63	13.15	13.48	12.00	---	8.05	10.25	---	---
---	---	15.30	---	---	---	---	---	---	---	---	---
---	---	15.79	19.24	---	---	---	---	---	---	7.90	---
115.23	---	12.60	3.68	4.70	---	---	---	---	---	---	---
---	---	1.80	---	---	---	---	---	---	---	---	---
4.65	---	59.69	51.57	4.30	---	2.02	2.14	15.30	---	---	---
2.60	---	4.47	---	---	---	---	---	---	---	---	---
12.97	11.74	23.32	21.31	20.02	16.82	7.20	15.20	6.44	5.86	18.56	26.65
---	---	11.70	6.76	4.59	2.93	---	---	---	---	---	---
---	---	---	---	84.00	---	---	---	---	---	---	---
---	---	---	---	---	---	25.20	---	---	---	---	---
---	---	17.32	28.93	---	---	9.40	---	---	---	---	---
9.51	8.75	14.10	17.14	24.49	49.21	10.47	4.19	8.33	8.69	26.93	---
---	---	---	---	1.60	---	---	---	---	---	---	---
---	---	32.06	27.46	2.70	2.97	14.40	20.47	30.73	32.62	---	---
---	---	16.90	---	---	---	---	---	---	---	---	---
---	---	34.40	---	---	---	---	---	---	---	---	---
15.03	17.35	21.64	21.02	3.20	2.61	2.23	1.33	---	---	---	---
1.50	---	16.28	7.18	---	---	6.90	---	---	---	---	---
---	---	14.63	14.03	---	---	---	---	---	---	---	---
---	---	---	---	8.60	---	---	---	---	---	---	---
17.20	---	---	---	36.30	---	---	---	---	---	---	---
14.98	10.38	37.35	21.28	18.71	27.30	15.30	---	11.78	4.97	---	---

Appendix 1 continued

VERNACULAR	**SPECIES**	**FAMILY**	**SEED MASS[1] CLASS**
FUKADI	*Terminalia amazonica*	Combretaceae	5
FUTUI	*Jacaranda copaia subsp. copaia*	Bignoniaceae	3
GALE, Almond	*Aniba citrifolia*	Lauraceae	6
GALE, Ginger	*Aniba kappleri*	Lauraceae	6
GALE, Greenheart	*Aniba excelsa*	Lauraceae	6
GREENHEART	*Chlorocardium rodiei*	Lauraceae	7
HACHIBALLI	*Simaba multiflora*	Simaroubaceae	4
HAIAWA	*Protium guianense*	Burseraceae	6
HAIAWABALLI	*Protium tenuifolium*	Burseraceae	5
HICHU	*Eugenia patrisii*	Myrtaceae	5
HIKURIBIANDA	*Simaba cedron*	Simaroubaceae	4
HISHIRUDAN	*Dulacia guianensis*	Olacaceae	6
HIWARADAN	*Chaunochiton kappleri*	Olacaceae	5
HURUEREROKO	*Cordia nodosa*	Boraginaceae	4
IMORO	*Palicourea guianensis*	Rubiaceae	5
ITIKIBOROBALLI	*Swartzia sprucei var. tessellata*	Leguminosae/Papil.	6
KABUKALLI	*Goupia glabra*	Celastraceae	2
KADITIRI	*Sclerolobium guianense*	Leguminosae/Caesalp.	5
KAIARIMA	*Maytenus myrsinoides*	Celastraceae	5
KAIRIBALLI	*Licania heteromorpha var. perplexans*	Chrysobalanaceae	7
KAKARALLI, Black	*Eschweilera sagotiana*	Lecythidaceae	6
KAKARALLI, Fine Leaf Thick Skin	*Eschweilera wachenheimii*	Lecythidaceae	6
KAKARALLI, Smooth leaf	*Eschweilera coriacea / Eschweilera decolorans*	Lecythidaceae	6
KAKARALLI, Wirimiri	*Lecythis confertiflora*	Lecythidaceae	6
WILD GUAVA	*Calycolpus goetheanus*	Myrtaceae	7
KARAMPAI	*Annona spp.*	Annonaceae	4
KARISHIRI	*Oxandra asbeckii*	Annonaceae	6
KAUTA	*Licania laxiflora*	Chrysobalanaceae	7
KAUTABALLI	*Licania alba*	Chrysobalanaceae	7
KOKORITIBALLI	*Licania majuscula*	Chrysobalanaceae	7
KOMARAMARA	*Duroia eriophila var. eriophila*	Rubiaceae	5
KOMARAMARABALLI	*Amaioua guianensis var. guianensis*	Rubiaceae	5

Appendix 1 continued

Class 1[2]		Class 2		Class 3		Class 4		Class 5		Class 6	
Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
---	---	24.70	13.29	---	---	---	---	---	---	---	---
---	---	12.60	16.97	17.56	3.91	2.25	2.33	14.92	8.52	---	---
7.90	---	17.60	22.03	36.07	36.86	---	---	---	---	---	---
---	---	38.67	---	---	---	---	---	---	---	---	---
---	---	24.84	17.85	---	---	7.63	6.64	0.95	1.06	42.20	---
12.72	11.74	18.38	17.81	12.95	15.24	11.11	11.68	7.14	9.83	9.78	7.08
---	---	14.94	4.04	15.30	0.00	---	---	5.48	4.63	---	---
16.26	17.45	14.41	12.66	3.70	5.47	3.23	3.08	---	---	15.22	14.83
---	---	3.80	---	---	---	15.90	---	---	---	---	---
---	---	17.90	16.97	73.70	99.42	---	---	---	---	---	---
---	---	---	---	---	---	57.53	---	---	---	---	---
---	---	11.00	---	---	---	---	---	---	---	---	---
---	---	31.19	16.55	11.01	7.39	13.06	13.24	---	---	---	---
22.03	---	27.87	---	---	---	---	---	---	---	---	---
---	---	35.60	---	---	---	---	---	---	---	---	---
3.15	---	23.12	17.90	24.82	47.24	13.80	10.89	2.00	0.28	---	---
---	---	22.27	24.36	11.38	13.16	32.45	26.03	15.38	16.49	---	---
7.53	5.52	16.39	22.35	11.26	4.97	1.62	1.27	7.57	1.08	---	---
---	---	---	---	---	---	1.80	---	---	---	---	---
11.65	11.51	17.53	15.79	25.57	35.46	7.73	8.39	10.10	8.59	26.17	39.59
53.23	74.06	19.97	26.83	15.05	39.88	6.24	4.65	3.10	---	---	---
13.75	---	21.57	29.55	10.41	9.65	8.38	13.14	9.30	7.95	---	---
11.42	14.21	26.89	30.15	12.77	16.67	6.78	7.05	4.30	---	---	---
16.25	19.17	16.50	15.96	14.83	20.44	18.57	26.02	15.82	25.98	27.10	39.28
22.13	20.74	27.98	24.24	16.98	18.73	13.96	26.06	8.44	3.10	---	---
---	---	---	---	1.23	---	---	---	6.00	---	---	---
14.39	16.77	24.28	35.01	16.82	23.08	16.43	31.19	5.85	5.69	8.67	10.69
---	---	16.37	15.18	8.95	7.14	---	---	---	---	5.27	---
16.29	17.08	19.88	20.80	15.42	13.44	3.73	2.25	1.40	0.57	36.37	---
---	---	6.10	5.52	31.72	33.49	28.20	---	8.45	9.69	9.07	---
---	---	19.33	8.07	15.77	3.98	42.24	40.91	---	---	---	---
42.40	---	15.30	---	---	---	146.00	---	4.70	---	---	---

