Foreword

Guyana and its neighbouring countries, Suriname and French Guiana are still endowed with large tracts of undisturbed forest, experiencing among the lowest deforestation rates in the world (Lanly 1982, Luning 1987, Burgess 1993, Bryant *et al.* 1997). Guyana is at crossroads where utilisation, conservation and preservation of its forests are concerned. As a country with little industry but rich in natural resources, the Government of Guyana has a need to exploit its natural resources for the development of the country and its people. The Government of Guyana has expressed its intention to do this in a sustainable manner (Chandarpal 1997, Ministry of Finance 1996). To effectuate this, large tracts of forest (approximately 4.5 million ha) have recently (1997) been designated as State Forest Lands and are available as exploratory concessions (no logging in the first two/three years). In addition, the granting of exploratory mining concessions is considered over large stretches of the country.

In 1998 the Tropenbos-Guyana Programme started with a project named "Conservation and Sustainable Use of Botanical Diversity in Guyana". In one subproject the aim was to collect and synthesise all information that was available on plant diversity in Guyana and potential effects of management thereupon. The first part of this sub-project was structured in such a way that it supported the process of the National Protected Area Strategy of Guyana as much as possible and worked closely together with the Environmental Protection Agency of Guyana and the Guyana Forestry Commission.

The second part of this sub-project started initially with data mainly from Guyana but was later expanded when in March 2001 we organised a workshop for and funded by the Utrecht University and the Tropenbos Foundation called "Changes in Forest Composition and Diversity". Emphasis was placed on long-term studies and studies that highlighted some of the mechanisms behind observed changes.

Our approach in the studies in the Guiana Shield was to use functional groups, based on a few life-history characteristics of species, notably wood density and seed size, and to a lesser degree dispersal. We asked our other contributors to take a similar approach.

The book that lies before you is the result of the efforts of the contributors to that workshop, which are listed at the end of this chapter.

bit more which has resulted in an extra chapter with a mathematical basis for the disturbance theories used.

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1   INTRODUCTION

Hans ter Steege

Introduction

Biodiversity is considered to be an important property of nature, especially in the context of the destruction and disturbance of the environment of which we, humans, are part. Due to the alteration and destruction of habitat the decline in species diversity proceeds at a rate that is considered unprecedented in geological history. This may threaten our very own survival on the planet.

Evolutionary biologists and ecologists are fascinated by the mechanisms determining the biological diversity of ecosystems. This has resulted in well-substantiated theories that explain part of the variation in diversity observed. However, clear and concise knowledge of the patterns of diversity and the processes regulating it is not yet operational. Ecologists and evolutionary biologists study diversity at different scales and what is becoming very clear at present is that scale is an important bridging element between theories.

In short, diversity is influenced by regional as well as local processes (Ricklefs & Schluter 1993, Rosenzweig 1995 but see Huston 1999), all operating at specific time-scales (Figure 1.1).
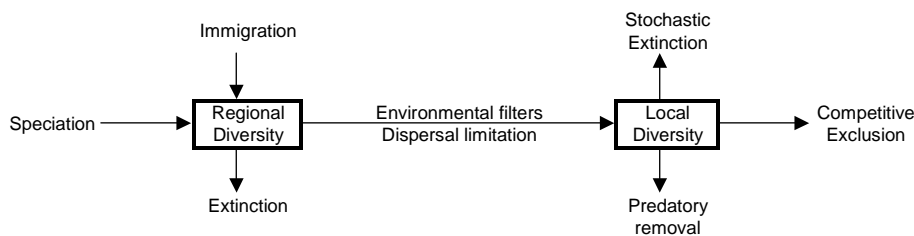
Figure 1.1   Diversity is influenced by regional and local processes (after Ricklefs & Schluter 1993, Hubbell 2001).

At large spatial and temporal scales, evolution is a main driving force behind diversity. Equilibrium in the rates of speciation and extinction determines to a large extent the size of the so-called 'regional species pool' (Rosenzweig 1995, Hubbell 2001). Understanding how geography, climate, and the species-specific life-history characteristics influence these rates is of crucial importance in understanding patterns of diversity.

At a more local level, which is the focus of this book, the regional species pool arguably determines the limits of local diversity but environmental filters or assembly rules (Keddy 1992) and local processes, such as predator-prey interactions

and competitive exclusion, also have a strong influence on the variation in diversity at this level (Figure 1.1).

Competitive exclusion, whereby species are removed from the community due to competition with better-adapted species has a negative effect on community diversity (Figure 1.1). The avoidance of competitive exclusion thus should result in maintenance of higher diversity. This could either be achieved by frequency-dependent mortality, whereby the most common species suffers most mortality or by disturbance.

Forests are not static entities and are disturbed continuously. Tree falls change the local environment, while larger disturbances such as storm damage are not uncommon. Even larger disturbances, such as caused by earthquakes, landslides and hurricanes are now known to have shaped many forest communities. Forest dynamics is thought to have a profound effect on species diversity. One hypothesis suggests that diversity peaks at "intermediate" levels of disturbance (Connell 1978) or productivity (reviews in: Huston 1979, 1994, Rosenzweig 1995).

The Intermediate Disturbance Hypothesis
The intermediate disturbance hypothesis (IDH) of Connell (1978) offers a suitable framework for the study of the effects of disturbance on species diversity in ecosystems (Figure 1.2). The theory is based on the assumption that in all systems superior competitors will exclude competitively inferior species up to a point that eventually just one or few species are left. Such species-poor communities are not rare, even among tropical forests (Richards 1952, Connell and Lowman 1989, Hart *et al*. 1989). When a community is disturbed space is created for other species to establish. After disturbance the community goes through a succession where the intermediate stages are thought to have the highest diversity. Finally, 'superior competitors' would exclude most other species and, in theory, would produce near single species stands. Intuitively, high diversity is expected not only in the middle part of a succession but also when disturbance are neither too frequent nor infrequent, and when disturbance are neither too large nor too small (Figure 1.2, but see chapter 9).

Huston (1979, 1994) later expanded the IDH into the 'dynamic equilibrium hypothesis' (DEH, Figure 1.3), that predicts that the highest diversity will be found where disturbance and population growth are in 'optimal' balance. Hence the optimum is not only dependent on the size and frequency of the disturbance but also on a general community growth parameter. When disturbance is greater (or more frequent) than their minimum regeneration time, populations of slow-growing species will no longer be able to recover from disturbance and fast growing (pioneer or r-type) species will prevail. Under low disturbance regimes the most competitive (climax or k-type) species will competitively exclude all other species. The species that will finally dominate the two low-diversity ends of the continuum predictably differ in a number of key characteristics associated with the varying environmental conditions (Huston & Smith 1987, Swaine & Whitmore 1988, Huston 1994), caused by trade-offs discussed below.

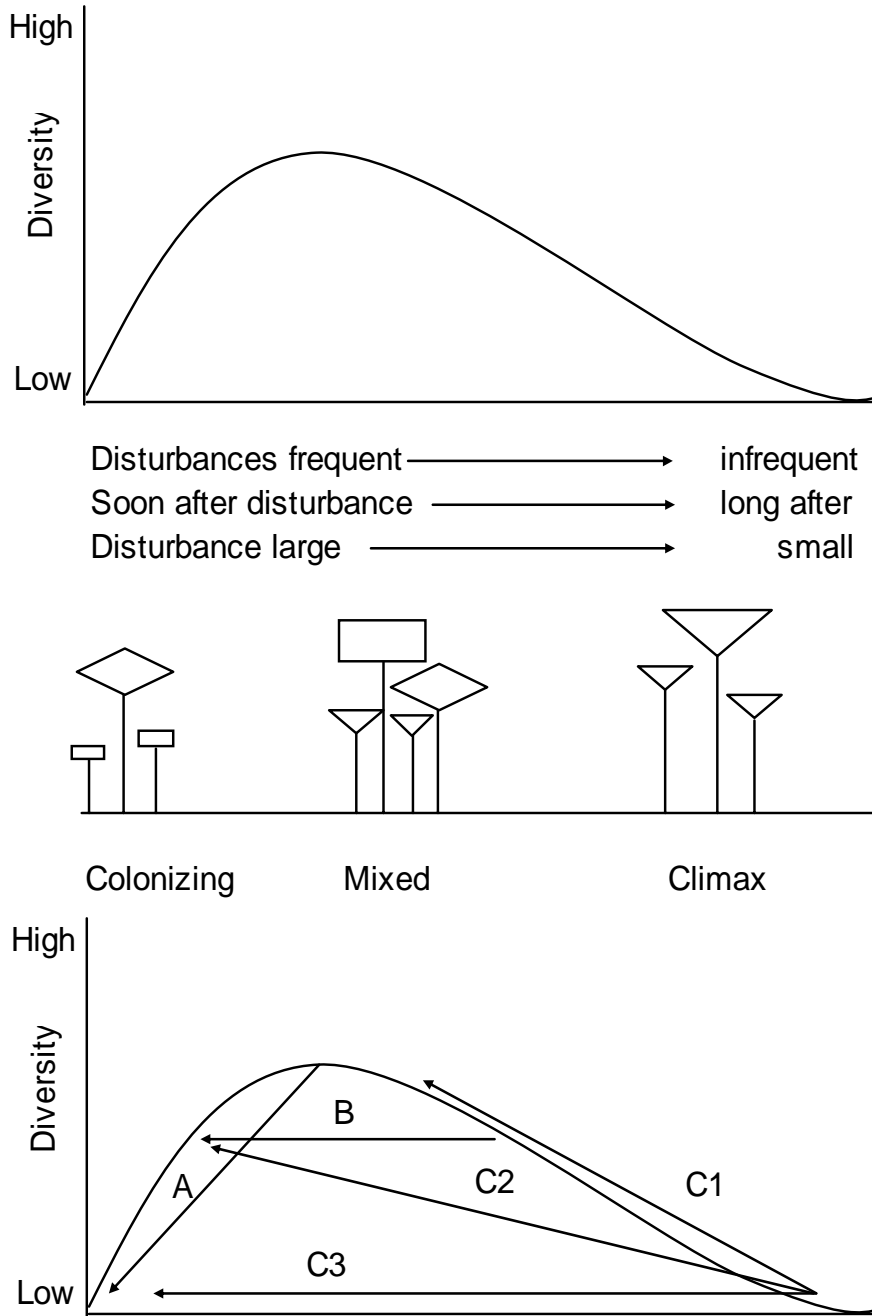Figure 1.2 The Intermediate Disturbance Hypothesis (Connell 1978). Above: Diversity is low after disturbance, especially large ones and in areas with continuous disturbance, highest in the intermediate stages and lowest in 'undisturbed' climax forest. Middle: types of forest Bottom: Depending on the successional stage of a forest, disturbance can lead to lower diversity (A), equal diversity (B, C3), higher diversity (C1, C2).
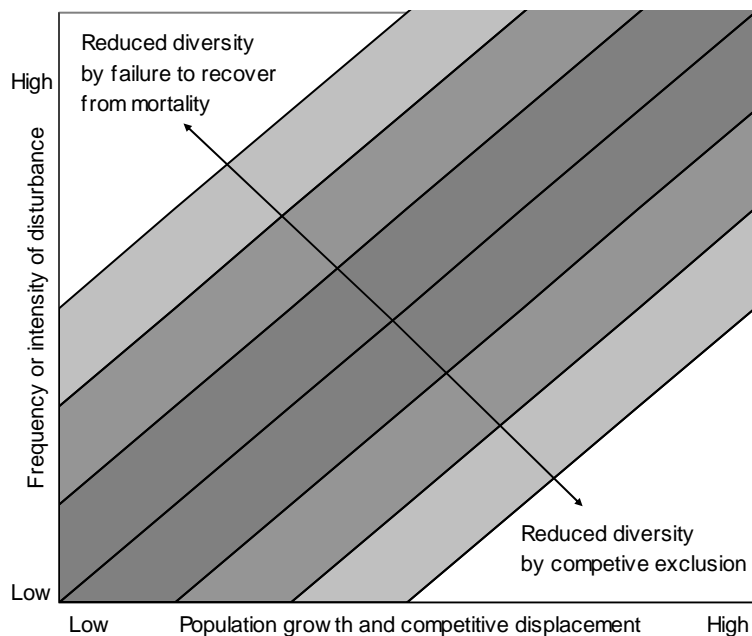
Figure 1.3   The Dynamic Equilibrium Hypothesis (Huston 1979, 1994). Diversity is influenced by disturbance and population growth/competitive exclusion and can be reduced by both. Diversity is highest where neither process dominates (Huston 1994).

Recent tests of the IDH have led to acceptance (Molino & Sabatier 2001) or rejection (Hubbell *et al.* 1999) of the theory. The theory has been used at very small scales (Molino & Sabatier 2001) and very large scales (ter Steege & Hammond 2001). A very up to date discussion can be found in Sheil & Burslem (2003).

Disturbance and productivity are not uniform throughout the tropics and spatial variation in tree diversity as a response to changes in these key environmental factors is predicted by the dynamic equilibrium hypothesis (Huston 1979). Not all tropical forest communities show particularly high tree alpha-diversity (Richards 1952, Connell and Lowman 1989, Hart *et al.* 1989) and low diversity typifies forests in central Guyana (e.g. Richards 1952, Fanshawe 1952, ter Steege et al. 1993, Johnston and Gillman 1995, ter Steege 1998a, ter Steege *et al.* 2003), central Africa (Hart *et* al. 1989) and Borneo (Richards 1996). Forests in the hurricane belt are potentially forest with low diversity due to relatively frequent high disturbance.

Selection on species can take place at two levels. Firstly at the individual level where certain species germinate and grow well in new and large gaps in forest and other seedlings show best establishment and recruitment in small gaps and forest understorey (see below). Secondly, character convergence may take place among species at the ecosystem level (Lugo & Scatena 1997, ter Steege & Hammond

2001). In highly disturbed ecosystems, such as forests regularly visited by hurricanes, selection will place a premium on species that grow fast and reproduce at an early age, while in contrast in ecosystems with very low levels of disturbance, longevity and shade tolerance will be the selected characteristics.

In addition to natural disturbance, human interference, which may also range from very small-scale, such as NTFP collecting, through slash and burn agriculture and small-scale timber harvesting, to clear-felling and forest conversion, has an effect perhaps similar or additive to what is naturally occurring.

Logging mimics natural disturbance in the fact that it removes biomass from the tree community. There are differences, too. The scale and intensity of the disturbance caused by logging may be different than those characterising natural disturbance. Logging, even when it disturbs small patches will affect large parts of forest landscapes at the same time, while natural disturbance except for the largest (fire, hurricanes) will affect smaller parts of the forest landscape at a time. Logging may be different from natural disturbance in its selectivity: certain species, often belonging to similar ecological groups, will be more affected than others. Logging damage, on the other hand, may be random like in natural disturbance. Unlike most forms of natural disturbance, logging creates new habitats if it is carried out by machinery that compacts the soil. Finally, logging and human presence affects animal populations on which trees depend, and logging may only be the start of intensified human interference with the forest. In the concepts presented below and throughout this book, the latter two aspects are not considered explicitly. Here, we are concerned with what happens to the composition of forest communities in areas that are managed for timber.