Appendix 1 continued

VERNACULAR	SPECIES	FAMILY	SEED MASS[1] CLASS
KONOKO	*Licania cuprea*	Chrysobalanaceae	5
KORAROBALLI	*Hymenolobium sp.*	Leguminosae/Papil.	5
KOYECHI	*Rollinia exsucca*	Annonaceae	4
KUDIBIUSHI	*Micropholis venulosa*	Sapotaceae	5
KULISHIRI, Black	*Cupania spp (2)*	Sapindaceae	5
KULISHIRI, Common	*Matayba sp1*	Sapindaceae	5
KULISHIRI, White	*Matayba sp2*	Sapindaceae	5
KURIHIKOYOKO	*Anaxagorea dolichocarpa*	Annonaceae	4
KUROKAI	*Protium decandrum*	Burseraceae	5
KUYAMA, Red	*Xylopia pulcherrima*	Annonaceae	4
KUYAMA, White	*Xylopia nitida*	Annonaceae	4
KWAKO	*Marlierea montana*	Myrtaceae	4
LANABALLI	*Gustavia hexapetala*	Lecythidaceae	3
LOCUST	*Hymenaea courbaril*	Leguminosae/Caesalp.	6
MAHO, Smooth Leaf	*Sterculia pruriens var. glabrescens*	Sterculiaceae	6
MANARIBALLI, Common	*Balizia pedicellaris*	Leguminosae/Mimos.	5
MANARIBALLI, Like	*Pseudopiptadenia suavolens*	Leguminosae/Mimos.	5
MANOBODIN	*Emmotum fagifolium*	Icacinaceae	5
MANYOKINABALLI	*Geissospermum sericeum*	Apocynaceae	5
MARISHIBALLI	*Licania densiflora*	Chrysobalanaceae	7
MARISHIBALLI, High Bush	*Licania sp.1*	Chrysobalanaceae	7
MORA	*Mora excelsa*	Leguminosae/Caesalp.	8
MORABALLI	*Pouteria coriacea*	Sapotaceae	5
MORABUKEA	*Mora gongrijpii*	Leguminosae/Caesalp.	8
MOROBALLI	*Talisia squarrosa*	Sapindaceae	5
MUNIRIDAN	*Siparuna sp.*	Monimiaceae	4
OKOKONSHI, BROAD LEAF	*Quiina indigofera*	Quiinaceae	5
OKOKONSHI, FINE LEAF	*Quiina guianensis*	Quinnaceae	5
PARAKUSAN	*Swartzia schomburgkii var. jenmanii*	Leguminosae/Caesalp.	6
PASTURE TREE	*Trymatococcus paraensis Ducke*	Moraceae	6
PERO-ISHI-LOKODO	*Tabernaemontana spp.*	Apocynaceae	5
PURPLEHEART	*Peltogyne venosa var. densiflora*	Leguminosae/Caesalp.	5

Appendix 1 continued

Class 1[2]		Class 2		Class 3		Class 4		Class 5		Class 6	
Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
---	---	---	---	---	---	4.25	3.32	---	---	---	---
---	---	---	---	---	---	---	---	---	---	19.57	18.24
---	---	20.40	---	---	---	---	---	---	---	---	---
8.90	6.36	18.70	11.80	8.65	9.97	53.35	69.93	11.60	11.38	1.40	---
39.67	---	26.65	29.74	29.85	20.63	13.43	3.32	17.62	3.28	---	---
16.60	---	8.80	9.19	8.50	---	9.25	1.06	---	---	---	---
---	---	17.76	14.12	6.88	7.05	10.30	1.13	---	---	0.10	---
---	---	4.93	3.01	0.20	---	36.00	29.27	---	---	---	---
29.97	21.89	19.31	17.00	19.38	7.07	6.53	6.50	3.55	0.78	4.53	---
---	---	---	---	2.70	---	---	---	---	---	---	---
---	---	---	---	6.58	6.10	5.20	---	---	---	---	---
24.69	21.63	12.96	22.04	13.05	6.01	11.03	3.53	1.60	---	25.00	---
---	---	---	---	15.30	0.00	3.53	1.29	---	---	---	---
30.98	42.17	---	---	---	---	---	---	---	---	---	---
---	---	---	---	6.00	1.13	---	---	---	---	---	---
7.80	---	0.40	---	16.95	9.90	5.14	6.96	1.95	2.19	---	---
8.83	---	---	---	11.30	---	---	---	---	---	---	---
---	---	---	---	15.30	---	---	---	---	---	---	---
---	---	---	---	---	---	---	---	---	---	12.80	---
3.30	---	21.92	22.59	15.41	23.50	10.38	13.88	18.13	20.55	---	---
30.70	45.75	13.29	13.71	21.65	20.25	2.55	2.20	---	---	---	---
---	---	3.20	---	---	---	---	---	---	---	---	---
---	---	13.78	12.52	1.60	---	7.67	---	3.63	2.35	---	---
23.05	18.60	16.65	22.61	31.62	47.46	18.87	17.88	15.79	14.98	---	---
---	---	11.44	6.03	---	---	4.80	5.09	---	---	11.57	8.86
---	---	---	---	8.20	---	---	---	---	---	---	---
32.61	25.95	22.25	25.04	11.11	10.22	14.15	23.25	29.17	40.32	---	---
11.10	9.72	5.17	4.75	---	---	---	---	---	---	---	---
1.73	---	37.20	36.41	---	---	---	---	---	---	---	---
---	---	15.30	---	10.67	15.91	---	---	28.77	---	---	---
2.70	1.84	32.98	41.58	16.25	15.23	7.55	6.56	18.52	22.37	---	---
9.42	11.19	45.42	80.73	10.84	6.02	15.25	20.61	2.92	2.67	4.25	3.99

Appendix 1 continued

VERNACULAR	**SPECIES**	**FAMILY**	**SEED MASS[1] CLASS**
ROKOROKO	*Macoubea guianensis*	Apocynaceae	5
RURI	*Chaetocarpus schomburgkianus*	Euphorbiaceae	5
SAREBEBEBALLI	*Vouacapoua macropetala*	Leguminosae/Caesalp.	6
SEREBEDAN	*Swartzia oblanceolata*	Leguminosae/Caesalp.	6
SHIBADAN, smooth leaf	*Aspidosperma album*	Apocynaceae	5
SHIBALLIDAN	*Hebapetalum humiriifolium*	Linaceae	3
SHIRADA	*Inga laterifolia*	Leguminosae	5
SILVERBALLI, Kereti	*Ocotea spp. (2)*	Lauraceae	5
SILVERBALLI, Others	*Ocotea spp.*	Lauraceae	5
SILVERBALLI, Pear Leaf	*Ocotea acutangula*	Lauraceae	5
WABAIMA	*Licaria cayennensis*	Lauraceae	5
SILVERBALLI, White	*Ocotea canaliculata*	Lauraceae	5
SIMARUPA	*Simarouba amara*	Simaroubaceae	4
TABLE TREE	*Cordia exaltata*	Boraginaceae	5
TATABU	*Diplotropis purpurea*	Leguminosae/Papil.	5
TRYSIL	*Pentaclethra macroloba*	Leguminosae/Mimos.	6
ULU	*Trattinickia spp.(2)*	Burseraceae	5
UNIKIAKIA	*Licania hypoleuca*	Chrysobalanaceae	7
UNKNOWN "A"	*Sandwithia guyanensis*	Euphorbiaceae	4
UNKNOWN "C"	*Eugenia sp.*	Myrtaceae	5
WAIABALLI	*Tapura guianensis*	Dichapetalaceae	4
WALLABA, Ituri	*Eperua grandiflora*	Leguminosae	7
WALLABA, Soft	*Eperua falcata*	Leguminosae/Caesalp.	7
WAMARA	*Swartzia leiocalycina*	Leguminosae/Caesalp.	7
WARAIA	*Miconia gratissima*	Melastomataceae	1
WARAKAIORO	*Laetia procera*	Flacourtiaceae	3
WARAKOSA	*Inga spp.*	Leguminosae/Mimos.	5
YARI YARI	*Duguetia negelecta*	Annonaceae	4
YARURU	*Aspidosperma exselsum*	Apocynaceae	5
YAWAREDAN	*Tachigali rusbyi*	Leguminosae/Caesalp.	5
YESHIDAN	*Duguetia yeshidan*	Annonaceae	4

Appendix 1 continued

Class 1[2]		Class 2		Class 3		Class 4		Class 5		Class 6	
Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
---	---	34.20	---	---	---	---	---	---	---	---	---
---	---	15.30	---	15.30	0.00	---	---	---	---	---	---
---	---	7.05	5.60	18.82	17.73	13.89	21.74	8.57	6.50	---	---
52.50	---	16.19	21.30	6.00	5.29	11.87	12.21	---	---	---	---
---	---	15.00	---	14.95	16.90	---	---	---	---	---	---
42.86	57.25	15.07	12.39	7.61	2.57	14.81	16.46	1.70	---	4.33	---
22.60	---	---	---	51.67	---	---	---	---	---	---	---
15.78	16.77	17.81	25.56	16.14	7.21	15.47	6.85	---	---	---	---
---	---	14.14	11.42	12.81	4.98	---	---	---	---	---	---
---	---	15.30	---	---	---	---	---	---	---	---	---
19.53	---	7.10	---	---	---	---	---	---	---	---	---
24.35	---	---	---	---	---	9.53	6.89	---	---	---	---
---	---	60.63	41.57	---	---	---	---	---	---	---	---
---	---	4.80	---	---	---	18.15	---	---	---	---	---
33.95	28.13	18.32	26.66	23.20	27.04	35.50	---	8.10	---	---	---
19.13	15.52	28.09	20.89	10.63	4.09	---	---	---	---	---	---
---	---	69.18	26.89	15.30	---	---	---	---	---	---	---
---	---	14.40	20.33	---	---	10.70	4.27	---	---	---	---
11.91	3.06	23.42	40.28	10.59	9.43	14.77	12.80	6.43	8.38	---	---
22.60	---	15.81	15.84	8.31	6.19	0.10	---	---	---	---	---
18.04	15.46	24.07	36.77	22.86	51.31	9.68	9.04	11.65	12.44	8.37	7.56
---	---	2.40	---	---	---	---	---	---	---	---	---
14.70	---	12.37	10.20	6.13	1.72	3.70	---	10.98	6.10	24.55	23.59
---	---	9.50	3.92	15.30	---	12.63	14.11	16.75	4.38	18.33	---
---	---	17.58	15.30	11.71	8.94	18.97	19.72	33.09	69.09	8.90	10.89
---	---	---	---	---	---	5.80	---	---	---	---	---
19.94	19.77	27.44	31.65	11.93	27.03	7.16	5.22	7.68	6.34	0.60	---
2.23	---	32.79	26.77	8.72	6.65	6.30	---	15.30	---	---	---
11.50	---	23.31	19.91	2.00	---	10.80	9.90	4.05	5.30	---	---
6.75	0.07	16.16	17.12	---	---	8.60	---	---	---	---	---
---	---	6.26	6.67	10.53	6.24	---	---	---	---	---	---

"Science is a wonderful thing if one does not have to earn ones living at it"
Albert Einstein 1879 - 1955

CHAPTER 7

DISCUSSION AND SUMMARY

The central theme of the present study is the relation between the heterogeneity in vegetation structure as caused by gaps, and the importance of the associated environmental heterogeneity for the regeneration of species populations. Two questions may be derived from the central theme above. First, to what extent does canopy openness and seed mass affect the regeneration potential of species? Secondly, to what degree are species differentiated in their gap requirements? The study analysed both of these questions from the viewpoint of controlled experiments and then via field experiments. Here, results from these two set-ups will be compared.

Species may be differentiated in the way they are adapted to gap associated environmental heterogeneity (Ricklefs 1976, Denslow 1980, Bazzaz & Wayne 1994, Ashton 1998, Brown & Jennings 1998, Poorter 1999). For some species, it is known that they require large gaps to be able to grow and complete their life cycle. Other species do very well in the shaded understorey of the mature forest. Gaps may play an important role in the maintenance of the high species diversity by maintaining a high environmental heterogeneity (Hubbell *et al*. 1999, Brokaw & Busing 2000).

Opposed to this is the view that species are only weakly specialised with respect to gap environments. Although several groups of species with similar gap requirements may be distinguished, within these groups differentiation is far from obvious. In this view, gap-dynamics creates small sites open for colonisation. For any newly created gap, the availability of seeds and the existent seedling bank are important for re-colonisation. Short-range dispersal mechanisms may prevent some seeds from reaching the gap while it is open to colonisation. Thus, any one gap may have a different subset of colonising species.

Variation in seedling survival and growth

Seedling growth increases with canopy openness, not only under controlled conditions (**chapter 2 & 3**) but also along a gap size gradient in the forest from very small to large gaps (**chapter 6**). However, the increase in height is much stronger in controlled experiments than the field experiments. Species survival, to a limited extent, is also affected by canopy openness, with shade tolerant and intermediate (see chapter 5 for definition) species showing relatively high survival rates in all gaps (**chapter 2 & 3**). Survival of high light demanding species was found to be dramatically lower in the understorey and small gaps. An increase in canopy openness is not always beneficial for plant performance, as extreme canopy openness led to reduced growth rates (**chapter 2**) and for some shade tolerant species to a decrease in survival (**chapter 3**).

In the last few years it has been found that high light demanding species are able to germinate and establish in the shaded forest understorey or small gap environments (Raich & Gong 1990, Swaine *et al*. 1997, Peña-Claros 2000). However, they demonstrate an obvious inability to survive for long periods in these conditions. Several reasons may be advanced for this observation, the first since the shade tolerance of a species is not so much related to growth but to other factors affecting persistence. Light demanding species may have low survival in the understorey as they suffer from high herbivory (Kitajima 1996). Another limitation may be their inherently high leaf turnover rate. Lost leaf area must be replaced at a high rate to sustain growth; a prerequisite which is difficult to meet in the forest understorey (King 1994). Furthermore, the leaf area ratio declines when plants increase in size, leading to a lower photosynthetic gain on a plant mass basis. Consequently, the whole plant light compensation point increases when plants increase in size (Givinish 1988). If pioneers do not encounter a brighter light environment in due time, they will grow themselves to death. Due to their slow growth, the shade tolerant species will reach this point much later in time, and have a higher likelihood that a gap is formed in the meantime.

Seedling growth is directly related to the way in which species can adjust their morphological and physiological characteristics to the environment. Pioneer and shade tolerant species show clear differences in morphological and physiological traits, with the intermediate species taking positions in-between. LMR, SLA and LAR are lowest for shade tolerant species and highest for light demanding species (**chapter 2**). Pioneer species realise higher relative growth rates than shade tolerant species, under intermediate and high canopy openness levels (**chapter 2**). At intermediate levels, this is due to a high SLA and LAR, whereas at high canopy openness, this is mainly due to a high NAR. A characteristic feature of pioneer species is a high plasticity in several plant traits, which is partly facilitated by their high growth rate. Pioneer species have relatively cheap throwaway leaves with a short leaf lifespan (**chapter 4**). This allows them to shed over shaded leaves in the top of the canopy of the re-growing gap vegetation. Due to their high SLA, high nitrogen content and low fibre content (Coley 1983), they are especially vulnerable to herbivory (*pers obs*.). Conversely, shade tolerant species have highly fibrous and often chemically defended leaves to protect them against herbivores, and a long leaf life span to allow for a return of construction costs of the leaves.

The importance of seed mass in determining shade tolerance

The availability of seed reserves has been reported in the literature as a major influence on seedling germination (Schaal 1980, Weis 1982, Dolan 1984), emergence (Stanton 1984, Yanful & Maun 1996), survival (Schaal 1980, Boot 1996), seedling size (Weis 1982, Boot 1996), and seedling competitive ability (Houssard & Escarré 1991, Boot 1996). However, the present study (**chapter 2 & 3**), reports strong seed mass influences only for a subset of the species, specifically those with seed masses less than 0.05g. With these species removed from the data set, no relation with seed mass is observed. In the field experiments there were no significant effects of seed mass on survival or growth in the field experiment (**chapter 5 & 6**). One reason for this may be the fact that less than 25% of the species encountered had seed masses < 0.05 (Table 1, Chapter 6). This casts some doubts on the general acceptance that seed mass is one of the most important components determining a species shade tolerance.

The idea that shade tolerant species have large seeds and light demanders small seeds goes back at least as far as the classic text of Salisbury (1942). However, dissent from this view has been expressed by Putz & Appanah (1987), Ellison *et al.* (1993), Kelly & Purvis (1993), Grubb (1996) and Grubb & Metcalf (1996). In fact, Metcalf & Grubb (1995) and Grubb (1996) have suggested that most of the smallest seeds (< 1 mg average dry mass) in the tropical Malaysian forests are produced by species that are shade tolerant at the stage of establishment. In contrast to such species, they found that most of the light demanding species that dominate the secondary forest in this region, have dry mass values > 1 mg. The sometimes-contradictory relationship between seed mass and light demand reported in the present study suggests that there is an overlapping spectrum of seed mass values of shade tolerant and light demanding species. That is also what was found by Foster & Janson (1985) for 202 species of trees, shrubs, and lianas at Manu in Peru. They found that pioneers had seed mass values ranging from 7 mg to 58.6 g, and shade tolerant species 1.2 mg to 54.7 g. Although the mean values for the two groups were significantly different, they were of the same order (1.39 and 2.19 g respectively). This certainly leads to the conclusion that although controlled experiments indicate that at the extremes of seed mass (in this case < 0.05 g), there may be strong relations between seed mass and species tolerance to shade, the vast majority of species does not exhibit this trend (**chapter 5 & 6**). There are too many light demanding large seeded species and shade tolerant small seeded species that minimise the importance of a simple seed mass to light demand relation.

What then is the role of seed mass? This study contends that while not relevant for determining shade tolerance, seed mass is still an important trait for seedlings. Small seeds are advantageous in that they allow species to have relatively higher seed production rates. This results in a large number of seeds being available for successful seedling establishment (Harper 1977, Foster 1986). This advantage is enhanced when establishment sites are unpredictably available. In addition to this, small seeds are generally transported farther by wind, and tend to be dispersed by a greater variety of dispersal agents (Foster 1986, Hammond & Brown 1995).

Large seeds on the other hand, can buffer seedlings better against drought (Leishman & Westoby 1994), because the seedlings become deep-rooted more quickly and gain access to a more persistent water supply. Similarly, they can buffer seedlings against losses of capital (leaves, meristems etc.) caused by herbivores (Armstrong & Westoby 1993) or by damage from fallen branches (Clark & Clark 1991), because survival is likely to be related to the absolute size of the undamaged part of the seedling. This maybe one of the reasons why large seeded species are found in higher abundances in the forest understorey (Table 1, Chapter 6).