An interesting challenge now is to interpret exogenous disturbance as caused by logging into the IDH/DEH concept. Communities that have adapted to low disturbance will show different successional trajectories after the same type of logging than communities that have adapted to high disturbance, because the ecological characteristics of the species that constitute the community will be different. While we expect that the successional trend will be structurally similar, we expect differences in the rate and species composition of these successions.

So a main question will be: How is tree community composition affected by a disturbance event and what is the difference in response between natural disturbance and logging?

A second question we have to answer before this is how actually such changes can be measured in forest communities?

Monitoring change vs. implied succession of changes

Changes in forest composition and/or biodiversity can be effectively monitored by permanent sample plots (PSP). If such plots were installed before intervention took

place there we can measure the direct effect of the intervention and the following changes. In many cases control plots are necessary for comparison with un-affected, but also dynamic, changing forest. A study where the same plots are censused several times over a period of time is often referred to as a time study.

Due to the high longevity of forest trees, their slow growth and turn-over, and consequently slow chain of events, which may run over the course of decades to a few hundred years, PSP's may not give answers in time. Chronosequences may provide an alternative way of assessing changes. A chronosequence can be defined as an assumed succession of plots – plots that can be ordered in time since a comparable intervention took place. Because interventions, such as slash and burn or larger-scale clearing have taken place continuously throughout history, the use of chronosequences is mainly limited by our ability to date previous disturbances and by the spatial variability in succession trajectories.

Diversity is a challenge

In many of these and other studies, diversity poses a challenge: only a few species are common and most species are rare (Figure 1.4). Thus, for the majority of species it will not be possible to obtain any statistically significant data in field plots of the size generally used for this type of studies. The form of the rank abundance curves is universal (Hubbell 2001) and theory suggests (and practice shows) that if plot size or sample size increase, rare species become even rarer. In practice this implies that
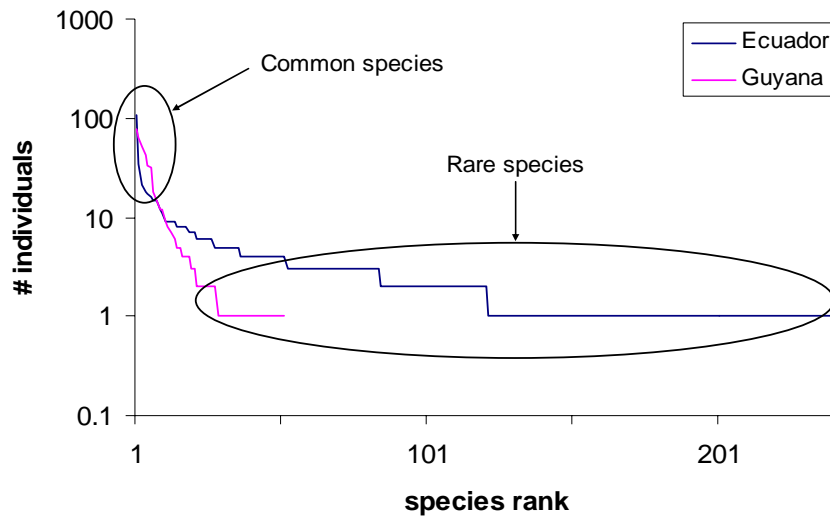

Figure 1.4   Rank abundance curve for a species-poor plot in Guyana (R. Zagt unpublished data) and a species-rich plot in Ecuador (Balsev *et al*. 1987). In both cases, but especially in the species rich case, the majority of the species is very rare at plot level.

much of our knowledge of species responses in tropical rain forest is based on the behaviour and study of just a few tree species (Turner 2001).

Another complicating factor is the way we describe diversity, a complete ecosystem with all its species, interactions and values compressed into one number. This number could simply be species richness, the number of species in a plot or larger area, or a more refined "information index" that takes the distribution of species over abundance classes into account, such as the Shannon index or Fisher's α (Magurran 1988). At present we have no information on the sensitivity of such measurements in forests that are subject to disturbance and change.

Functional Groups – a way out?

Classifying species into groups that behave similarly in ecological sense, so-called functional groups, has been suggested as a way out of this problem. This method has been used with some success in modelling changes in forest a result of climate change or human interventions.

Grouping species simplifies the system by reducing the number of distinct behavioural units and, as a result of that, it enlarges the number of individuals for each unit at the expense of resolution in ecological responses. A first and long standing plant functional type division is the one described by Swaine and Whitmore (1988) – pioneers vs. climax (Table 1.1). With simple rules based on this division, a simple succession can 'accurately' be modelled (see e.g. Huston and Smith 1989, Huston 1994).

Several classifications have been proposed e.g. Grime (1974, CSR: Competitor-Stress Tolerator-Ruderal), Swaine & Whitmore (1988, pioneers vs. climax), Condit *et al.* (1996a), Westoby (1998, LHS: Leaf-Height-Seed), Gitay *et al.* (1999: Seed – Growth), Turner (2001). Each of these classifications is based (at least partially) on the replacement of individuals based on competition for space and light, which is very relevant when disturbance is being discussed. It is obvious that, when other ecological phenomena are being investigated functional groups will be different all together (e.g. nitrogen-fixers vs. non nitrogen-fixers). This requires an analysis of those functional aspects of plant life which are relevant for disturbance or rather regeneration.

Weiher *et al.* (1999) discuss in detail the merits of functional classifications and suggest that all plants face identical challenges, which can be summarised into dispersal, establishment and persistence. Each of these challenges are characterised by one of a number of life history characteristics on which selection can take place and which are often characterised by well-known trade-offs (Table 1.2). In dispersal the best known trade-off is that of seed size and seed numbers (Smith & Fretwell 1974). With limited resources to invest in the production of seeds, plants must find a balance between producing a few large seeds or many small seeds. Seed mass is also of importance for subsequent seedling growth. Seed mass is very well correlated

Table 1.1.   The classic Pioneer- Climax dichotomy of tropical trees (Swaine & Whitmore 1987)

	Pioneer	**Climax**
Alternative name	Light-demander, (shade-) intolerant, secondary, vagrants, nomads	Shade-bearer, (shade-) tolerant, primary, dryads
Germination	In gaps, receiving full sunlight, influenced by RFR, and temperature fluctuations	Usually under shade
Seedlings	Low survival in shade	Sufficient survival to form seedling banks
Seeds	Small, produced in large amounts	Large, produced in much smaller amounts
Seed longevity	Usually long, many species in seedbank	Short, few species in seedbank
Dispersal	Wind, birds, bats	Variable, also unassisted, gravity
Dormancy	Yes, possible	Germination usually immediate
Growth rate	Max A, NAR, and RGR high, high plasticity	Lower, low plasticity
Light compensation point	High	Lower
Height growth	Fast	Slow
Branching	Sparse	Often copious
Growth periodicity	Indeterminate, no resting buds	Determinate, with resting buds
Leaf life	Short, high turn-over	Long, slow turn-over
Leaf defence	Low, high herbivory	High (chemical, structural), herbivory low
Wood	Low density, not silicious	Low to high density, sometime silicious, sometimes rich in alkaloids
Ecological range	Wide	Sometimes narrow
Stand table	Negative	Positive
Longevity	Short	Long
Maximum adult size	Low	High

with several aspects of seedling growth. Larger seeds produce larger seedlings with greater structural mass and lower RGR, LAR (leaf area ratio) and SLA (Kitajima 1994, Osunkoya *et al*. 1994, ter Steege 1994). Seed mass also influences shade tolerance (Hart *et al*. 1989, Hammond and Brown 1995). This results in a well-known trade-off of high growth in high light vs. survival in shade (Hubbell 1998). Fast growth, small adult size (and copious small seeds) characterise one end of the pioneer-climax continuum. Slow growth, large adult size (and few large seeds) characterise the other end. It is obvious that these trade-offs were also the basis for the pioneer-climax dichotomy of Swaine & Whitmore (1987, Table 1.1 above). When classifying large sets of species it has become obvious that a dichotomy is too simple but that species can very well be ordered along these trade-offs, for example the "fast growth in light – low mortality in shade trade-off" (Hubbell 1998, 2001).

Based on the above, three soft traits emerge, as being of value for many 'challenges' faced by trees. These are seed mass, specific leaf area, stem density, providing information on dispersal, growth and persistence.

Table 1.2. Common challenges as faced by trees and some suggested traits. The hard traits are in fact the life-history characteristics we are interested in but that are hard to measure (expensive, time-consuming). The soft traits are more easily measured traits that are thought to correspond well with the hard traits for which they are listed (modified after Weiher *et al*. 1999).

Challenge	Hard trait	Soft trait
Dispersal		
in space	Distance	Seed mass; dispersal mode
in time	Propagule longevity	Seed mass; seed shape
Establishment		
Seedling growth	Relative Growth Rate	Seed mass; SLA[1]; LWC[2]
Sapling/adult growth	Growth Rate	Wood density
Persistence		
Seedling persistence	Shade tolerance	Seed mass
Seed production	Fecundity	Seed mass
Competitive ability	Competition	Height
Longevity	Life span	Wood density
Plasticity	plasticity	SLA; LWC
Acquisition of space	Vegetative spread	Clonality
Resistance	Palatability	SLA; LWC

[1] Specific Leaf Area
[2] Leaf Water Content

The importance of seed size – a simple model

Seed size ranges seven orders of magnitude in some rain forests (Hammond & Brown 1995, ter Steege & Hammond 2001). How would the 'high light growth low shade mortality' trade-off work out in a dynamic environment? Whereas seedling size and residence time may determine the success of seedlings in the understorey and small gaps in tropical rain forests, the ability to increase relative growth rate (RGR) under high light conditions may determine to a large extent success in large gaps (Boot 1996, ter Steege & Hammond 1996). This is shown in Figure 1.5.

This simple model (only based on growth) predicts that under low light seedlings of large seeded species will start off with larger initial size. Due to low growth rates of seedlings of small seeded species under these circumstances, the seedlings of the large seeded species will be able to keep their initial advantage. High mortality among the small seeded species will further tip the balance in favour of the large seeded species. Under high light conditions, however, the higher RGR of seedlings of small seeded species allows these species to overtake that seedlings of the large seeded species that are not capable of increasing their growth rate much.

Thus seed mass may be one reasonable estimator of the place of a species in the continuum of regeneration strategies and we expect to find a high relative abundance of seedlings of small seeded species in new, large openings, early stages of primary succession and a preponderance of such species in highly disturbed or dynamic
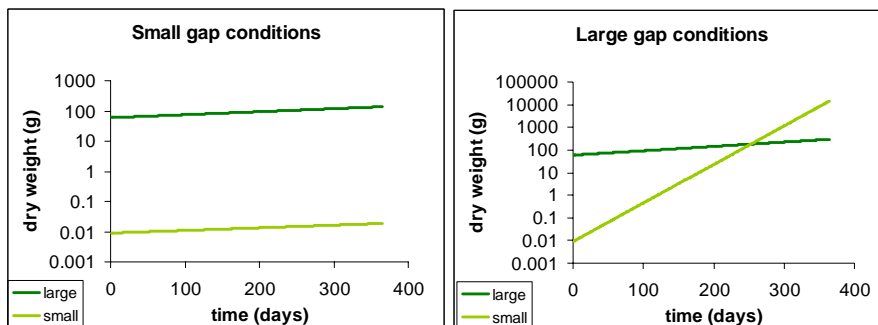
Figure 1.5   Modelled growth of shade tolerant, large seeded, *Mora gonggrijpii* (ter Steege 1993) and small seeded, pioneer species *Cecropia obtusa* (Boot 1995), based on seed weight and RGR. Under dark conditions RGR of both species is similarly low but the due to its large seed mass *Mora* seedlings attain more weight and height. Due to higher survival rates, the large-seeded species is likely to outlast the small-seeded species. Under equal high light conditions the small-seeded species is capable of increasing its RGR much more than the large-seeded species and eventually overcomes its initial size disadvantage. Based on a conceptual model of Boot (1996).

areas. We also expect timber harvesting, which results in more and larger gaps and higher forest dynamics to cause an increase in small seeded species at the expense of large seeded ones.

From this we derive one of our first working hypotheses: in highly disturbed systems the proportion of small seeded species will be large and disturbance in most systems will result in an increase in the smaller seeded species of that system.

The importance of wood density – another simple model
Seed size is unlikely to have a large influence on growth of larger woody individuals but wood density (or stem density) will (ter Steege & Hammond 1996, 2001). We suggested earlier (ter Steege and Hammond 1996, Figure 1.6) that increasing disturbance rates should have a significant effect on the recruitment of slower-growing species. Individuals that reside in smaller size classes for longer periods, due to slow growth, are more likely to die in tree fall events (see Clarke & Clarke 1991) and they are thus less likely to reach reproductive sizes. The simple model of Figure 1.6 also suggests that an increase in mortality will affect the slower growing species more than the faster growing species.

The advantages given to fast-growing trees in a highly disturbed environment suggests that wood density, as a measure of long-term growth performance, may also be a proximate measure of the place of a species in the continuum of regeneration strategies. From this we derive our second working hypothesis: We expect a higher proportion of soft wooded species in early successional stages and more dynamic environments. We also expect to see an increase of soft wooded species at the expense of hard wooded species in areas that have been harvested for periods of time.
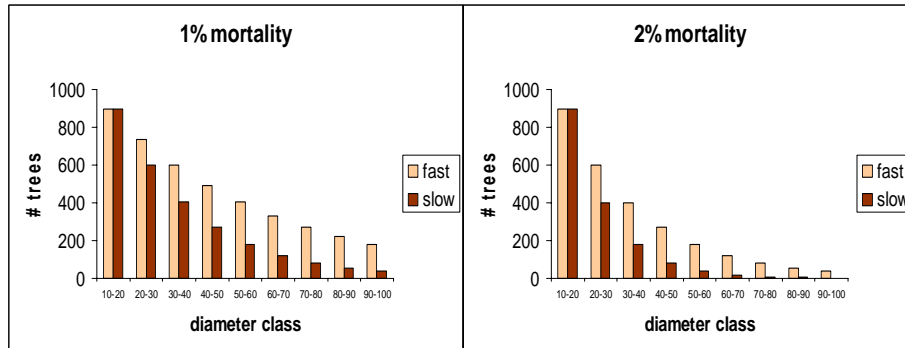
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Figure 1.6   Modelled size class distributions of a slow (2.5 mm/y, solid bars) and fast grower (5 mm/y, open bars) based on fixed mortality rates. An increase in mortality from 1 to 2%, as could be caused by logging and silvicultural treatments, may have a 60% larger effect on the slow growing species.

Like large seed weight, a large stem size and long lifespan are typical of climax species (Huston and Smith 1987, Table 1.1). Maximum height and diameter are therefore important characters in functional classifications of both temperate (Brzeziecki and Kienast 1994) and tropical (Favrichon 1994) trees.

Based on this a preferred list of soft traits for tropical trees would include:

1.   Seed mass; which can easily be obtained from many tropical flora's; Is relatively constant within a genus (Casper *et al*. 1992, ter Steege & Hammond 2001); and relates to several trade offs or life cycle processes.
2.   Wood density; for which also large databases are available; relatively constant within genus but some (large) genera are very variable (e.g. *Ocotea*, *Shorea*)
3.   Adult size; Can in some cases be found in regional flora's or derived from large PSP sets.

and (Weiher *et al*. 1999):

4.   SLA or LWC; which provides better proxy information for maximum RGR of seedlings than does seed mass but is not available for many species and highly variable.