The importance of gap size

Gap size is said to be the most important characteristic of gaps because it often correlates with biologically functional parameters (Denslow 1980, Turner 1990, Turner & Newton 1990, Denslow & Hartshorn 1994). The environment within a gap is strongly dependent on the size of the gap. The larger the gap, the greater the amount of radiation incident on the forest floor, resulting in higher temperatures and light levels and lower humidity and topsoil moisture. It has been suggested that such microclimatic differences influence the species composition of gap regeneration. In fact, the theories of niche differentiation are all hinged around gap size (Swaine & Whitmore 1988, Turner 1990, Osunkoya *et al.* 1993, Poorter 1998).

Seedling growth is strongly limited by canopy openness. All species increase their growth rates as canopy openness increased (**chapter 2, 3 & 6**). Generally, light availability on the forest floor is between 1-2% of the light above the canopy (Zagt & Werger 1997). Hence, any moderate opening of the canopy will lead to enhanced growth. Most seedlings showed the strongest responses in terms of their relative growth rates between 14 (200 m^2) and 17% (800 m^2) canopy openness and with the exception of 3 species, RGR was highest at 17% (**chapter 2**). This implies that any opening in canopy in this range will allow species to realise higher growth. Any additional opening may lead to a decrease in RGR as observed for some species (**chapter 2**).

When the canopy is opened up, not only will the target species (the economically important species) benefit from this increase in light availability but also the less desirable species (species with no economic value) (Rose 1997). When the canopy is opened up too far, it is likely that desirable species will be overtopped by the inherently fast growing pioneer species or strangled by lianas, which profit most from the increased light availability. Results from **chapter 3** indicate that in the very large gaps, in approximately one month, the pioneer species out compete the more slow growing shade tolerant species, irrespective of the initial size difference. These pioneers will intercept most of the light and continue to respond with vigorous growth, whereas the smaller shade tolerant species will be left behind in the shade. Unless there are some silvicultural interventions, the decreased light availability may lead to mortality of the over shaded plants in the course of time.

Gap partitioning?

Why have so many ecologists been concerned with gap dynamics in forests? One compelling reason is that gap dynamics might promote the coexistence of competing tree species and thus help explain tree diversity (but see Hubbell *et al.* 1999). The question remains however: how much does gap partitioning contribute to the diversity of tree species regenerating in gaps and what path does this partitioning (if it exists) take? The thought behind this concept relies on the fact that most species depend on gaps for regeneration. Hence, they might compete for, and partition gap resources. For example, if light and soil resources vary predictably among gaps (this may also happen within gaps), competition could lead to specialisation by species on different levels of these resources.

Results in **chapter 5** indicate that in the field, seedlings of tree species do not show enough differences in distribution behaviour to suggest that coexistence of many species is maintained via partitioning of gaps. For example, light demanding species often occur in large gaps (**chapter 5**), but most species overlap too much on the gradient of gap size to indicate substantial partitioning. It has been suggested that many tropical studies are not large enough in space, time and number of species to test for this partitioning at appropriate scales (Brokaw & Busing 2000). Zagt & Werger (1998) suggest that partitioning in gaps might operate for certain size classes, for example it may be observed for saplings but not for seedlings and vice versa. In an attempt to correct for these scale problems ecologists working in Central America examined the performance of trees in a range of sizes, over time, and relative to a variety of light and canopy environments in the field (Welden *et al.* 1991, Lieberman *et al.* 1995, Dalling *et al.* 1998, Hubbell *et al.* 1999). However, they recorded very little evidence of partitioning. In **chapter 5**, seedling abundances of light demanding pioneer species, which should seem most sensitive to gap environments, were not directly related to gap size. All these results on populations contradict the hypothesis that species coexistence and diversity are maintained by specific species preferences.

This study suggests that the potential for gap partitioning exists. However, this was found only in the controlled studies where a few species were tested, and seedlings were protected from many of the variables that may act and interact with seedling survival and growth. This finding was not supported by uncontrolled field studies with a much larger suite of species growing in natural conditions. This implies that while controlled experiments can be useful in explaining species specific growth patterns these mechanisms may operate differently in the field and hence these experiments may not be good indicators of field realities.

Some reasons for the lack of partitioning in the field experiment have been discussed in **chapter 5** and will only be briefly mentioned here. One of the most important reasons was suggested to be, the relative size difference when the gap is created, and the suite of species already present. In the tropical rain forest in Sabah, Brown and Whitmore (1992) followed the height growth of three Dipterocarp species after gap formation. After four years, initial height at the time of gap formation was the most important factor explaining seedling survival and growth.

Fast growing light demanding species are potentially able to catch up with taller slow growing shade tolerant species (**chapter 3**), but these species are usually never present at the time a gap is created. In fact, **chapter 5** indicated that there was no significant change in the total species composition in gaps even after four years of regrowth, which indicates that pre-gap rather than post-gap patterns largely determine the species composition in the gaps.

Tilman (1982) has suggested that a trade off may exist between the maximum rate at which a plant may exploit an abundant resource and it's tolerance of that resource's scarcity. If we use that resource in this case to mean gap size (light), then this theory may explain the observed species performances in high and low light environments. As **chapters 2 and 3** indicate, pioneer species have much higher growth rates than shade tolerant species in the larger gaps. This is because of their higher light saturated rates of photosynthesis, which enables them to effectively exploit the available light. However, in the understorey or small gap where light is limiting this high photosynthetic capacity is not an advantage. They cannot maintain a positive carbon balance in the understorey and this ultimately results in the death of these pioneer species.

The carbon balance of a plant is affected by among other things the longevity of this photosynthetic tissue (i.e. the leaf life span). Pioneer species have an inherently high leaf turnover rate (Bongers & Popma 1990, Chapter 4). They must replace lost leaf area at a high rate to sustain growth (King 1994), a pre-requisite that is difficult to meet in the understorey where carbon gain and thus fixation rates are low (Poorter 1999). Consequently, there is a 'trade off' between growth in large gaps and survival in small gaps or the understorey, as suggested already by the results of chapter 2 (see also Hubbell & Foster 1992, Zagt 1997, Poorter 1998).

This trade off has frequently been found (Hubbell 1998, Poorter 1998) and also in this study (Figure 1). It is this trade off coupled with the better species performance that leads to a shifting competitive hierarchy along this gap size gradient. Chapter 3 presents strong evidence for this and the pattern of growth of the three dipterocarp species reported by Whitmore & Brown (1996) and Brown (1996) appears to also confirm this.

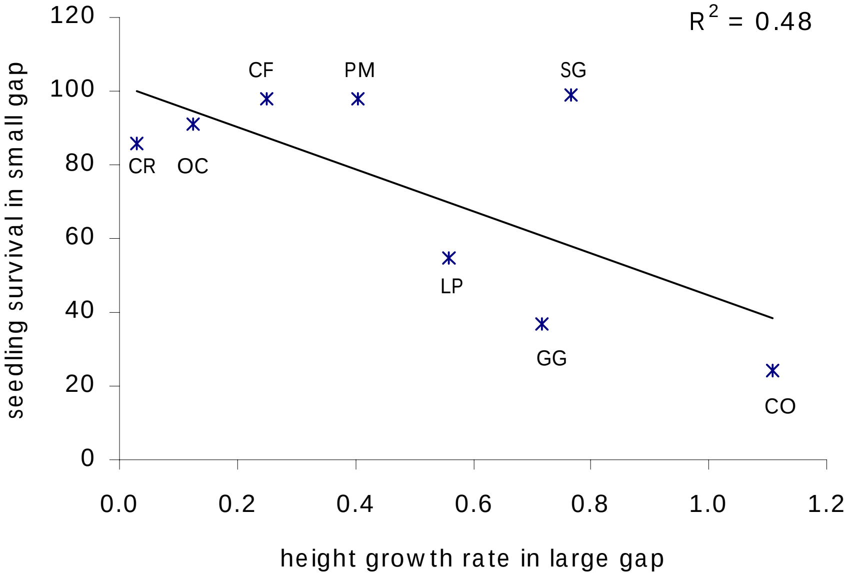

Figure 1 *The relation between seedling height growth rates in a large gap and seedling survival in a small gap. (CF - Catostemma fragrans, CO - Cecropia obtusa, CR - Chlorocardium rodiei, GG - Goupia glabra, LP - Laetia procera, OC - Ormosia coccinea, PM - Pentaclethra macroloba, SG - Sclerolobium guianense)*

Conclusions

This study suggests that most species show their maximum growth rates between 200 - 800 m^2 gap sizes. If the timber species of interest were high light demanding species with appropriate morphological and physiological characteristics for fast growth, then it would perform as well in this gap size range as it would in larger gaps. However, if it is a slow growing species that is adapted to shaded environments the only way it can maintain itself after gap creation is by having a size advantage over the fast growing pioneers. This is possible since these shade tolerant species may already be present in the forest understorey and the light demanding species not. The larger this head start is, the more likely it is that this species becomes the leading dominant in the regrowing gap vegetation. Consequently, damage to seedlings and saplings of desirable species should be kept at a minimum during logging exercises. Further, if the gaps created are larger than 800 m^2, this initial size advantage may quickly disappear in the presence of high pioneer species abundances.

Understanding the mechanisms by which species respond to gaps in tropical forests is essential if these forests are to be managed for repeatable timber extraction. While small controlled experiments may be useful in determining inherent species characteristics, the ability of these experiments to accurately predict species behaviour in the field is quite limited. This study suggests that the only way the 'true' nature of the forest regeneration process will be fully understood is by also undertaking long-term studies under natural field conditions.

Implications for timber harvesting

In their thought provoking article, Brown and Jennings (1999) suggested that instead of searching for species specific growth responses to gap size it would be better to study species performance (establishment and growth) under different conditions of species composition and vegetation structure. This study sought to do both because when silvicultural interventions are being considered it is necessary to know under what conditions will the target species exhibit their maximum performance (in terms of survival and growth) and how these species are likely to perform in the absence of an intervention.

The studies in natural forest (in this thesis) were carried out after reduced impact logging (RIL). Van der Hout (1999) suggests, that while gap sizes between areas that were subjected to RIL and conventional logging (CL) did not differ significantly, damage to the residual stand (especially the seedling bank) and the soil was much higher in the case of CL. Indiscriminate skidder activity as observed in conventional logging (van der Hout 1999) results in a large network of skid trails. The seedling bank, which consists mainly of shade tolerant species, may be destroyed while dormant seeds of pioneer species may benefit strongly from this soil disturbance (Putz 1983, Riéra 1985, Ek 1997). When two areas subjected to RIL and CL were examined, there were almost two times as many pioneer species in the CL areas as compared to the RIL areas (Figure 2). The number of stems of shade tolerant and intermediate species was slightly less in CL areas. These differences in species composition may be directly attributed to the differences in the amount of damage caused by the two methods of logging.

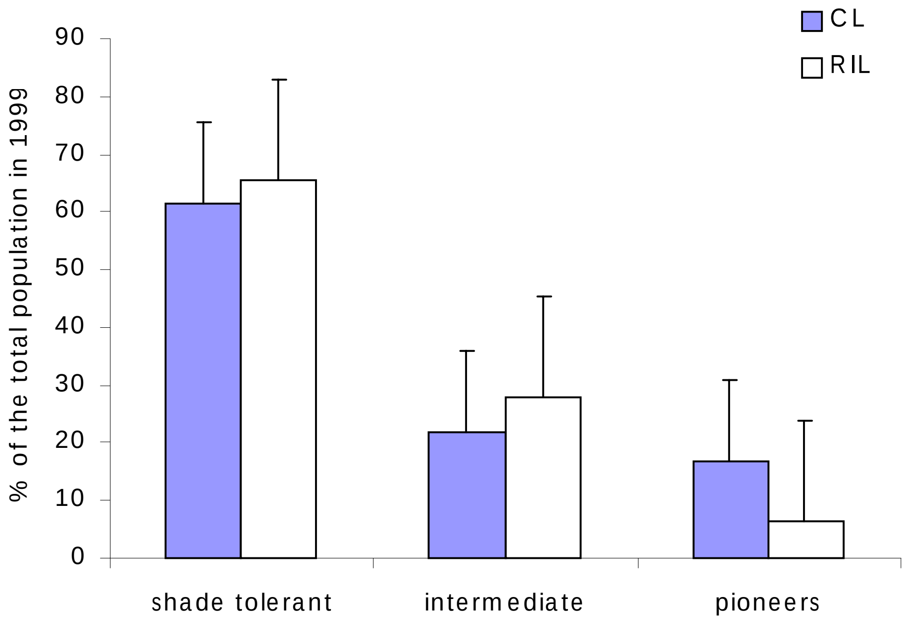

Figure 2 *The species composition of two areas exposed to reduced impact logging (RIL) and conventional logging (CL).*

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SAMENVATTING EN DISCUSSIE

Het centrale thema van deze studie is de relatie tussen de heterogeniteit in de vegetatiestruktuur als gevolg van openingen in het kronendak en het belang van de daarbij behorende heterogeniteit in microklimaat en andere omgevingsfactoren voor de regeneratie van populaties van boomsoorten. Twee onderzoeksvragen volgen uit dit centrale thema. Ten eerste wat is de invloed van de kronendakbedekking en van de zaadmassa's van de boomsoorten op de potentiele regeneratie van die soorten? Ten tweede, in hoeverre verschillen de soorten in hun voorkeur voor een bepaalde grootte van een opening in het kronendak?

Soorten kunnen verschillen in hun aanpassing aan de ruimtelijke variatie in groei-omstandigheden (Ricklefs 1976, Denslow 1980, Bazzaz & Wayne 1994, Ashton 1998, Brown & Jennings 1998, Poorter 1999). Het is bekend dat sommige soorten erg grote openingen nodig hebben om te kunnen groeien en hun levencyclus te vervolmaken. Andere soorten doen het juist ook goed in de ondergroei van het bos. Op deze manier kunnen openingen in het kronendak aan de grote soortsdiversiteit bijdragen, doordat ze bijdragen aan een grote ruimtelijke milieu-heterogeniteit (Hubbell et al 1999, Brokaw & Busing 2000).

Hier kan men tegen inbrengen, dat soorten slechts in beperkte mate gespecialiseerd lijken te zijn op het exploiteren van de verschillende milieu-omstandigheden, die door openingen in het kronendak ontstaan. Men kan verscheidene groepen soorten met onderling overeenkomende ‘omgevingswensen’ onderscheiden, maar binnen deze groepen is het erg moeilijk om verschillen in milieu-eisen vast te stellen. Daarom scheppen openingen in het kronendak slechts beperkte mogelijkheden for kolonisatie. De aanwezigheid van een zaadbank of zaailingbank zijn juist belangrijk voor kolonisatie. Maar omdat zaden zich slechts over beperkte afstanden verspreiden zullen veel zaden de openingen nooit bereiken. Met andere woorden, iedere opening heeft een eigen, verschillende subset van soorten.

Variatie in overleving en groei van zaailingen

De groei van zaailingen neemt toe met toenemende openheid van het kronendak. Dit geldt niet alleen onder gecontroleerde omstandigheden (**hoofdstuk 2 & 3**) maar ook in het veld over een reeks van hele kleine tot grote openingen in het kronendak (**hoofdstuk 6**). De hoogtegroei van de zaailingen is echter veel groter in gecontroleerde experimenten dan in veldexperimenten. De overleving van individuen wordt, in mindere mate, ook door de openheid van het kronendak beinvloed. Sterk en matig schaduwtolerante soorten (definitie in **hoofdstuk 5**) hebben een relatief hoge overlevingsratio in alle kronendakopeningen (**hoofdstuk 2 & 3**). De overleving van lichtbehoevende soorten is veel lager in de ondergroei van het bos en in kleine openingen. De groei-prestaties van planten nemen echter niet altijd onbeperkt toe met de grootte van de openingen in het kronendak – zeer grote openingen in het kronendak leiden tot verminderde groeisnelheden (**hoofdstuk 2**) en bij sommige schaduwtolerante soorten tot verminderde overleving (**hoofdstuk 3**).

Het is de laatste jaren opgevallen, dat lichtbehoevende soorten ook kunnen kiemen en zich ook kunnen vestigen in de donkere ondergroei of in kleine openingen (Raich & Gong 1990, Swaine 1997, Peña 2000). Zij kunnen onder deze omstandigheden echter niet erg lang overleven. Hier zijn verscheidene verklaringen voor aan te voeren. Ten eerste is de schaduwtolerantie van een soort niet zozeer gerelateerd aan de groei maar aan andere factoren die invloed hebben op de overleving. Lichtbehoevende soorten hebben meestal een geringe overleving in de ondergroei omdat ze veel last van vraat hebben (Kitajima 1996). Zij worden ook in hun succes beperkt door hun snelle inherente bladwisseling. Om hun groei te kunnen waarborgen moeten ze verloren blad weer snel aanvullen, iets dat in de ondergroei moeilijk te volbrengen is (King 1994). Daarbij komt nog dat de LAR (bladoppervlak per eenheid plantgewicht) afneemt wanneer de planten in grootte toenemen, hetgeen tot een lagere fotosynthese-opbrengst per eenheid biomassa leidt. Als gevolg hiervan komt het lichtcompensatie punt hoger te liggen als een plant groter wordt (Givnish 1988). Een pionier (sterk lichtbehoevende soort) zal zichzelf doodgroeien in de ondergroei als hij niet op een gegeven moment in lichtere omstandigheden komt te verkeren. Door hun langzame groei bereiken schaduwtolerante soorten dit punt veel later in de tijd en hebben ze meer kans, dat er in de tussentijd een opening in het kronendak onstaat.