Wood density and seed mass as prime traits for TRF trees
With the classic scheme of Swaine and Whitmore or the above suite of important traits it is still difficult to actually classify species and many people have classified pioneers and climax species subjectively on the basis of circular field observations (pioneers occur in secondary forests – secondary forests are composed of pioneers).

To make a subdivision more 'objective', ter Steege *et al*. (2002, Chapter 8) looked at classifications of Finegan (1996) and Favrichon (1994) and observed that all species

classified as pioneers had an air-dry wood density below 700 kg m^{-3}. This was then used as the difference between softwoods and Hardwood species (HWD, most climax species fell into this class). Among the pioneers the so-called short lived pioneers tended to have the smallest seeds (< 0.1 g). They then classified as Small Seeded Softwoods (SSW, most short lived pioneers fell into this class) and as Large Seeded Softwoods (LSW, most long lived pioneers fell into this class) on the basis of their seed mass (Hammond and Brown 1995, ter Steege and Hammond 2001). Because of the fixed classifications some trees 'switched' class. The three functional groups thus derived can be summarised as:

1.   SSW: wood density < 0.7 g cm^{-3}, seed mass < 0.1 g
2.   LSW: wood density < 0.7 g cm^{-3}, seed mass ≥ 0.1 g
3.   HWD: wood density ≥ 0.7 g cm^{-3}

All species regardless of their previous classification or behaviour could then be classified according to this objective scheme.

Where ter Steege *et al*. (Chapters 5, 8) used a wood density of 0.7 g cm^{-3} as class boundary, Arets *et* al. (Chapter 6) used 0.8 g cm^{-3} and Verburg & van Bos-Eijk (Chapter 7) used three classes (0.4 and 0.7 g cm^{-3}). In addition to that the latter could not use seed mass due to low data availability but did use maximum adult tree height, for which data was readily available. Thus, although the final classification is objective, the selection of the class boundaries is still a subjective choice. However, as the classification is based on theoretical considerations and made on forehand it can be tested with experimental field data. Using field performance of species to classify them (e.g. Favrichon 1994), prevents the possibility of validating that classification with the field data. In addition to that the classification is not based on theoretical considerations but on behaviour of individuals and their interaction with other individuals and can thus not be extrapolated to other species.

Set up of the book

This book consists of the reports of a number of studies that take a long term view of forest disturbance and its effects on composition and diversity. The authors of the papers were asked to use wood density and seed size as potential life history characteristics on which to base functional groups (if possible). Locations of a number of such studies, used as examples in this book, are found in Figure 1.7 and listed below:

1.   Barama/Pibiri NW and Central Guyana, Arets *et al*. (Chapter 6). Bartica, Guyana (mixed), ter Steege *et al*. (Chapter 8).
2.   Mapane, Kabo, Suriname (PSP's), ter Steege *et al*. (Chapter 5).
3.   Budongo, Uganda (chrono-seq.; time study), Sheil (Chapter 3).
4.   ITCI, Borneo (PSP's), Verburg & van Eijk-Bos (Chapter 7)
5.   Kolombangara, Solomon Islands (PSP's), Burslem & Whitmore (Chapter 4).

Figure 1.7   Location of long-term studies of disturbance on forest composition and diversity. In west to east order: 1) NW-Guyana & central Guyana; 2) Mapane, Suriname; 3) Budongo Forest, Uganda; 4) ITCI, Borneo; 5) Kolombangara, Solomon Islands.

In Chapter 2 Simmoné Rose and and Lourens Poorter discuss the importance of one of the characteristics, seed mass, for early regeneration in tropical rain forest and is a review of a number of 14 (!) case studies on various locations of all tropical continents. This chapter is a further elaboration on the importance of seed size for the regeneration strategy of species.

The following two chapters are mainly concerned with succession and disturbance in 'natural' forest.

Chapter 3 by Douglas Sheil offers a historic permanent sample plot view of almost 70 years, based on the original data set of Eggeling (1947, in itself already a chronosequence). The original dataset inspired Connell to develop the IDH. However, as the IDH is developed from this dataset, it cannot be tested with it.

David Burlsem and Tim Whitmore show responses over a 30 year period to three major disturbances, caused by hurricanes, in a lowland tropical rain forest of the Solomon Islands in chapter 4.

This is followed by three studies at PSP level.

In chapter 5 Hans ter Steege, Bram Laumans, Denise Laumans-Bus, Gerold Zondervan and Frans Bongers discuss the effect of two harvests and subsequent treatments on composition and diversity of permanent sample plots in north Suriname with a 43 year time span.

Chapter 6 by Eric Arets, Peter van der Hout and Roderick Zagt discusses the effects of timber harvesting based on permanent sample plots in two areas in Guyana, with a 6 year time span for one study.

In Chapter 7 René Verburg and Clara van Eijk-Bos discuss changes after logging in permanent sample plot study of 20 years in a Bornean rain forest.

One study discusses changes more at the landscape level.

In Chapter 8 Hans ter Steege, Ivan Welch and Roderick Zagt offer a view of the effects at landscape level of 75 years of continuous timber harvesting in a large watershed area in central Guyana.

And finally

Because the mathematical basis for the IDH and DEH has not been worked out in detail, in Chapter 9 René Verburg and Feike Schieving develop a mathematical model for the IDH and DEH, necessary for a discussion of the previous studies.

Then in chapter 10 René Verburg, Hans ter Steege and Roderick Zagt integrate the results of the studies and discussed some implications for ecology, policy and management.

2 THE IMPORTANCE OF SEED MASS FOR EARLY REGENERATION IN TROPICAL FOREST: A REVIEW

Simmoné Rose, Lourens Poorter

Abstract

Seed mass is an important component of the shade tolerance of rain forest tree species. Using a meta-analysis we evaluate till what extent seed mass affects the survival, initial size, and growth of seedlings in light environments that are typical of forest gaps and understorey.

Early seedling survival in low light was positively correlated with seed mass, and about two-fold larger for large-seeded species (>0.1 g) compared to small-seeded species (<0.1 g). Survival of the two seed size groups was comparable in high light. Initial size (height, leaf area, biomass) was positively correlated with seed mass. The relationship was stronger when seedlings were compared shortly after emergence and when seedlings were grown at low irradiance. Height ranged from 1-68 cm, leaf area from 1-1500 cm^2, and biomass from 0.007-28g for the smallest-seeded species compared to the largest seeded species. A large initial size enables the seedling to penetrate the leaf litter layer, to escape size-dependent mortality, to be more resilient after disturbance, and to get a better access to resources. Seed mass is a good predictor of plant traits under high-light conditions. At high irradiance seed mass is negatively correlated with the Relative Growth Rate (RGR), Net Assimilation Rate (NAR), Leaf Area Ratio (LAR), Specific Leaf Area (SLA) and Leaf Mass Fraction (LMF), with average coefficients of determination ranging from 0.19 to 0.52. At low irradiance seed mass is only negatively correlated with LAR and SLA For all growth parameters but LMF, the small-seeded species show a more plastic response to an increase in irradiance than the large seeded species.

Small-seeded species have a similar RGR at low irradiance compared to large-seeded species, whereas at high irradiance they realise a higher RGR. The RGR of small-seeded species tends to cross-over with the RGR of large-seeded at irradiance levels below 5%. Large-seeded species have a large initial size but an inherently low RGR. Under high light conditions as found in forest gaps, it would take small-seeded species such as *Cecropia* 6 months to overtake the large-seeded species in size. Small-seeded species need therefore a small time-window of opportunity to attain a dominant position in the regrowing vegetation before the gap is closed.

Introduction

Seed mass varies over 10 orders of magnitude in weight amongst species, from 10^{-6}g in orchids to more than 10^4g for the double coconut *Lodoicea seychellarum* (Harper 1977). Even within plant communities, the seed mass may span a range of 10^5 (Westoby *et al*. 1992). In a Guyanan rain forest, for example, the dry seed mass of woody species ranges from 0.1 mg to 82 g (Figure 2.1, Hammond & Brown. 1995).

Seed mass is considered an important ecological attribute of plants, reflecting interactions between past environment pressures and the evolutionary history of taxa (Westoby *et al*. 1992, Westoby 1998). It has been shown that seed mass plays an important role in seed dispersal (Augspurger 1984b, Westoby *et al*. 1996), seedling establishment (Grime & Jeffrey 1965, Gross 1984, Leishman & Westoby 1994, Lusk 1995, Kidson & Westoby 2000), initial seedling size (Boot 1993 1996), early seedling growth, and competitive ability (Westoby *et al*. 1992, Grubb 1996, Kidson & Westoby 2000).
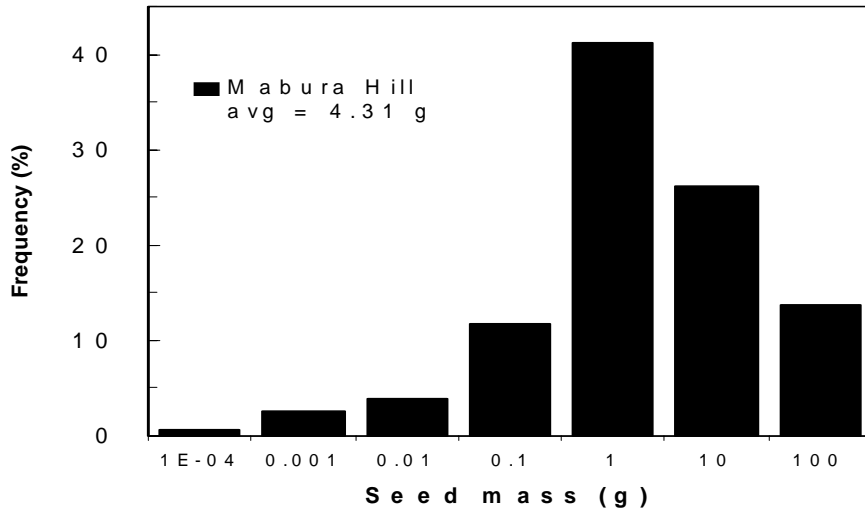
Figure 2.1   Frequency distribution of dry seed mass of 153 woody species in Mabura Hill, Guyana. The average dry seed mass is 4.31 g. Labels: 100 refers to the size class 10 – 100g. Data from Hammond & Brown (1995).

Seed mass is especially seen as an important component of shade tolerance (Leishman & Westoby 1994). Shade tolerance here is defined as the ability of a species to establish, persist, and grow in the shade. A large seed may enable a seedling to survive for a longer period while the seedling is in net carbon deficit (Grime & Jeffrey 1965, Saverimuttu & Westoby 1996), allowing the seedling to survive in the understorey until the formation of a canopy gap. A large seed produces also a larger seedling and thus results in an initial size advantage. The duration of this size advantage, however, depends on the light environment: in large gaps the initially large seedlings of large-seeded species may soon be overtaken by seedlings of small seeded species with higher growth rates (Boot 1993, Rose 2000).

Rain forest trees have been divided into shade-tolerant and shade-intolerant species according to their responses to light. The first group tends to have large seeds that can germinate and persist in the shaded forest understorey, while the second typically has small, widely dispersed seeds from which seedlings establish mainly in gaps (Swaine & Whitmore 1988). In the Guyanan forest of Mabura Hill, for example, shade-tolerant species have about four times the average seed mass of pioneers (Hammond & Brown 1995). Both groups, however, show widely overlapping ranges in seed mass (Figure 2.2). Indeed, in many tropical rain forest floras, there are shade-tolerant understorey species that have minute seeds (< 50 mg) (Grubb 1996).

In this review, we evaluate the importance of seed mass for tropical forest regeneration by examining the relationship of seed mass with early seedling growth, morphology and physiology.
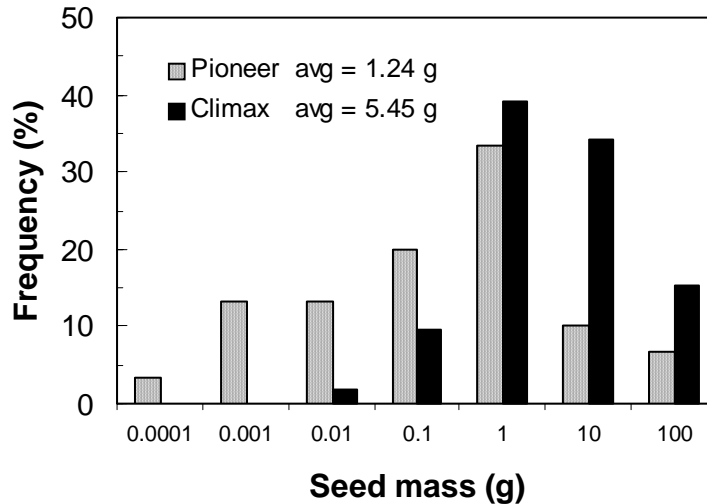
Figure 2.2   Frequency distribution of dry seed mass of woody pioneer species (n=30, grey bars) and climax species (n=105, filled bars) in Mabura Hill, Guyana. The average dry seed mass of pioneer and climax species is respectively 1.24 and 5.45 g. Labels: 100 refers to the size class 10 – 100g. Data from Hammond & Brown (1995).

We address the following questions:

1.   Does seed mass increase seedling survival in low light?
2.   Do large seeds give rise to large seedlings?
3a.   Is seed mass a good predictor of the inherent growth rate of species, and plant traits related to growth?
3b.   Are small seeded species more plastic in properties underlying RGR and hence better capable of adjusting RGR to an increase in light?
4.   At what level of irradiance and after how much time does the initial size advantage of large-seeded species disappear, and are they overtaken by small-seeded species with high RGRs?

We selected 14 published studies, in which seedling germination, recruitment, survival and growth of a wide range of species with varying seed masses was studied in different light environments (Table 2.1). Subsets of these studies were used for the different aspects reported on in this paper because they met the specific criteria required for the questions posed. The assessment of seedling survival required that studies included at least six species with 1000-fold difference in seed mass (< 0.1 g were considered small seeds, > 0.1 g were considered large seeds), grown in at least two different light environments. To address the influence of seed mass on initial seedling size, studies in which seeds of at least 5 species were germinated at low irradiance and/or high irradiance. The evaluation of the seed mass – seedling growth relationship required that a growth analysis had been carried out,

21

Table 2.1   Studies reviewed in this paper. The table shows the number of species included in each study, the light levels (as % of full light, with the exception of the study of Peña-Claros and Rose, for which respectively successional age and gap size are given), and for which type of analysis the study has been used. In bold it is indicated which light levels of each study are selected as being representative of low and high irradiance.

Reference	Nr. species	Light levels (%)	Survival	Initial size	Growth	Cross-over
Agyeman *et al.* (1999)	16	**1.9**, 6, 10, **28**, 44, 66			x	x
Augspurger (1984a)	18	**1, 20**	x			
Barigah *et al.* (1998)	10	**4**, 10, **25**, 45, 65			x	
Boot (1996)	6	**2.2**, 9, **30**			x	x
Boot (1993)	6	0.9, **1.8**, 4.3			x	
Huante & Rincon (1998)	10	**20**, 70		x	x	
Kitajima (1994)	13	**1.9**, **23**		x	x	
Osunkoya *et al.* (1994)	12	**2.5**, 10, **37**		x	x	x
Peña-Claros (2001)	6	**1**, 10, **20** year old secondary forest	x		x	
Poorter (1999)	15	**3**, 6, 12, **25**, 50, 100			x	x
Popma & Bongers (1988)	10	**1.6**, 4, **46**		x	x	
Rose (2000)	8	**understorey**, 50, 100, 200, 400, 800, 1600, **3200** m^2 gap	x	x	x	x
Swaine *et al.* (1997)	6	**5**, 8, 16, **27**, 60	x		x	x
Veenendaal *et al.* (1996)	8	**4**, 8, 16, **27**, 60/ 100			x	

at low irradiance (<5%), and/or high irradiance (20-40%) using seedlings of at least 6 species ranging from small seeded to large seeded.

Does seed mass increase seedling survival in low light?

Early survivorship of seedlings in low light varies widely and continuously among tropical tree species (Augspurger 1984a, b, Brokaw 1985, Li *et al.* 1996). In the past few years it has been found that small-seeded light-demanding species are able to germinate and establish in the shaded forest understorey or small gap environments (Raich & Gong 1990, Kyereh, *et al.* 1999, Peña-Claros 2001). These species, however, lack the ability to survive for long periods under these conditions (Li *et al.* 1996, Peña-Claros 2001). If low irradiance is a key factor determining seedling mortality in the shaded understorey, then survival of seedlings in shade will depend on, among other things, the total amount of reserves in the seed and the rate of carbon fixation and respiration of the seedlings under the prevailing light conditions. It follows therefore that seedling survival should be positively related to seed mass

in low light with this relation becoming obscure as irradiance increases. To answer this question a meta-analysis of early survival was carried out for four greenhouse and field studies in which species were grown at two light levels (Table 2.1).

From this analysis is becomes clear that seed mass is positively related to survival in low light, whilst both groups of species survived equally well in high light conditions (Figure 2.3). Small seeded species showed on average 34 % survival in low light when compared with 79 % in high light. Large seeded species on the other hand, recorded 75 % survival in low light and 84 % in high light. Many other studies have also found that large-seeded species persisted longer in shaded conditions and survival chances of small-seeded species increased with an increase in irradiance (Denslow *et al*. 1990, Alvarez-Buylla & Martinez-Ramos 1992, Boot 1996). For the species included here, larger seed size resulted in a two-fold increase in survival in the shade. Such an increase in survival enhances the chance of large-seeded species to survive until a canopy gap is formed, and profit from the increased light availability.

Why is the influence of seed mass on survival restricted to low light environments? Boot (1996) has argued that seed mass is only influential on seedling survival at irradiance levels below the whole-plant light compensation point. At such low irradiance, species with a low metabolic activity (expressed by a low inherent RGR) have an increased longevity (Saverimuttu & Westoby 1996), but at higher irradiance
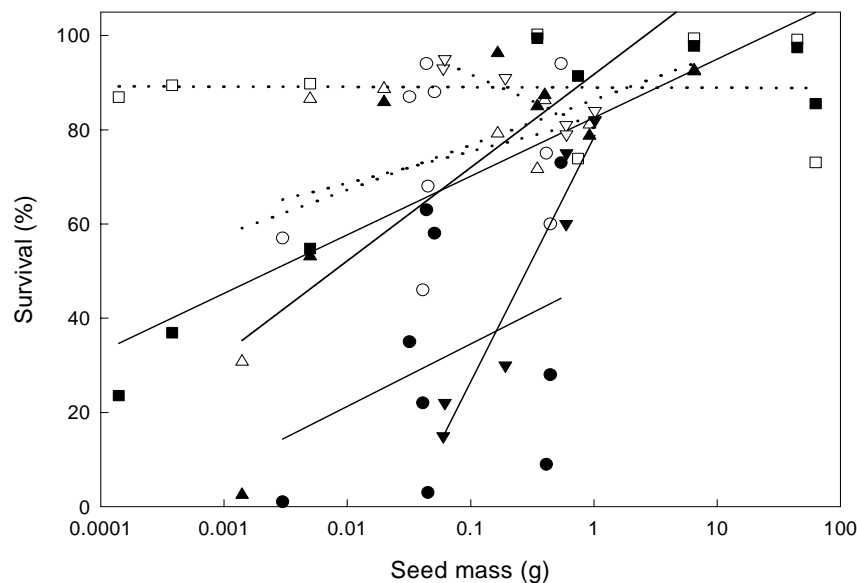

Figure 2.3   Survival rates after approximately two months for tropical rain forest species growing at high irradiance (open symbols, broken regression line) and low irradiance (filled symbols, continuous regression line). Data are from Augspurger 1984 (circle), Swaine *et al*. 1997 (downward triangle), Rose 2000 (square), Peña-Claros 2001 (upward triangle).

23

levels the amount of stored reserves and the rate at which these are reallocated to stem, roots and leaves are less important for survival, since light is not limiting. Another reason may be that small-seeded species are prone to herbivory (Kitajima 1996). With so little reserves available, they are not able to recover in the understorey, as a large seeded species with abundant resources may be able to do (Harms & Dalling 1997).

Do large seeds give rise to large seedlings?

To address the question if large seeds result in large seedlings, we evaluated three size-related traits (height, leaf area, and whole-plant biomass) that are crucial for plant performance in a forest environment. Plant height after emergence determines whether seedlings are able to emerge from the litter layer, and whether they are able to overtop neighbouring understorey plants and get access to light. The leaf area determines the ability to capture light. The total biomass is closely associated with the size of the foraging organs, and the resistance to falling debris and herbivores.

We selected five greenhouse and field studies (Table 2.1) in which seeds of different species were germinated at the same time and in which seedlings were compared within 2 months of germinating. These studies were carried out at low irradiance (<5%) and/or a high irradiance (20-40% of full light).

Correlations with seed mass
All three size variables showed a close, positive, correlation with seed mass (Figure 2.4). The strength of the correlations changed with the duration and irradiance level of the study. Responses were greater when seedlings were compared shortly after emergence (e.g., the study of Kitajima (1994), in which seedlings were evaluated after 8 weeks), and when seedlings were grown at low irradiance (Figure 2.4).

Height was positively correlated with seed mass for three out of four comparisons, with the slopes being almost identical (Figure 2.4a). Height ranged from 1 cm for small-seeded species to 68 cm for large seeded species. A similar positive relationship with seed mass has been found amongst 50 temperate species (Ganade & Westoby 1999). The greater height of large-seeded species is both the result of a greater biomass and a stronger etiolation response (Leishman & Westoby 1994, ter Steege *et al*. 1994).

Figure 2.4   (Opposite page) The relationship between seed mass and a) seedling height, b) leaf area, and c) total biomass. Data are based on a literature compilation. Species were grown at low irradiance (0-5%, filled symbols) or high irradiance (20-40%, open symbols). Each data point represents a different species. Regression lines are shown for each study separately (significant regressions as continuous lines, insignificant regressions as broken lines). Data are from Popma & Bongers 1988 (circles), Osunkoya *et al*. 1994 (diamonds), Kitajima 1994 (triangles), Huante & Rincon 1998 (hexagonals), Rose 2000 (squares).
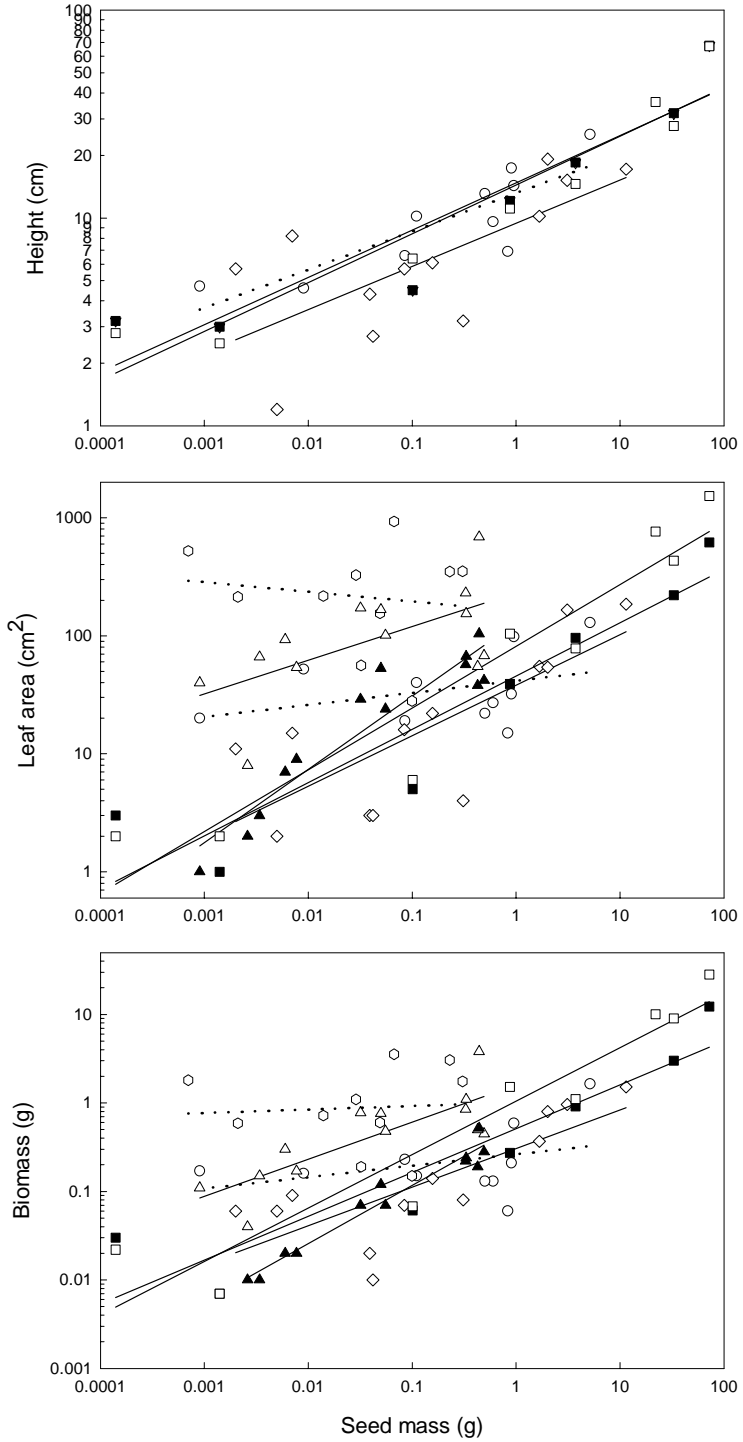
Total leaf area was positively correlated with seed mass for 5 out of 7 studies. Leaf area ranged from 1 cm^2 in the smallest seeded species, to 1500 cm^2 in the largest seeded species (Figure 2.4b). The total leaf area is a function of the leaf mass, and the amount of leaf area species can deploy with a given leaf mass (the Specific Leaf Area; SLA). The total leaf mass is tightly correlated with the seed mass, but the SLA tends to be larger for small-seeded species compared to large-seeded species (see the section on growth analysis). As a consequence, the relationship between total leaf area and seed mass is less tight than first expected. There was considerable variation in leaf area at a given seed mass between studies. This is probably caused by differences in length of the growing period and environmental conditions between studies. As noted above, the total leaf area is strongly affected by SLA, which varies substantially with ontogeny and irradiance (see the section on growth analysis, Veneklaas & Poorter 1998, and Poorter 1999).

Biomass was significantly correlated with seed mass for 5 out of 7 studies. Biomass ranged from 7 mg in the smallest seeded species, to 28 g in the largest seeded species (Figure 2.4c). A similar positive relationship with seed mass was found between 80 temperate woody species (Cornelissen *et al.* 1998). The larger amount of energy and nutrients stored in the endosperm allows large-seeded species to produce bigger seedlings (Kitajima 1996).

Penetration of the litter layer
What is the functional significance of having a large initial size? In a Bolivian moist forest, most species start to germinate at the onset of the rainy season. Similar patterns have been found in Panama and Guyana (Garwood 1983, ter Steege *et al.* 1994). At this moment the leaf litter layer is on average 3.6 cm thick (measured as the distance between the soil and the upper leaf of the loose litter layer). Only 5% of the forest floor consists of bare soil, while 23% has a litter thickness of more than 5 cm (L. Poorter, unpublished data). The presence of a litter layer may hamper the germination and establishment of plants (Molofsky & Augspurger 1992, Peña-Claros 2001) and reduce their photosynthesis (Facali & Pickett 1991). The establishment of tiny-seeded species (with a seed mass < 50 mg) is therefore confined to litter-free places, rocky microsites (Grubb 1996) or logs (Lusk 1995, Van der Meer *et al.* 1998). While small seed reserves may not permit seedling radicles to penetrate the thick litter layer (Putz 1983), large-seeded species do form a longer radicle or hypocotyl, which allows them to penetrate the litter layer successfully (Kidson & Westoby 2000). Also, for seeds that germinate under the litter layer a large initial seedling size allows them to pass through it. Indeed, Molofsky and Augspurger (1992) found that large seeded species had a larger establishment success in a litter treatment compared to small seeded species.

Escape from size-dependent mortality
Large seedlings have a considerably higher survival rate compared to small seedlings (section 1 and references therein). For example, survival rates of the understorey tree *Duguetia neglecta* increase rapidly with size, from 75% y^{-1} for seedlings < 15 cm height, via 94% y^{-1} for seedlings between 15-30 cm, to 100% y^{-1} for seedlings between 30-65 cm (Zagt 1997). It is likely that size drives differences

in survival, rather than age; larger seedlings have a higher survival rate because they can explore a larger air and soil volume to capture resources, and because they are more resistant to damage. Probably the same mechanism operates between species, if their seedlings are dissimilar in size.

Access to resources
Vertical expansion is especially important when resource gradients are unidirectional, as is the case for light, or for soil water in the dry season. Tall seedlings may overtop neighbouring plants and herbs and get access to light, especially in dense seedling banks. However, the vertical light gradient in the understorey is not very steep (Yoda 1974, Zagt 1997, Arets 1998), and therefore it is not likely that a 40 cm tall plant receives considerably higher light levels than a 10 cm tall plant, which may have its leaves at the same height or above the carpet of seedlings and herbs at the forest floor. The greater height may confer an advantage, once a gap is opened up in the canopy and there is a strong competition between the plants during gap-phase regeneration (Zagt & Werger 1998).

A larger leaf area allows seedlings to intercept more light. Whether such a large leaf area also implies a more positive carbon balance, depends on the ratio between leaf area and plant respiring tissue (the Leaf area Ratio; LAR) (Boot 1996).

Tall seedlings take advantage from a better access to soil water. Poorter and Hayashida-Oliver (2000) studied the performance of *Cedrela odorata* seedlings during the dry season, and found that large plants had a deeper root system, and disproportionally better access to soil water compared to small plants (cf. Veenendaal *et al*. 1996a, b). As a consequence, large seedlings experience less drought stress, and a shorter leafless period (Poorter & Hayashida-Oliver 2000).