De groei van een zaailing is direct afhankelijk van de manier waarop een soort zich in zijn morfologische en fysiologische eigenschappen aan de omgeving kan aanpassen. Pioniers en schaduwtolerante soorten vertonen duidelijke verschillen in hun morfologische en fysiologische eigenschappen en er zijn veel soorten die een positie daartussenin innemen. De LMR (bladmassa per eenheid van plantmassa), SLA (specifiek bladgewicht) en LAR zijn het laagst bij schaduwtolerante soorten en het hoogst bij lichtbehoevende soorten (**hoofdstuk 2**). Pioniers zijn in staat hogere relatieve groeisnelheden onder gemiddelde en hoge licht-intensiteiten te bereiken dan schaduwtolerante soorten (**hoofdstuk 2**). Bij gemiddelde licht-intensiteiten is dit te wijten aan een hoge SLA en LAR, terwijl bij hoge licht-intensiteiten dit vooral aan een hoge NAR (netto assimilatie-snelheid) te wijten is. Een typische eigenschap van pioniers is hun grote plasticiteit in meerdere eigenschappen, gedeeltelijk mogelijk gemaakt door hun hoge groeisnelheid. Pioniers hebben relatief goedkope ‘wegwerpbladeren' met een korte levensduur (**hoofdstuk 4**). Dit stelt ze in staat, om in een snel groeiende vegetatie in een opening in het kronendak, beschaduwde bladeren af te werpen en te vervangen. Met hun hoge SLA, hoge stikstofconcentratie en een laag gehalte aan vezels zijn ze erg vatbaar voor vraat (*pers obs*.). Schaduwtolerante soorten hebben daarentegen sterke, vezelrijke bladeren, vaak met chemische afweerstoffen om hen tegen vraat te beschermen. Om deze hogere investeringkosten te kunnen terugverdienen is de levensduur van die bladeren langer.

Het belang van zaadmassa voor schaduwtolerantie

Zaadreserves zijn belangrijk voor de kieming (Schaal 1980, Weis 1982, Dolan 1984), het opkomen (Stanton 1984, Yanful & Maun 1996), de overleving (Schaal 1980, Boot 1996), de zaailinggrootte (Weis 1982, Boot 1996) en het concurrentie-vermogen van een zaailing (Houssard & Escarré 1991, Boot 1996). In deze studie (**hoofdstukken 2 & 3**) werd echter alleen bij een klein aantal soorten een effect van de zaadmassa gevonden, met name bij soorten met een zaadmassa van minder dan 0.05 g. Behalve voor deze soorten kon er in veldexperimenten geen effect van de zaadmassa op de overleving en groei worden aangetoond (**hoofdstukken 5 & 6**). Misschien dat dit resultaat beinvloed is door het feit dat minder dan 25% van de onderzochte soorten zaadmassa's van minder dan 0.05 g hadden (Table 1, Hoofdstuk 6). Maar het is dus maar de vraag of zaadmassa een van de belangrijkste eigenschappen is die schaduwtolerantie bepalen.

Het idee dat schaduwtolerante soorten grote zaden hebben en lichtbehoevende soorten kleine, gaat terug op een klasieke publikatie van Salisbury (1942). Putz & Appanah (1987), Ellison *et al.* (1993), Kelly & Purvis (1993), Grubb (1996) en

Grubb & Metcalf (1996) hebben kritiek op deze visie geuit. Metcalf & Grubb (1995) en Grubb (1996) vonden zelfs dat de kleinste zaden (< 1 mg gemiddeld drooggewicht) in de tropische regenwouden van Australasia gewoonlijk van schaduwtolerante soorten waren, terwijl de meest lichtminnende soorten zaadmassa's van meer dan 1 mg hadden. Ook in deze studie bleek, dat schaduwtolerante en lichtminnende soorten sterk in zaadmassa's overlappen. Dit is ook gevonden door Foster & Janson (1985) in een studie aan 202 soorten bomen, struiken en lianen in Manu, Peru. Zij vonden dat pioniers zaadmassa's hadden van 7 mg tot 58.6 g hadden, terwijl schaduwtolerante soorten zaadmassa's van 1.2 mg tot 54.7 g hadden. Hoewel de gemiddelden van deze twee groepen significant verschilden (1.39 en 2.19 g voor de twee groepen), waren zij van dezelfde orde van grootte. Hoewel men dus uit gecontroleerde experimenten kan concluderen dat er bij kleine zaden (hier < 0.05 g) een sterk verband is tussen zaadmassa en schaduwtolerantie, volgen de meeste soorten deze trend niet (**hoofdstukken 5 & 6**). Er zijn teveel lichtminnende soorten met grote zaadmassa's en teveel schaduwtolerante soorten met geringe zaadmassa's om een simpel, eenduidig verband tussen zaadmassa en lichtbehoefte vast te stellen.

Wat is dan de betekenis van zaadmassa? Uit dit onderzoek blijkt, dat zaadmassa weliswaar niet relevant is voor het bepalen van de schaduwtolerantie van een soort, maar het heeft wel belangrijke implicaties voor zaailingen. Kleine zaden zijn gunstig in die zin dat de plant grotere aantallen zaden kan produceren, die beschikbaar zijn voor vestiging (Harper 1977, Foster 1986). Dit voordeel is nog groter wanneer de beschikbaarheid van ‘gunstige’ standplaatsen niet te voorspellen is. Verder worden kleine zaden vaak verder door wind of door diverse andere zaadverspreiders getransporteerd (Foster 1986, Hammond & Brown 1995).

Aan de andere kant kunnen grote zaden gunstig zijn bij droogte (Leishman & Westoby 1994), omdat de zaailing snel een diepe wortel kan produceren en zo een betrouwbaarder watervooraad kan aanboren. Ook kunnen de reserves een rol spelen bij het opvangen van verliezen door vraat (Armstrong & Westoby 1993) of schade door vallende takken (Clark & Clark 1991), omdat overleving waarschijnlijk afhangt van de absolute grootte van het deel van de zaailing dat overblijft. Dit zou een van de redenen kunnen zijn waarom soorten met grote zaden in grotere aantallen in de ondergroei worden gevonden (Table 1, Hoofdstuk 6).

Het belang van de grootte van de opening in het kronendak

De grootte van de opening in het kronendak wordt geacht van groot belang te zijn, omdat dit direct verband houdt met biologisch functionele parameters (Denslow 1980, Turner 1990, Turner & Newton 1990, Denslow & Hartshorn 1994). Het microklimaat in een opening wordt in sterke mate door de grootte van de opening bepaald. Hoe groter de opening, hoe groter de hoeveelheid straling die de bodem bereikt. Dit resulteert in hogere temperaturen en lichtwaarden, lagere luchtvochtigheid en minder vocht in de bovenste bodemlaag. Er wordt gespeculeerd dat juist die verschillen in het microklimaat de regeneratie beinvloeden. Alle niche-differentiatie-theorieen zijn daarop gebaseerd (Swaine & Whitmore 1988, Turner 1990, Osunkoya *et al.* 1993, Poorter 1998).

De groei van zaailingen is sterk afhankelijk van de openheid van het kronendak. Alle soorten vertonen hogere groeisnelheden in grotere openingen (**hoofdstukken 2, 3 & 6**). Normaal gesproken is de hoeveelheid licht in de ondergroei 1-2% van het licht boven het kronendak (Zagt & Werger 1997). Dus iedere kleine opening zal tot verhoogde groei leiden. De meeste soorten vertoonden de sterkste respons in hun relatieve groeisnelheid bij 14% (200 m^2) en 17% (800 m^2) openheid van het kronendak en, met uitzondering van 3 soorten, werd de hoogste RGR bij 17% gerealiseerd (**hoofdstuk 2**). Dit betekent dat iedere extra opening tot aan 17% tot verhoogde groei zal leiden. Gaat het kronendak nog verder open, dan kan dit weer tot afname van de groei leiden, zoals bij sommige soorten ook werd waargenomen.

Als er gaten in het kronendak ontstaan profiteren niet alleen de economisch belangrijke houtsoorten (commerciele soorten) van deze lichttoename maar ook de minder gewenste soorten (soorten zonder economische waarde) (Rose 1997). Wanneer het kronendak te veel wordt geopend, zullen de commerciele soorten door sneller groeiende pioniers overschaduwd of door klimmers verstikt worden, omdat die beide groepen soorten het meest van de toegenomen hoeveelheid licht zullen profiteren. Resulaten uit **hoofdstuk 3** laten zien, dat in heel grote openingen de pioniersoorten de climaxsoorten binnen een maand overschaduwen, onafhankelijk van het oorspronkelijke grootteverschil. Deze pioniers zullen het merendeel van het licht invangen en sterk uitgroeien, terwijl de langzamer groeiende climaxsoorten in de schaduw achterblijven. Dit zal voor de climaxsoorten uiteindelijk tot verhoogde mortaliteit leiden, tenzij er bosbouwkundige behandelingen volgen.

'Gap partitioning'?

Waarom houden zo veel ecologen zich met de dynamiek van openingen in het kronendak bezig? Een duidelijke reden is gegeven door het feit dat deze dynamiek de coexistentie van soorten bevordert en dus een verklaring biedt voor soortsdiversiteit (maar zie Hubbell *et al.* 1999). Het blijft echter de vraag hoeveel 'gap partitioning' (waarmee bedoeld wordt dat verschillende soorten zich verschillend specialiseren op de benutting van verschillende milieu-omstandigheden binnen een opening in het kronendak) werkelijk bijdraagt aan de diversiteit van boomsoorten, die opgroeien in openingen in het bos. Ook blijft het de vraag hoe dat dan zou moeten werken. De gedachte achter dat begrip steunt op het feit, dat de meeste soorten voor hun regeneratie afhankelijk zijn van openingen in het kronendak. Het zou kunnen dat ze in die openingen concurreren en uiteindelijk niet allemaal in dezelfde mate dezelfde hulpbronnen gebruiken. Bijvoorbeeld, als lichtbeschikbaarheid en bodemfactoren in openingen voorspelbaar varieren, dan zou concurrentie tot gespecialiseerde benutting van verschillende (niveau’s van deze) hulpbronnen kunnen leiden, die per soort anders is.

De resultaten in **hoofdstuk 5** geven aan dat zaailingen in het veld niet voldoende verschillen in hun voorkomen vertonen om er vanuit te gaan dat de coexistentie van veel soorten door 'partitioning' van de openingen in het kronendak wordt bepaald. Lichtminnende soorten komen, bijvoorbeeld, vaak in grote openingen voor (**hoofdstuk 5**) maar de meeste soorten vertonen te veel overlap over de reeks van openingen van verschillende grootten om 'partitioning' als waarschijnlijk te beschouwen. Het is mogelijk dat de meeste studies niet voldoende ruimte, tijd en individuen in acht nemen om deze hypothese toereikend te toetsen (Brokaw & Busing 2000). Zagt & Werger (1998) denken dat 'partitioning' wellicht van belang is voor bepaalde grootte-klassen. Het is bijvoorbeeld mogelijk, dat het belangrijk is bij jonge boompjes maar niet bij zaailingen en vice versa. Om aan deze schaalproblemen het hoofd te bieden bestudeerden ecologen in Centraal Amerika de groeiprestaties van bomen in diverse grootte-klassen gedurende langere tijd en in een veelvoud van licht- en andere kronendak-omstandigheden (Welden *et al.* 1991, Lieberman *et al.* 1995, Dalling *et al.* 1998, Hubbell *et al.*

1999). Ook zij vonden echter erg weinig bewijs voor 'partitioning'. In **hoofdstuk 5**, bleek dat de dichtheid van zaailingen van lichtminnende pioniers, die het meest gevoelig zouden moeten zijn voor verschillen in omgevingsfactoren, niet direct gerelateerd was met de grootte van de opening in het kronendak. Al deze resultaten spreken de vooronderstelling, dat coexistentie van soorten en diversiteit door soortspeciefieke voorkeuren in relatie tot de grootte van een opening in het kronendak bepaald worden, tegen.

De uitkomsten van deze studie suggereren dat 'partitioning' potentieel toch kan optreden. De aanwijzingen hiervoor werden echter alleen in de gecontroleerde experimenten gevonden, waarin een klein aantal soorten werd getoetst en waarin de zaailingen tegen de vele variabelen, die de groei en overleving van zaailingen kunnen beinvloeden, werden beschermd. Deze aanwijzingen werden niet versterkt door de resultaten van de ‘ongecontroleerde’ veldstudies met een veel groter aantal soorten onder natuurlijke omstandigheden. Het blijkt dus dat, hoewel gecontroleerde experimenten nuttig zijn om soortspecifieke groeipatronen te verklaren, de werking in het veld heel anders kan zijn. Men moet dus concluderen dat zulke experimenten geen goede indicatoren zijn voor de realiteit in het veld.

Een aantal redenen die mogelijk verklaren waarom het veldexperiment geen aanwijzingen voor 'partitioning' opleverde zijn al in **hoofdstuk 5** genoemd en worden hier kort herhaald. Als een van de belangrijkste redenen werd het relatieve grootteverschil tussen de zaailingen op het moment dat de opening in het kronendak gemaakt wordt genoemd en het aantal soorten dat dan al aanwezig is. In het tropisch regenwoud in Sabah volgden Brown en Whitmore (1992) de hoogte-groei van zaailingen van drie soorten Dipterocarpaceae na het openen van het kronendak. Na vier jaar was de beginhoogte van de zaailingen inderdaad de belangrijkste verklarende factor voor de overleving en groei.

Snel groeiende, lichtminnende, soorten zijn mogelijk in staat om grotere, langzaam groeiende zaailingen van schaduwtolerante soorten in te halen (**hoofdstuk 3**). Deze soorten zijn echter vrijwel nooit aanwezig op het moment dat er een opening onstaat. **Hoofdstuk 5** toonde aan dat er geen significante verandering in de soortensamenstelling tot vier jaar na het openen van het kronendak optrad. Dit suggereert, dat de soortensamenstelling van voor het moment van het onstaan van een opening in het kronendak in grote mate bepaalt wat de soortensamenstelling in de opening zal zijn.

Tilman (1982) meent dat er een ‘trade-off’ bestaat tussen de maximale snelheid waarmee een plant een hulpbron kan exploiteren en de tolerantie van de plant voor schaarste van diezelfde hulpbron. Als we nu voor hulpbron hier de grootte van de opening in het kronendak (licht) invullen, dan kan deze theorie de waargenomen verschillen in de prestaties van de zaailingen onder veel en weinig licht mogelijk verklaren. Zoals **hoofdstukken 2 en 3** lieten zien, vertonen pioniersoorten een veel hogere groeisnelheid dan schaduwtolerante soorten. Dit wordt voornamelijk veroorzaakt door de hogere maximale fotosynthese-snelheid van de pioniers, die ze in staat stelt beter gebruik te maken het beschikbare licht. In de ondergroei of in een kleine opening in het kronendak, daar waar licht beperkend is, is deze potentieel hoge maximale fotosynthese-snelheid geen voordeel. Deze snel groeiende soorten kunnen in die omgeving geen positieve koolstofbalans behouden en dit leidt uiteindelijk tot de dood van deze soorten.

De koolstofbalans van een plant wordt onder andere door de levensduur van de bladeren beinvloed. Pioniersoorten hebben een inherent hoge ‘turn-over’ van hun bladeren (Bongers & Popma 1990, **hoofdstuk 4**). Zij moeten het verloren bladoppervlak snel aanvullen om hun snelle groei te kunnen handhaven (King 1994) en, in de ondergroei waar de koolstofopbrengst laag is, dit is moeilijk te volbrengen (Poorter 1999). Er dus een 'trade off' tussen snelle groei onder veel licht en overleving in de ondergroei. De resultaten in **hoofdstuk 2** suggereren dit (zie ook Hubbell & Foster 1992, Zagt 1997, Poorter 1998).

Deze 'trade-off' wordt vaak gevonden (Hubbell 1998, Poorter 1998, deze studie) (Figuur 1). Het is deze 'trade-off' , gekoppeld aan de betere groei-prestaties, die leidt tot een verschuiving in de concurrentie-kracht van de soorten over een gradient van groottes van openingen in het kronendak. **Hoofdstuk 3** presenteert hiervoor goede aanwijzingen en de resultaten van Whitmore & Brown (1996) en Brown (1996) ondersteunen dit.