Susceptibility to, and resilience after disturbance
Large seedlings suffer less from disturbance than do small seedlings. Falling debris, and herbivory are important disturbance agents in tropical forests. Twenty five percent of the understorey seedlings are exposed annually to falling debris (Clark & Clark 1989), and on average 10% of the leaf area is removed annually by herbivores (Coley & Barone 1996). Litterfall-induced stem damage is larger than 20% y^{-1} for small seedlings, whereas this declines to 7% y^{-1} for plants > 50 cm tall (Clark & Clark 1991). Large seedlings are, in addition to that, more resilient after biomass loss due to disturbance. The larger pool of non-structural carbohydrate reserves stored in the stem and roots enables them to recuperate from biomass loss due to herbivory or falling debris, and produce new sprouts and leaves (Armstrong & Westoby 1993, Harms & Dalling 1997).

Is seed mass a good predictor of the inherent growth rate of tree species and their plasticity?

In addressing this question we specifically sought to determine whether this relationship varied with irradiance, and what were the underlying mechanisms. To

evaluate this, one should compare the growth of different species. The absolute growth rate of seedlings is strongly size dependent. Comparisons between species and individuals differing in size are therefore most straightforward using the Relative Growth Rate (RGR, biomass growth per unit plant biomass, in mg g^{-1} d^{-1}). To analyse what underlying plant traits give rise to interspecific differences in RGR, we analysed the RGR as the product of a "physiological" plant trait, the Net Assimilation Rate (NAR; biomass growth per unit leaf area, in g m^{-2} d^{-1}), and a morphological plant trait, the Leaf Area Ratio (LAR; leaf area per total plant mass, in m^2 kg^{-1}). LAR can be factored into the biomass allocated to the leaves, the Leaf Mass Fraction (LMF; leaf mass per unit plant mass, in kg kg^{-1}), and the leaf area constructed with this leaf biomass, the Specific Leaf Area (SLA; leaf area per unit leaf mass, in m^2 kg^{-1}).

We selected 13 published studies, in which: a) a growth analysis was carried out, b) at least 6 species were compared, and c) seedlings were grown at low irradiance (<5%), and/or high irradiance (20-40%) under greenhouse conditions or in the field. The low irradiance is typical for the light levels encountered in the forest understorey, whereas the high irradiance is typical for large treefall gaps and logging gaps. In most studies the first harvest was carried out after the cotyledons were exhausted, or had been abscised. The seed mass was therefore not included in the calculation of the RGR (but see Kitajima 1994, Rose 2000). If data on NAR were not available (e.g., Kitajima 1994), we calculated NAR as the ratio of RGR over LAR.

For each combination of study and light level, we regressed RGR and its components on log-transformed seed mass (in g), using species as data points (Figure 2.5 a-e). If a regression slope differed significantly from zero, then seed mass is correlated with growth-related species traits. To evaluate whether all studies show a similar trend with seed mass, we used a t-test to determine whether the mean slope differed from zero, using independent studies as data points. It is often hypothesised that small-seeded species have a more plastic response to increased irradiance than do large-seeded species. If this is true, then the regression slope at high irradiance should be steeper than the slope at low irradiance. Therefore, we compared the regression slopes for each study at both high and low irradiance, using a paired t-test.

Relative Growth Rate
At high irradiance the RGR decreased with the seed mass of the species (Figure 2.5a, Table 2.2, t-test, P<0.01) (cf. Swanborough & Westoby 1996). A similar, negative relationship was found in an experiment with 80 temperate woody species (Cornelissen *et al.* 1996). Small-seeded pioneer species are able to profit from high irradiance, and realise a higher growth rate than the large seeded species. At low irradiance the relationship between growth and seed mass can be negative, absent, or positive, dependent on whether the light levels are well above (3%, Poorter 1999), around (2.5%, Osunkoya *et al.* 1994) or below (1.9%, Popma & Bongers 1988) the light compensation point of the pioneer species. As a consequence, the overall relationship between RGR and seed mass is not significant at low irradiance (t-test,
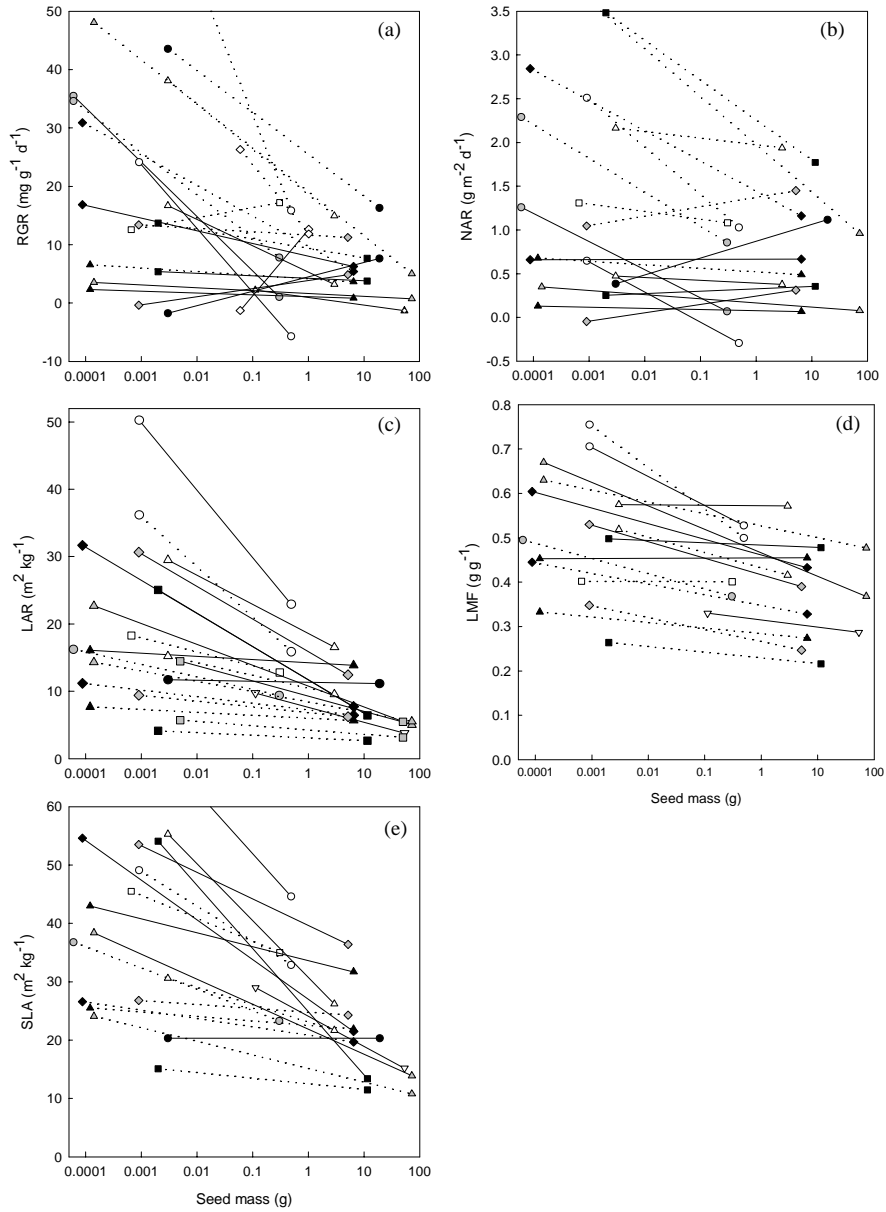
Figure 2.5 Regression lines of growth analysis parameters regressed on log(seed mass), for low light (continuous lines) and high light (broken lines) grown plants. Regression lines connect the lowest and highest seed mass included in each study. The different symbols at the extremes of the regression lines indicate the different studies. Data are from Agyeman *et al*. 1998 (black circles), Boot 1993 (open downward triangles), Boot 1995 (grey circles), Huante & Rincón 1998 (open squares), Kitajima 1994 (open circles), Osunkoya *et al*. 1994 (black squares), Peña-Claros 2001 (black triangles), Poorter 1999 (black diamonds), Popma & Bongers (grey diamonds), Swaine *et al*. 1997 (open diamonds), Veenendaal *et al*. 1996 (open triangles), Rose 2000 (grey triangles).

29

Table 2.2　Regression coefficients of growth analysis parameters (RGR, NAR, LAR, SLA and LMF) regressed on log(seed mass), for low light (LL, <5% irradiance) and high light (HL, between 20 and 40% irradiance) grown plants respectively. The regression slope (b), coefficients of determination (r^2), and significance level (P) are shown for each study separately, and for all studies combined (Overall). N indicates the number of species in LL and HL respectively.

REF	N	RGR						NAR					
		LL			HL			LL			HL		
		b	r2	p	b	r2	p	b	r2	p	b	r2	p
Agyeman et al. (1999)	17/17	2.46	0.11	ns	-7.17	0.38	ns	0.193	0.03	ns			
Barigah et al. (1998)	9/9												
Boot (1993)	6/0	-1.32	0.59	ns									
Boot RGA (1995)	4/6	-5.57	0.08	ns	-7.24	0.84	*	-0.095	0.11	ns	-0.367	0.66	ns
Huante & Rincon (1998)	0/10				-3.52	0.13	ns				-0.086	0.04	ns
Kitajima (1994)	13/13	-10.91	0.73	***	-23.66	0.78	***	-0.344	0.59	**	-0.541	0.38	*
Osunkoya et al (1994)	12/12	-0.42	0.10	ns	-1.61	0.57	**	0.028	0.09	ns	-0.455	0.19	ns
Pena-Claros (2001)	5/7	-0.31	0.67	ns	-0.62	0.45	ns	-0.013	0.56	ns	-0.040	0.40	ns
Poorter (1999)	15/15	-2.17	0.38	*	-5.23	0.65	***	0.001	0.00	ns	-0.345	0.28	*
Popma & Bongers (1988)	10/10	1.40	0.34	**	-0.57	0.04	ns	0.095	0.36	ns	0.107	0.10	ns
Rose et al. (2000)	7/8	-0.49	0.17	ns	-7.54	0.93	***	-0.048	0.10	ns	-0.545	0.55	*
Swaine et al. (1997)	6/6	11.29	0.60	ns	-11.75	0.43	ns						
Veenendaal et al. (1996)	8/8	-4.51	0.77	**	-7.74	0.49	ns	-0.032	0.04	ns	-0.075	0.01	ns
Overall		-0.96	0.41	ns	-6.97	0.52	**	-0.02	0.21	ns	-0.26	0.29	*

P>0.05). The small-seeded species, however, show a stronger increase in growth with an increase in irradiance (paired t-test, n=10, P<0.05) (cf. Leishman & Westoby 1994). An opening in the canopy due to natural treefall or to logging favours small-seeded species therefore more strongly than the less plastic large-seeded species.

There are two reasons why small seeded species have a high inherent RGR. First, RGR declines with the size of plants. When plants grow taller, they have a larger part of their biomass in stem and a smaller part of their biomass in leaves, leading to a low LAR and thus a low RGR. Since large seeds give rise to large seedlings, it is likely that part of the association of RGR and seed mass is caused by this decreasing RGR (ter Steege 1990, Walters *et al*. 1993). Second, small-seeded species are characterised by a high NAR and LAR, which allows them to realise a high growth rate, as discussed below.

Net Assimilation Rate
Light-dependent changes in RGR are paralleled by the changes in NAR. NAR decreases with the seed mass at high irradiance (Figure 2.5b, Table 2.2, t-test, P<0.05), while this relationship breaks down at low irradiance (t-test, P>0.05). As a consequence, small-seeded species show a stronger increase in NAR with an increase in irradiance (paired t-test, n=8, P<0.05). The NAR is closely related to the whole-plant rate of photosynthesis (Poorter & van der Werf 1998). In general, plants adjust their photosynthetic capacity to the light environment (Rijkers 2000). There is little scope for a high photosynthetic capacity in the understorey, as the maintenance costs are high, and the probability of high irradiance during sunflecks is low. Large-seeded climax species that are adapted to the forest understorey have therefore a low inherent photosynthetic capacity. Small-seeded pioneer species are adapted to the high irradiance of gaps. In such an environment it is advantageous to have a high light-saturated photosynthetic rate. However, such a high photosynthetic capacity cannot be maintained in the understorey. As a result, small-seeded pioneer species

Table 2.2   Continued.

LAR						SLA						LMF					
LL			HL			LL			HL			LL			HL		
b	r2	p	b	r2	p	b	r2	p	b	r2	p	b	r2	p	b	r2	p
-0.15	0.00	ns				0.01	0	ns									
-2.25	0.35	ns	-0.64	0.27	ns												
-2.21	0.49	ns				-5.17	0.62	ns				-0.016	0.08	ns			
-17.02	0.79	ns	-2.10	0.81	*	-29.39	0.34	ns	-3.99	0.5	ns	-0.239	0.73	ns	-0.038	0.84	*
			-2.06	0.18	ns				-3.95	0.08	ns				0.000	0.00	ns
-10.01	0.69	***	-7.43	0.59	**	-10.63	0.47	*	-5.92	0.24	ns	-0.065	0.30	ns	-0.093	0.73	***
-4.95	0.56	**	-0.39	0.12	ns	-10.82	0.41	*	-0.95	0.16	ns	-0.005	0.01	ns	-0.013	0.02	ns
-0.46	0.04	ns	-0.43	0.08	ns	-2.37	0.07	ns	-0.76	0.09	ns	0.000	0.00	ns	-0.012	0.02	ns
-4.91	0.71	***	-0.97	0.14	ns	-6.80	0.43	**	-1.42	0.1	ns	-0.035	0.14	ns	-0.024	0.06	ns
-4.84	0.12	**	-0.85	0.92	ns	-4.55	0.15	ns	-0.65	0.02	ns	-0.037	0.29	ns	-0.027	0.19	ns
-3.09	0.92	**	-1.54	0.48	ns	-4.27	0.87	*	-2.31	0.36	ns	-0.053	0.98	***	-0.027	0.27	ns
-4.32	0.35	ns	-1.89	0.15	ns	-9.73	0.57	*	-2.98	0.14	ns	-0.001	0.00	ns	-0.034	0.13	ns
-4.93	0.46	**	-1.83	0.37	*	-8.37	0.39	**	-2.55	0.19	**	-0.05	0.28	0.078	-0.03	0.25	**

have a high plasticity in both their photosynthetic capacity and their NAR (Raaimakers *et al*. 1995, Strauss-Debenedetti & Bazzaz 1996).

Leaf Area Ratio and its components
The Leaf Area Ratio (LAR) indicates the "leafiness" of the plant. LAR is negatively correlated with the seed mass in both light environments (Figure 2.5c). This relationship is more pronounced at low irradiance than at high irradiance (paired t-test, P < 0.05 in both cases). A high LAR in the understorey allows plants to enhance their light interception in a light-limited environment. Surprisingly, the large-seeded climax species, which are supposedly adapted to the understorey, are characterised by a low LAR (cf. Veneklaas & Poorter 1998)! The higher LAR of small seeded species is mainly caused by a high Specific Leaf Area (SLA, Figure 2.5e) and, to a lesser extent, by a high Leaf Mass Fraction (LMF). The SLA indicates how efficient leaf area is deployed per unit leaf biomass invested. The LMF is negatively correlated to seed mass at high irradiance (t-test, P<0.01), but this relationship disappears at low irradiance (t-test, P>0.05) (Figure 2.5d). The high LAR helps small-seeded pioneer species to grow faster than shade-tolerant species at moderate shade. This rapid growth, however, is at the expense of an increased risk of mortality. Kitajima (1994) found a positive relationship between the LAR of species, and their mortality rate in the shade. This is most probably caused by the high SLA, which is characteristic of species with a high LAR. A high SLA is associated with thin, watery leaves, thin cell walls, low lignin content and low leaf toughness (Coley 1983, van Arendonk & Poorter 1994, Cornelissen *et al*. 1999).