Conclusies

Deze studie laat zien, dat de meeste soorten hun maximale groei bereiken in openingen in het kronendak tussen de 200 - 800 m^2. Als commerciele houtsoorten

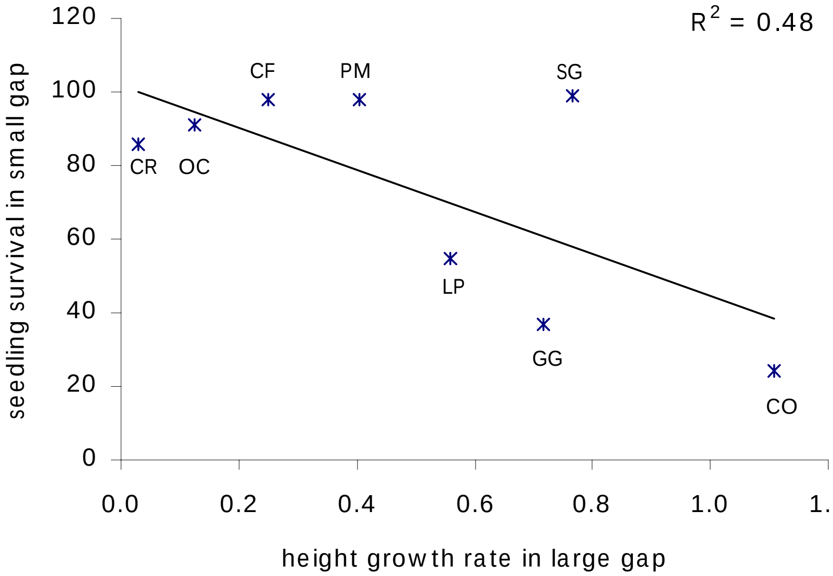

Figure 1 *De relatie tussen hoogtegroei-snelheden van zaailingen in een grote opening in het kronendak en de overleving van zaailingen in een kleine opening. (CF - Catostemma fragrans, CO - Cecropia obtusa, CR - Chlorocardium rodiei, GG - Goupia glabra, LP - Laetia procera, OC - Ormosia coccinea, PM - Pentaclethra*

lichtminnend zouden zijn en ze de daarbij passende morfologische en fysiologische eigenschappen zouden bezitten, dan zouden zij in deze relatief kleine openingen even goed groeien als in grotere openingen. Maar als het langzaam groeiende soorten zijn, aangepast aan de schaduwrijke omstandigheden van de ondergroei, dan kunnen zij zich alleen handhaven wanneer ze bij het onstaan van de opening groter zijn dan de sneller groeiende pioniers. Dit is mogelijk omdat deze schaduwtolerante soorten al in de ondergroei aanwezig zijn, in tegenstelling tot de pioniersoorten. Hoe groter het verschil in grootte, hoe groter de kans dat die soort een overheersende positie in de hergroei in de opening zal krijgen. Dat betekent, dat de schade aan zaailingen tijdens een oogst-operatie zo klein mogelijk gehouden moet worden. Bovendien mogen openingen in het kronendak niet groter dan 800 m^2 zijn, omdat bij grotere openingen het oorspronkelijke verschil in zaailinggrootte snel zal verdwijnen als gevolg van de snelle groei van de pioniers, die zich vestigen.

Goed inzicht in de mechanismen waarmee soorten reageren op openingen in het kronendak is essentieel als we in deze bossen duurzaam hout willen exploiteren. Terwijl kleine gecontroleerde experimenten nuttig zijn om soortspecifieke eigenschappen te bepalen, is de mogelijkheid om met de resultaten van deze experimenten het gedrag van soorten nauwkeurig te voorspellen erg beperkt. De enige manier om goed inzicht te krijgen in de regeneratie van het bos is door ook lang lopende studies, onder natuurlijke omstandigheden, te implementeren.

Implicaties voor de houtkap

In hun stimulerende artikel suggereerden Brown en Jennings (1999) dat het beter zou zijn om, in plaats van te zoeken naar soortspecifieke eigenschappen, de vestiging en groei van soorten te bestuderen in vegetaties van verschillende soortensamenstelling en vegetatiestructuren. Dat is in deze studie juist geprobeerd, want als men bosbouwkundige interventies overweegt, is het nodig te weten onder welke omstandigheden de commerciele soorten optimaal presteren en hoe deze soorten waarschijnlijk zullen reageren bij het uitblijven van zulke interventies.

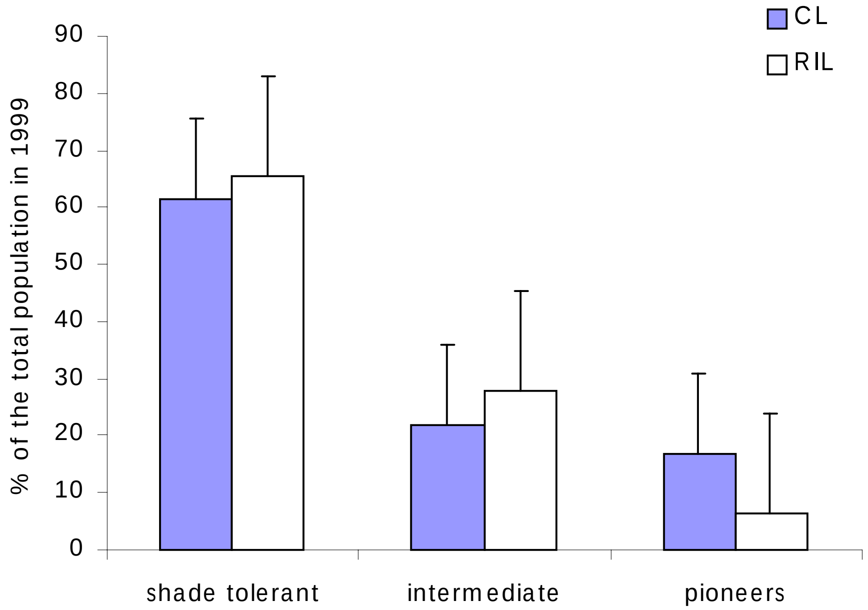

Figure 2. *De soortensamenstelling van twee gebieden waarin schadebeperkende houtkap (RIL) of conventionele houtkap (CL) werd uitgevoerd.*

Het deel van dit onderzoek dat in natuurlijk bos is uitgevoerd, werden gedaan na kap met schadebeperkende maatregelen. Van der Hout (1999) stelde vast, dat de groottes van de openingen in het kronendak in gebieden waar met schade reducerende maatregelen en in gebieden waar conventioneel werd gekapt, niet significant verschilden. De schade aan de overgebleven bomen, en in het bijzonder de zaailingbank en de bodem, was echter veel groter in het geval van conventionele houtkap. Ongeremde activiteiten van de uitsleepvoertuigen (skidders) resulteerden in een dicht netwerk van paden en sleepsporen (van der Hout 1999). De zaailingbank, voornamelijk bestaande uit schaduwtolerante soorten, wordt daarbij over het algemeen zwaar verstoord, terwijl dormante zaden van pioniersoorten sterk van de bodemverstoring kunnen profiteren (Putz 1983, Riéra 1985, Ek 1997). Bij een vergelijking van twee gebieden, waarvan in de een met schade beperkende maatregelen en in de ander conventioneel gekapt is, valt op, dat er in het conventionele deel bijna twee maal zoveel pioniers voorkomen (Figuur 2). Het aantal individuen van schaduwtolerante soorten is iets minder in het conventionele deel. Deze verschillen in soortensamenstelling kunnen in direct verband worden gebracht met de verschillen in schade veroorzaakt door de twee methodes.

"The clearest way into the universe is through a forest wilderness"
John of the Mountain 1938

Acknowledgements

"It's not an easy road
Many see de glamour an' de glitter so dem think a' bed a' rose
Me seh who feels it knows
Ooooooooh, lawd help me sustain these blows"

Not an easy road ('til Shiloh) – Buju Banton

The road that led me to Mabura, Pibiri and then to the Netherlands was certainly not an easy one. However, there were many people along the way, who made my life and work over the last four years an unforgettable and rewarding experience. In January 1996, I became a member of the Tropenbos-Guyana 'family'. The road into this family was paved for me by Drs. George Walcott, Thijs Pons and Hans ter Steege. Their confidence in my ability to undertake the study and their unstinting support and encouragement were greatly appreciated, and to these persons I would like to express my heartfelt gratitude! The exhaustive discussions that sets in motion all ecological studies are designed to give shape and direction to the study. Hans ter Steege, Thijs Pons and Peter van der Hout provided invaluable advice and support during this phase. I am grateful for their knowledgeable guidance in the experimental designs, plot selection and sampling techniques.

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Thank you for everything! Bedankt voor alles!!!

Curriculum Vitae

I was born on the 7th April 1972 in Cumberland Berbice. I attended St. Agnes Primary School until 1982 and then obtained my secondary education at St. Stanislaus' College. In 1988, I commenced studies for a Bachelor of Science degree at the University of Guyana, majoring in Biology with Chemistry as a minor. During these four years I was introduced to plant taxonomy, plant physiology and plant ecology. In 1992, I was admitted to study for the Master of Science degree in Forest Biology, also at the University of Guyana. This programme was a collaborative effort between the Department of Biology and the Tropenbos-Guyana Programme. This programme provided me with my first forest experiences and an opportunity to undertake research in the tropical rain forest in central Guyana. I focussed specifically on the temporal variation of light, temperature, humidity and recovery in man-made gaps. From January until June of 1995, I was an assistant researcher at INRA - Institut National de la Recherché Agronomique - Kourou French Guiana. In January 1996, I begun work f or my PhD thesis as part of the Tropenbos Guyana Programme and the Department of Plant Ecology, Utrecht University.