Such leaves are more susceptible to fungal pathogens (Augspurger 1984b), and more attractive to herbivores (Coley 1983, Cornelissen *et al*. 1998). A loss of biomass, due to wilting or herbivory, is especially deleterious in the shade, as carbon gain is

low and lost biomass is not easily replaced. As a consequence, the small-seeded species trade high growth for high survival.

Is seed mass a good predictor of plant traits related to growth?

Seed mass appears to be a good predictor of plant traits under high-light conditions. At high irradiance seed mass is negatively correlated with RGR, NAR, LAR, SLA and LMF, with average coefficients of determination ranging from 0.19 to 0.52 (Table 2.2). At low irradiance seed mass is only negatively correlated with LAR and SLA, with corresponding mean coefficients of determination ranging from 0.39 to 0.46. For all growth parameters but LMF, the small-seeded species show a more plastic response to an increase in irradiance than the large seeded species.

Differences between small and large seeded species in inherent growth rate and morphological and physiological traits closely parallel the observed differences between pioneer and shade tolerant species (Veneklaas & Poorter 1998, Walters & Reich 1999). There are also important exceptions: *Carapa guianensis*, one of the large-seeded species in this study, has an RGR comparable to small seeded species and the high RGR of *Cecropia obtusa* in the study of Rose (2000) was not based on a high SLA but a high NAR (thick leaves with a high photosynthetic capacity) (Pons *et al.*, in press). Classifying species into functional groups, based on their seed mass is, however, still far less arbitrary, than classifying species into pioneers and shade tolerant species, based upon observed habitat preferences in the field. Such a seed mass based classification may provide in addition a powerful tool to predict species responses to (changes in) the light environment (cf. Westoby 1998).

When do small and large seeded species cross-over?

At what irradiance level do small and large seeded species cross-over?
Small-seeded species have a lower, similar, or higher RGR at low irradiance compared to large-seeded species, whereas at high irradiance they realise a higher RGR. It is still unclear at what light levels the RGR of small-seeded species crosses over with the RGR of large-seeded. The light level of this cross-over point may have large implications for the coexistence of tree species (Sack & Grubb 2001), and the changes in species composition after disturbance (see Chapters 3 – 8). We selected 6 published studies that examined RGR of small and large-seeded species (Table 2.3). All had (a) a minimum of 6 species with a range of small to large seeds, (b) a seed mass range large enough to arbitrarily distinguish between large and small-seeded species (species with seed masses < 0.1g were considered to have small seeds, species with seeds > 0.1g to have large seeds, sensu Chapters 1, 8), (c) at least three light levels, the lowest levels being smaller than 4% and the highest light level being between 20 and 60%.

RGR was regressed on log-transformed light values (% of full light). This was done for each study separately, each data point representing one species and the slopes groups of species with similar seed mass. The regression coefficient of small-seeded

Table 2.3   Regression of RGR on log-transformed percentage of full light, for small and large seeded species. For each study, the number of species in each seed mass class (n), the coefficient of determination (r^2); the slope (b), the significance level (P) and the calculated light level at which the regression lines cross over (x, in % of full light) are shown for the group of small seeded species (S) and large seeded species (L).

Study	Seed mass	n	r^2	b	p	x
Boot (1993)	S	3	0.05	6.16	ns	0.4
	L	3	0.35	2.98	ns	
Osunkoya *et al.* (1994)	S	6	0.71	2.82	***	0.7
	L	6	0.63	1.72	***	
Poorter (1999)	S	3	0.01	3.84	ns	0.2
	L	10	0.00	0.99	ns	
Popma & Bongers (1988)	S	3	0.63	2.16	*	$1 * 10^{-8}$
	L	6	0.69	2.25	***	
Rose *et al.* (2000)	S	3	0.29	18.00	ns	3.1
	L	5	0.45	4.48	***	
Swaine *et al.* (1997)	S	3	0.31	14.92	*	11.2
	L	3	0.10	0.06	ns	

species is expected to be larger than that of large-seeded species because they are expected to show a stronger response of RGR to irradiance. We used a paired t-test to test this hypothesis, comparing the slopes of large and small seeded species per study.

The regression slope of the small-seeded species was significantly steeper than large-seeded species in four of the six studies (t-test, p<0.05). Further, in five of the studies the RGR of the small seeded species crossed over with the RGR of the large-seeded species, below 5% full sunlight (Table 2.3). From these comparisons it is evident that although the absolute difference in RGR between large and small-seeded species increases with increasing irradiance, small seeded species have, in general, a higher RGR than large seeded species. This is reflected in their ability to grow much faster than large seeded species at low light levels. They, however, are unable to maintain their high growth rate in the shade (see above). The study of Swaine *et al.* (1997) was the only exception with small-seeded species realising higher RGRs at approximately 11% full sun than their large seeded counterparts. This may be due to the fact that the seed mass range in this study was not as large as in the other studies.

Sack and Grubb (2001) hypothesised that the irradiance level at which species cross-over increases with the size of the plants. If this is the case, then small seeded pioneer species may grow faster than large-seeded climax species when compared as seedlings, but they may grow slower when compared as saplings.

After how much time does the initial size advantage of large-seeded species dissipate in large gaps, and are they overtaken by the small-seeded species?
To address this question, we carried out a theoretical exercise. Using data from Rose (2000), we compared the growth of 8 species in a large logging gap. We assumed that all species experience similar light conditions, start at 60% of their initial seed mass (thus excluding the seed pericarp which does not provide any carbon to the

developing seedling), and maintain their maximum RGR over time. The increase in log plant mass over time was calculated for each species as seed mass x $e^{(rgrmax \times time)}$).

Assuming constant RGR, it would take *Cecropia obtusa* 174 days to attain the same plant mass as *Mora gongrijpii* that has a 6 orders of magnitude heavier seed. *Hymenaea courbaril* on the other hand would take 786 days respectively to attain equal mass as *Mora* (Figure 2.6). This is a conservative estimate, as the small-seeded species is likely to start from seed, whereas the large-seeded species will be present as advanced regeneration. Nevertheless, if the re-growing gap vegetation is not too dense shortly after a large disturbance, the small seeded pioneers can exploit their inherently higher growth rate to compensate for the small initial plant size and gain advantage over the slow growing climax species. Similar results were found in a growth experiment in French Guiana. *Jacaranda copaia*, a pioneer species with tiny seeds and a low initial biomass, by the end of the experiment attained a larger biomass than two *Carapa* species, which started off with a considerably larger seed mass (Barrigah *et al*. 1998). Fast growth of small seeded pioneers in large gaps was also demonstrated in an experiment where eight species were planted in gaps and allowed to grow for a longer period (Rose 2000). The initially small *Cecropia obtusa, Goupia glabra* and *Sclerolobium guianense* dominated the canopy after one year in the larger gaps (1600 and 3200 m^2). In the small gap, the large-seeded
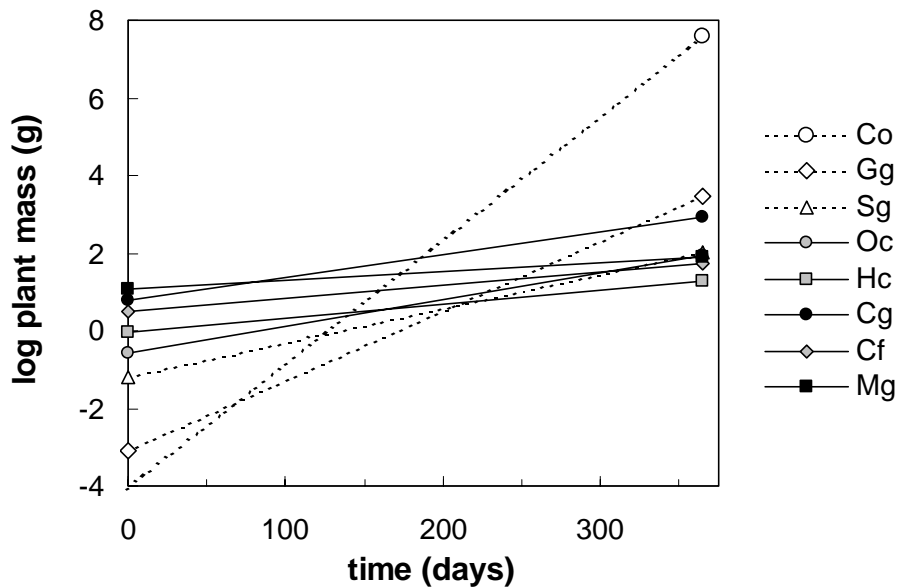

Figure 2.6 Biomass growth of eight species and their cross-over points in time. Log plant mass was calculated on the basis of the seed mass and maximum RGR (log plant mass = seed mass x $e^{(rgrmax \times time)}$) for each species over one year (365 days). The figure is from Pons *et al*. (in press) and based on data from Rose (2000).

34

species were amongst the tallest species. *Pentaclethra macroloba*, a species with intermediate seed size, showed the fastest growth in the small gap, and also substantial height growth in the largest gaps. The remarkable combination of tolerance of deep shade and fast growth in gaps was also demonstrated for this species in Costa Rica (Fetcher *et al.* 1994).

Concluding remarks

The general ideas about the role of seed size in establishment (Foster 1986, Leishman *et al.* 2000) have been supported, and expanded by our meta-analysis. One of the advantages of a large seed is associated with survival in shade. If seed reserves are not immediately allocated to the slow growing seedling, then the reserves in the cotyledons can sustain the seedling for a prolonged period until conditions become more favourable. This is particularly evident in the very large seeded *Chlorocardium rodiei* that keeps it reserves for up to a year after germination in the understorey, and even for five years when growing in gaps (Boot 1993, ter Steege *et al.* 1994). In the process, plant mass including cotyledons gradually decreases due to a negative carbon balance in the shaded understorey environment, but survival is high. Another advantage of a large seed is associated with the competitive advantage of the large initial size. Large seeds always come with the disadvantage of the trade-off with small numbers. Large numbers of seeds are essential for species that exploit the unpredictable window for establishment after an occasional heavy disturbance. Small seed size improves dispersal (Hammond *et al.* 1996) and also survival in the soil seed bank (Leishman *et al.* 2000). Chance to be there at the right time and place are thus maximised. A high RGR is however, important to compensate for the low initial plant mass as argued above.

The observed relationship between seed size, initial seedling size and RGR varies with irradiance. In disturbed areas, where the primary competitors for space and resources are other seedlings, species with large seeds may only have a competitive advantage when seedling densities are high (Gross 1984). In that case competition is largely asymmetric, and large seedlings may shade the smaller ones. However if seedling densities are low, then species with small seeds and high RGRs will have a competitive advantage since they are able to quickly overgrow seedlings with lower growth rates. Grime (1979) has suggested that high RGR may be adaptive for small seeded pioneer species as it allows them to monopolise available space rapidly and reproduce before being replaced by slower growing species. Clearly, the importance of seed size in determining seedling establishment success depends on this relationship between seed (or seedling) size and other life history characteristics such as RGR.

3 OBSERVATIONS OF LONG-TERM CHANGE IN AN AFRICAN RAIN FOREST

Douglas Sheil

Abstract

This account summarises studies based on tree data from plots established during the 1930s and 1940s in Budongo, a Ugandan rain forest. The original interpretations of forest change provoked controversies that continue to the present day. Analyses have yielded three categories of results: the first is descriptive; the second is a more focused evaluation of the relationship between forest change and species persistence; and the third is methodological. This summary focuses on the first two by examining stem, species and stand level patterns of change and introduces some previously unpublished results relating to trends in species traits and characters.

Evidence confirms the successional nature of the original series of plots. However, the time series changes are complex and while the younger vegetation plots develop more or less as expected the older plots do not. Disturbances caused by silvicultural intervention in four of the five longer-term plots compromise some evaluations, but also allow the effects of such disturbances to be observed.

Various anticipated aspects of forest change are verified. Examples include the slowing of forest dynamics with maturity, and the increase in potential canopy height. However, other observations, such as the real-time increase in tree recruitment are less expected and require explanation. Viewed overall, the results suggest an interplay of many factors that must be explored in greater depth. The importance of truly long-term studies is highlighted.

Introduction

Interpretations of forest change at Budongo have been both influential and controversial in the discussion of theories of forest succession, stability and species diversity. But before dwelling on these broader preoccupations, the context and history of the study require introduction. Budongo is situated in Bunyoro County, Uganda, at 1°37'-2°03' N and 31°22'-46' E, at an altitude of 1000-1100 m, just east of the Albertine Rift Valley escarpment (Figure 3.1). The Budongo plots are believed to be the oldest surviving in the humid tropics. It is this, as much as the high profile references, which ultimately make the Budongo study important.

During the 1920s and 1930s, the British Ecological Society emphasised the need to evaluate and quantify tropical vegetation (see Sheil 1998). This ideology shaped W.J. Eggeling's outlook so that when he was posted to manage Budongo Forest, he set out to systematically assess the flora. Aside from a considerable body of taxonomic work he became intrigued by the different forest formations he encountered. Together with his colleagues, he established a range of vegetation sample plots during the 1930s and early 1940s in order to examine composition, productivity and natural change (Uganda Forest Department, UFD., records, various unpublished).

Eggeling eventually published an account of the plot-based work (Eggeling 1947a) which asserted that the main forest types could be understood as a successional progression from *grasslands*, to a *colonising forest*, to a *mixed forest*, to the near monospecific (c.f. Hart *et al.* 1989) *ironwood forest* climax of *Cynometra alexandri*,

Figure 3.1   Location of Budongo.

the 'ironwood'. According to this view, changes in species composition were associated with stand level properties, such as a progressive increase in overall canopy height and preponderance of large buttressed stems. Crucial in terms of subsequent reference was the assertion that species richness first rose and later fell with successional status (Eggeling 1947a).

Since Eggeling's study was published, challenges and modifications have been suggested. Philip (1964) called attention to the considerable longevity of some trees which arrive in early formation but remain as relics in later formations, the role of climatic history, and also the mosaic nature of the older forest in which pioneer trees can be found in larger tree-fall gaps: factors which can distort Eggeling's idealized progression. Richards (1952) expressed general misgivings about reconciling a monoclimax view of tropical forests, such as Eggeling's, with the many types of variation that he had himself described in supposedly ancient forest types. Hewetson (1956) went further and argued that Eggeling's interpretation was overly gestaltic in

nature, i.e. that Eggeling was seeing order in a random assemblage of species (c.f. Gleason 1936). While Hewetson never set-foot in Uganda, or made an analysis of Eggeling's data, his views provides a clear and useful null model. A role for soil was proposed when Langdale-Brown *et al.* (1964) suggested that *Cynometra* forests are edaphically determined – a still untested idea that warrants further research. That the *Cynometra* forest is animal induced was proposed by Laws *et al.* (1970, 1975) as they had noted that elephant caused selective tree damage and mortality, with *Cynometra* being more likely to survive than most species. This idea, as is explained below, remains credible but unproven.

Eggeling's (1947a) account gained a new prominence in 1978 when Connell used it as the main example of a famous *Science* article in which he singled it out as the 'best evidence' for the Intermediate Disturbance Hypothesis. Some still imply that increasing richness is actually characteristic of late successional forest communities (e.g. Brünig 1973, Phillips *et al*. 1997, Hubbell *et al.* 1999). Others, like Connell, insist that high local richness is a transient successional property that can only be maintained by an appropriate disturbance regime (e.g. Huston 1994, Connell 1978, Sheil 2001, Molino & Sabatier 2001). Disagreement thus centres upon diversity patterns in relation to histories and forest age, and the stability and determinants of such patterns (Sheil 1996a, 1997a, Phillips *et al*. 1997, Phillips & Sheil 1997). This debate has implications for the interpretation of broader species richness patterns and community richness per-se (e.g. Sheil *et al.* 1999). While interpretations of available data are contested (e.g. Phillips 1995, Phillips & Gentry 1994, Phillips *et al*. 1994, 1997, Sheil 1995a, 1996a, 1997a, Sheil *et al.* 1999, Molino & Sabatier 2001) there is consensus on the need for further evaluations (Phillips & Sheil 1997).

Study site

The gazetted area of the Budongo Forest Reserve covers almost 800 km^2 of which *c.* 430 km^2 is closed forest. The heavily weathered pre-Cambrian geology has given rise to a gentle topography with relatively homogeneous deep and ancient, non-volcanic clay soils. Annual rainfall is generally between 1200-1800 mm, with most falling during September-November and March-May (see Sheil 1997b). Despite the homogeneity of the landscape, Budongo has the most forest tree species recorded in a Ugandan forest (Howard 1991, Synnott 1985, UFD *pers. comm.*).

Budongo is undocumented prior to the 20th century. The forest was probably avoided due to diseases such as river blindness (*Onchoceriasis*). The Uganda Protectorate did not gain control of the area until 1901 when many traditional land use patterns were disrupted, and interference in traditional burning patterns led to an increase in tsetse (*Glossina* spp.). Sleeping sickness became a major issue and regional evacuations followed in 1909 and 1912. Extraction of poles and larger building timbers by local populations was recognised in the 1930s but harvest, especially of larger trees, was considered negligible (Harris 1934).

The gazetting of the Budongo reserves and various modifications were completed during the 1930s and the objective of all management plans from 1935 until 1965-74 was sustainable timber harvesting (with a commitment to control and monitoring). The records and evaluations associated with each plan mean that the management history of Budongo is well documented. One highly relevant management activity was the arboricide treatment of low value species, during the 1950s and 60s. The death of any treated tree was not assured and some patchy results occurred.

The felling operations were mostly orderly and systematic. Until 1965, the size limit was 1.2 m dab (diameter above buttress) for African mahoganies (*Khaya, Entandrophragma* spp.) and *Milicia*, and 0.58 m dab for other species that were not compulsorily harvested. In 1965, obligatory felling of several species in addition to the mahoganies was introduced, and the size limit for mahogany and *Milicia* decreased to 1.07 m diameter. The regulation for *Cynometra* was adjusted; having been compulsorily cut before 1966 it was later classified as a 'weed' and was henceforth poisoned during treatments, as there was too much of this hard, and difficult to work, timber to find economic use. Little monodominant *Cynometra* forest has survived in Budongo. In recent years unregulated cutting and pit sawing has increased while mechanised extraction has decreased.

There have been changes in the fauna also. In particular, elephants were previously relatively abundant and were viewed as a problem due to their impacts on forest regeneration (Laws et al. 1970, 1975), but by the 1970s were considered locally extinct. Eggeling (1947a, b), Philip (1965), Plumptre (1996), Sheil (1996b, 1998) and Synnott (1985) provide further information about Budongo.

Sample plots

Plots establishment started in 1933 and continued into the 1940s. The plot series used in Eggeling's account were numbered from 1-10 according to successional status: Plot 1 being the youngest, and Plot 10 the most mature (Table 3.1). In addition to these there were several other specialized plots: Plot 15, was established in wooded-grassland at the forest edge (an earlier 'developmental stage' than Plot 1) and Plot 11 was situated on water-logged ground and termed 'swamp forest', and is not discussed further in this account. All these plots were established in the south of the forest.

Five of the original plots, (15, 2, 5, 6 and 7), have been maintained. The plots are 1.86 ha in size, except for Plot 6, which is 2.12 ha. They have been measured at various times since establishment, most recently in 1992/93. Some of the older records have been lost, but much useful information remains. Plot 7 is perhaps the most interesting of the plots and provides a 53 year record of pristine old-growth forest. The remaining four plots were subjected to tree poisoning as part of an effort to examine the efficacy of such treatments in increasing the yield of commercial species. The data for these four treated plots include about 20 years of pre-disturbance and 35 years of post-disturbance measurements.

Table 3.1   The plots. Plot maintenance and ultimate re-measurement in 1992 is shown by ●.

Plot	Vegetation in 1940	Vegetation in 1992	Intervention (arboricide treatments)	Net Basal Area Loss m²ha⁻¹ (min - max estimate)
●15	*Terminalia* grassland	Mixed (with *Maesopsis*)	1955, 56, 58	8 - 15
1	Colonising (Woodland)	nr*		
●2	Colonising (with mixed *Maesopsis*)	Mixed	1960, 64	6 - 10
3	Colonising (with *Maesopsis*)			
4	Ecotone to Mixed			
●5	Mixed	Mixed	1960, 64	25 - 30
●6	Mixed	Mixed	1956, 58, 59	15 - 25
●7	Ecotone to Ironwood	Ecotone to Ironwood	None	None
8	Ecotone to Ironwood			
9	Ironwood			
10	Ironwood			
11	Swamp forest			

Measurement conventions have varied (see Sheil 1995b). Most stem diameters have been measured at 1.3 m but buttressed, fluted or deformed stems have usually been measured also at three meters. Where multiple measurements have been taken, the highest point has commonly been used for analysis, and is known as the 'diameter at reference height' (hereafter 'drh'). For growth data by time interval the highest point measured in the consecutive periods was taken. In the 1992-93 evaluation, we measured stems using all known previous points of measurement.

In the following account, Eggeling's original plot series serve as a recurring backdrop against which other dynamic trends can be examined. These data suffer some limitations: no individual-stem records (only summaries by species and stem size classes, the original data are lost); an end strip was excluded from the established plots (making them 1.49 instead of 1.86 ha); and dates are not recorded and appear lost (W.J. Eggeling *pers. comm.*). A full list of species including notes on their ecological guilds, characteristic height, successional status and commercial timber significance is provided in Sheil *et al.* (2000). Further information regarding the plots and the assessment methods are available in Eggeling (1947a) and Sheil (1995b, 1996b, 1998).

Data have been comprehensively evaluated (Sheil 1995b), and the quality of the original studies – the botany in particular – are high. We can pinpoint various problems *because* there is such a long history of conscientious data collection and we have been able to seek out and analyse discrepancies. Many of these errors *can* be corrected. Stems are individually documented and so can be revisited; careless errors are identified by comparison with other records (Sheil 1995b).

To assess broad patterns of change tree species were allocated *a-priori* (without reference to the plot data) to Hawthorne-Guilds (c.f. Hawthorne 1995, 1996, and pers. comm. see Sheil *et al.* 2000). Trait level examinations provide more detail but remain complex to assess. A systematic list of ecological traits was developed for each tree species (Sheil *unpublished*, Paterson 1995). These related to maximum height, stem morphology, leaf size and form, implied pollination syndrome, fruit and seed size and morphology and dispersal syndrome. Growth-data from the five long-term plots was also compiled as a per-species 'trait'. Local floras (Eggeling & Dale 1952, Hamilton 1991, Flora of Tropical East Africa, Kew RBG) generally provided the required morphological information. Various classification techniques were used. Pollinators were classified from blossom traits (Faegri & van der Pijl 1979, Richards 1986, Weberling 1989, Bell & Bryan 1991, Willemstein 1987, Dafni 1992) with wind pollination determined in accordance with Bullock (1994, see also Regal 1982, Domínguez *et al.* 1989, Mayer & Charlesworth 1991). These techniques are imprecise and neglect rare syndromes (e.g. Gautier-Hion & Maisels 1994), but provide a practical approach to broad community patterns (Bawa *et al.* 1985). Dispersal of seeds can take many forms (van der Pijl 1982), frugivore-plant relations are generally less specific than for pollinators (Wheelright & Orians 1982) and generalisations more limited (Janzen 1984, Gautier-Hion *et al.* 1985b, Howe 1986). Classifications of fruit and seed types were based on fruit maximum dimension, seed size (*c.f.* Hladik & Miguel 1990), food reward, and structural adaptations.

There is a large literature on traits, including trade-offs, adaptations, relic characters, and phylogenetic constraints (Gould & Lewontin 1979, Bradshaw 1987, Grafen 1989, Stearns 1989, Harvey & Pagel 1991, Pagel 1992, Reeve & Sherman 1993, Hay 1994, Westoby *et al.* 1995, Harvey *et al.* 1995). A more in-depth treatment would heed these complexities but here we only summarise some exploratory analyses. These take two general forms: first a plot by plot weighting of each trait, and second a comparison of species-successional-position for each trait assessed.

Is the successional interpretation justified?

Perhaps most importantly, we need to determine whether Eggeling's successional interpretation of the plot series is valid. This series features repeatedly in the following account as *the* consistent model of successional change. Are we confident that these plots provide such a model or are there discrepancies that force reconsideration? A full answer requires us to look beyond the plot data.

Eggeling's (1947a) interpretation pre-dated his plots, which were established as illustrations (W.J. Eggeling pers. comm. 1993). Firstly, there was the general observations of community differences alluded to previously, and that the understorey of younger forest types usually included numerous saplings of species found in the canopy of older types – a pattern of replacement considered by Eggeling as a general fact (pers. comm. 1993). In addition it was known that forest cover in the south of Budongo had expanded into surrounding grasslands since the earliest observations in the 1920s (Eggeling 1947a) and these areas were of the

colonising forest type. The general distribution of forest types prior to logging, with *Cynometra* in the centre and progressively 'younger' types nearer the edges, was consistent with gradual forest expansion over several centuries (Eggeling 1947a, Philip 1965).

Recent examinations fail to undermine the successional model. Continuing expansion of forest cover through the 20th century is confirmed by aerial imagery (Sheil 1996b). An age-gradient across the outer younger forest is inevitable. Multivariate analyses of the plot series (Sheil 1999a and summarised below) are found to be consistent with predictions of succession in size-structured data. Additional aspects of successional consistency both direct and indirect, such as reduced turnover with maturity, are provided in this account (also Sheil *et al.* 2000, Sheil 2001). Further, an extensive review of UFD records and discussions with many past observers fail to identify a single charge of biases associated with Eggeling's plot locations (Sheil 2001).

A specific analytical evaluation of the successional interpretation is provided in Sheil (1999a) and is recounted here in brief. A formalised numerical approach examines predicted temporal patterns from the plot data. C*orrespondence analysis* (or *reciprocal averaging*, Hill 1973) was applied to canopy-tree composition of large trees ($\geq$ 60 cm drh) in the original plot series (Eggeling 1947a). This procedure ranks the original sequence data (1 to 10) in perfect correspondence to the implied
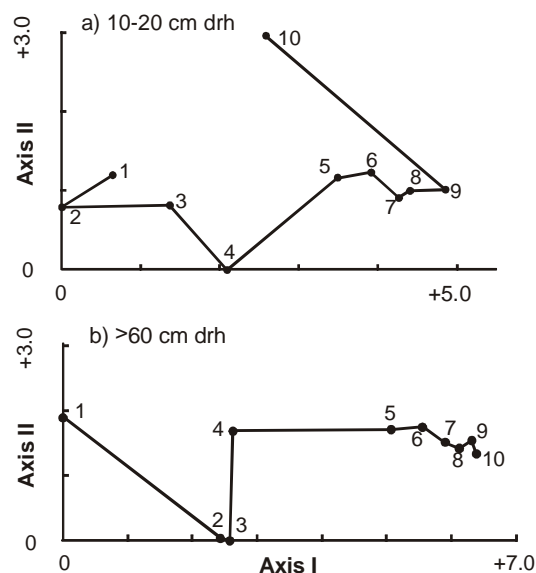

Figure 3.2   a) DCA of original data for stems between 10 and 20 cm drh (first two axes). Axis I accounts for 25% of variation in abundances (subsequent axes 5%, 2%, 0.4%). b) As in 2a, but for stems $\geq$ 60-cm drh. Axis I accounts for 30% of variation (subsequent three axes account for 6% 3% & 2%).

43

successional sequence (Figure 3.2). A 'development-scoring' procedure was developed using a 'passive-ordination approach'[1] against this DCA reference sequence; this was then applied to each plot by stem-size classes so that each observation is positioned on this univariate-scale (first axis of ordination) according to its composition.

The analyses assess predictions of compositional progression and convergence implicit in the succession model. Four distinct hypotheses are involved and the original data are consistent with each prediction assessed (see Sheil 1999a). Considering each of these in turn the analyses show:

1   Compositional progression *across* the plot series. The series show a clear trend in composition sequence in both the larger and smaller stems (this result is also a requirement of the analytical procedure in order to demonstrate logical consistency). As noted already the ordination procedure ranks the large stems $\geq$ 60 cm drh in perfect correspondence to Eggeling's successional sequence (exact probability using a random null hypothesis is given by p = 1/10! or 2.8×10^{-7}), this order is consistently maintained, though imperfect in other stem sizes.

2   Apparent convergence *across* the plot series, meaning that composition tends to an equilibrium or limit ('apparent' as this cannot be quantified without observations of real change), but we do not observe new forest types regenerating in *Cynometra* dominated forest but an increase in local dominance by a limited number of species.

3   Progression within each plot, meaning that the composition of smaller stems is 'more advanced' than that of larger stems. The relative rankings of the size-classes within plots demonstrate the expected order in eight of the ten plots (a one-sided binomial probability of 0.05). Plots 5 and 6 both show perfect correspondence (exact probability *p* =1/6!, = 0.004 for each).

4   Convergence within each plot. The compositional 'difference' between larger and smaller trees gets less and less until (in the abstract theory) a steady state community is developed. This convergent pattern is pronounced in the series when all size classes (10 cm classes from 10 cm drh up to 60 cm and $\geq$ 60) are examined together - either as maximum to minimum spread of scores, or standard deviation, of scores by plot (τ = 0.689 *p*= 0.0056, n= 10, for both). Compositional convergence is also seen more generally, e.g. in the second axis of the ordination (see Sheil 1999a for a fuller description).

The analytical approach is logical, includes few assumptions, and many of the test-statistics reach high levels of significance. It is however, also true that the 'generality' of the results are somewhat compromised. Eggeling's plots were chosen

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[1] In passive ordination the plots that are *passive* do not effect the location of other plots but are themselves located with reference only to the pre-defined ordination of the reference data [here the successional sequence] rather than to each other

to illustrate his model, and do not objectively represent the whole forest (though he was attempting to illustrate all major types and sub-types). The null-model in all the tests is an extreme version of Hewetson's (1956) claim of disorder, i.e. that Eggeling's data are randomly assembled. Non-conformation of the model with the original data would have undermined Eggeling's model, i.e. falsification, or lack of corroboration, *were* logical possibilities. On the other hand, confirmation of the model with the original data provides credibility to the original hypotheses, and to the model. While Hewetson's total disorder is clearly denied the suggestion of 'biased selections' and 'spurious interpretation' is harder to assess. Though Eggeling was undoubtedly a careful observer, such consistent patterns results appear difficult to generate by selection alone in a non-successional system. None of the notable, and in some cases sceptical, individuals visiting or working on these plots has ever reported any selection biases (e.g. W.J. Eggeling, H.C. Dawkins, M.S. Philip, A. Katende, A. Aubreville, T. Synnott – Sheil 1996a and unpublished correspondences).

Because of these results and the auxiliary information summarised above, the successional account appears well validated. Using the same multivariate approach the time-series results, though in apparent agreement for the early successional Plot 15, not all do accord so clearly with a progressive succession. This is especially true in the most advanced plots, though interpretations are complicated by the disturbances in all but Plot 7 (see Sheil 1999a for a complete account of the patterns observed). These analyses though not presented in any more detail here are in general accord with the many other results considered below.

Results and observations

General
One hundred and eighty-eight tree species, including two exotics, have been recorded from the combined data sets. This represents over 80% of Budongo's forest tree flora. The time series observations added forty species not recorded in the initial evaluations (Eggeling 1947a).

Some species have dramatically increased their representation in samples. The past botanical collection efforts need be emphasized to place these observations in context: a large number of botanists have worked in Budongo and floristically it is the best-known forest in Uganda (see Synnott 1985). *Tetrorchidium didymostemon* (Baill.) Pax & K.Hoffm. had previously been recorded once in the forest but in 1992 the species was recorded in two plots. *Trichilia martineaui* Aubrev. & Pellegrin, was also only ever recorded once before 1992 but was found in four of the five plots in 1992 (Sheil *et al.* 2000). Though possibly chance fluctuations, these species changes appear to be part of a more general change in forest composition.

The observed pattern of shade-tolerance (using Hawthorne's guilds see Methods above) in the original plot series conforms to patterns expected for succession: an increasing proportion of shade-tolerant species, with large stems appearing to 'lag
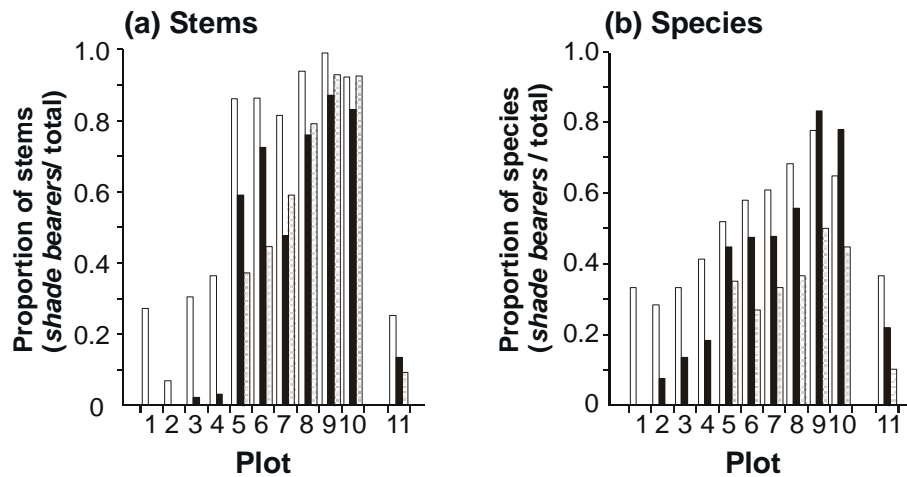
Figure 3.3   Relative abundance of the 'shade-tolerant' guild in Eggeling's original data set by, a) stems and b) species in three diameter classes: 10 to 30cm (open bars), 30 to 60cm (black bars), and 60 and over (hatched bars).

behind' smaller stems in this respect (Figures 3.3 & 3.4). The time series data are less consistent, but the younger plots follow predicted patterns. However, while Plot 7 increases in the proportion of shade-tolerant *stems* through time, the recruitment of additional species means that the proportion of shade-tolerant *species* actually declines (Sheil *et al.* 2000).

Rates of stem-turnover vary from plot to plot and period to period. In Plot 7, the overall mortality rate (c.f. Sheil *et al.* 1995) decreased with initial stem size (Sheil *et al.* 2000). In general, stem-turnover slows with assumed succession (Sheil 1998, Sheil *et al.* 2000). This slow-down is also observed in stand level growth by both diameter and basal area (Sheil 1997c). Most species have a higher recruitment than mortality rate and stem numbers have thus increased in all plots. Using simple tests that assume mortality and recruitment counts are independent events (c.f. Sheil 1999c) many of these imbalances are significant (Sheil *et al.* 2000). Such differences are most pronounced in the 'early successional' Plot 15. Related to this recruitment stem size structure has changed within all the plots, as the proportion of smaller stems increases. The general patterns of turnover appear consistent with a successional process that involves a period of colonisation and then periods of development followed by intensive canopy thinning and senescence leading to renewed cycles of recruitment (Figure 3.5).

In all the plots there is high variation in mortality and recruitment rates of different species. Recruitment and mortality rates for the more common species are correlated in both of the better data sets the 'late successional' Plot 7 and the 'early successional' Plot 15. This indicates a dynamic component to compositional maintenance (see Figures 3.6 and 3.7). As total stem number is increasing, species by species recruitment rates are also generally outpacing mortality.

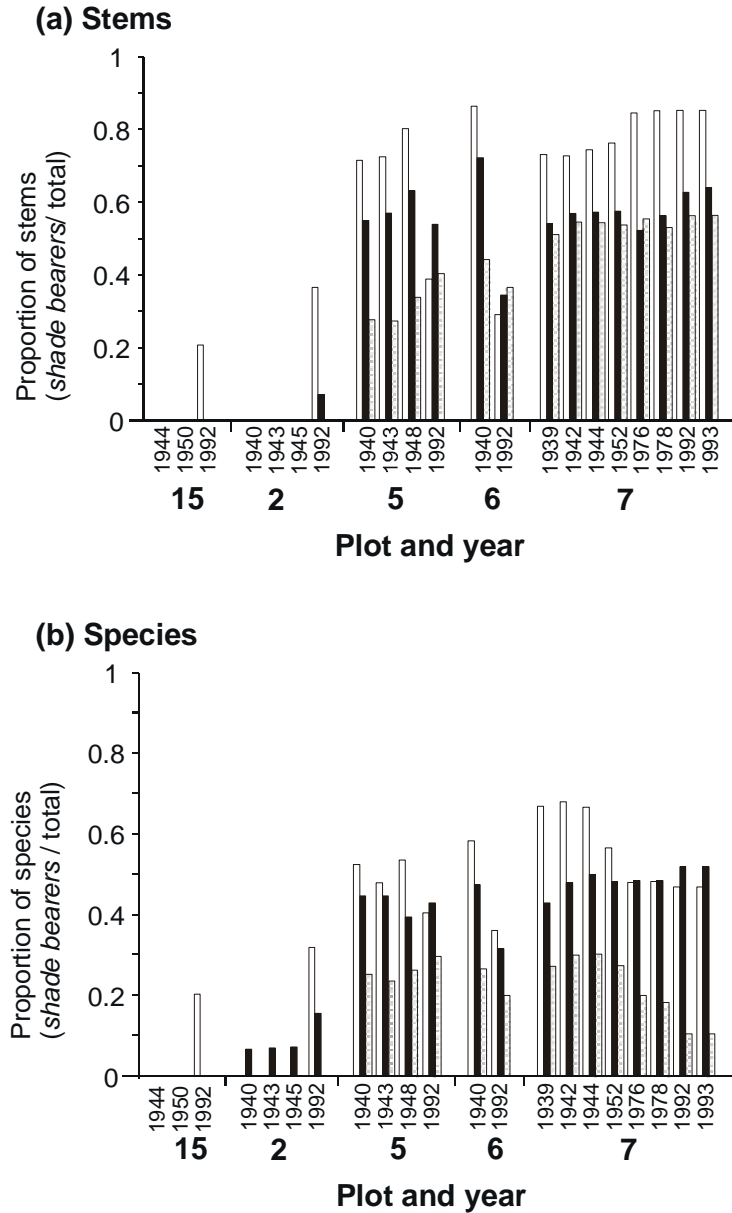**(a) Stems**

(b) Species

Figure 3.4   Relative abundance of the 'shade-tolerant' guild over time in plots 15, 2, 5 and 6 , by a) stems and b) species. Three diameter classes are shown: 10 to 30cm (open bars), 30 to 60cm (black bars), and 60 and over (hatched bars). Plot 6 has no early all species record apart from the original series (Eggeling 1947a) data and this is repeated in the time series (as '1940') to allow comparison with the 1992 data. All enumerations in which all species were recorded are shown, but the lower diameter class used in some observations is greater than 10 cm which may reduces the value of the 10-30 cm comparisons for these observations (see Sheil *et al*. 2000 for a species by species listing of the height data used here).
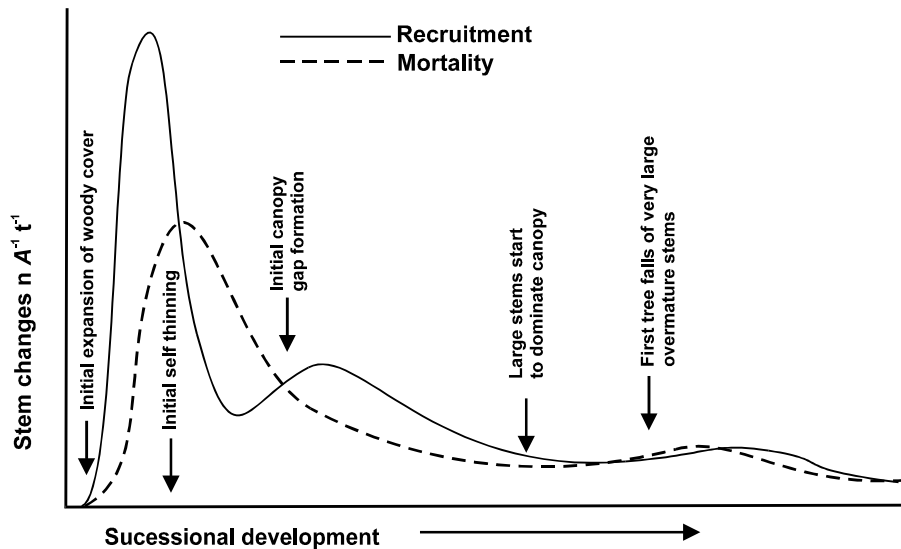
47

Figure 3.5   A speculative view of recruitment and mortality rates over succession that is consistent with the Budongo data, and suggesting how the rates interact over a long time period. The trend in total stem counts would rise and start to fall again and then finally level out, but would have additional minor peaks and troughs due to the imbalances between recruitment and mortality processes.

However, despite the long history of the sample plots the data remain inadequate to fully address certain critical phenomena. For example, the mortality rates of some species, such as the *Cynometra*, appear so low that simple estimates imply they may live longer than 500 years (Sheil *et al.* 2000). The persistence of such species is hard to examine as, senescence and catastrophes aside, we can expect current adult populations to reflect climatic conditions centuries ago – and steady state models or a century of data seem of questionable relevance given known climate flux (e.g. Olago *et al.* 2000).

Change in late successional forest

Plot 7 is probably of greatest general interest as it shows how a late successional forest has developed over 54 years without silvicultural interventions. According to Eggeling's (1947a) interpretation this plot was in transition between a rich mid-successional forest and a lower diversity *Cynometra* dominated formation. Of the total of 259 stems ($\geq$ 20 cm drh) recorded in 1939, 146 survived to 1993, when 212 additional stems were recorded. The highly significant differential in mortality and recruitment is also demonstrated by the derived mortality and recruitment rates for these stems (1.05 %yr^{-1} and 1.64 %yr^{-1} respectively). These rates are low in comparison with records elsewhere in the tropics (Phillips 1996). Though accentuated by the long census period (c.f. Sheil 1995a) this remains true when shorter periods are examined.
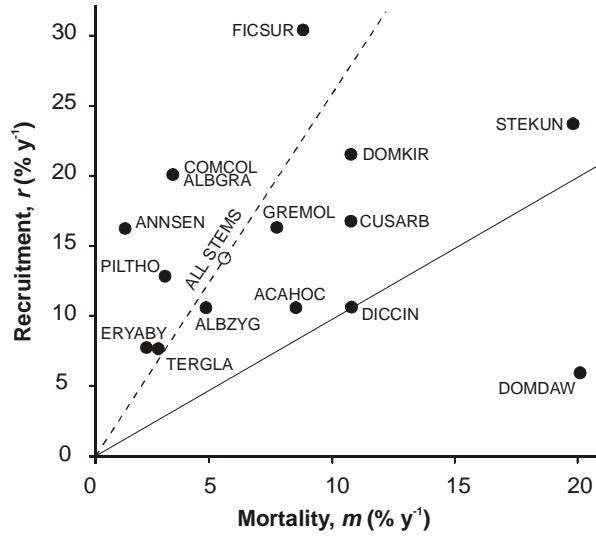
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Figure 3.6   Annualised mortality (*m*) and recruitment (*r*) rates between 1944 and 1950 for those species in Plot 15 that provide data for both rates. There is a significant relation between the size of gain and loss by species ($\tau = 0.488$, $p = 0.013$*, n = 15. Dotted line shows the overall plot mean, full line shows equality. Species names are designated by six-letter codes provided in Sheil *et al.* 2000.
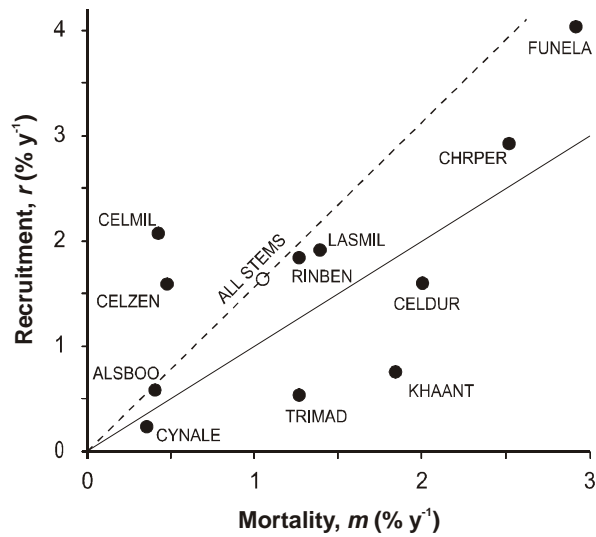

Figure 3.7   Annualised mortality (*m*) and recruitment (*r*) rates for stems $\geq$ 20 cm drh in Plot 7 from 1939 to 1993, for those species that provide data for both rates. The scale on the Y axis is reduced. Dotted line shows the overall plot mean, full line shows equality. Species names are designated by six-letter codes provided in Sheil *et al.* 2000.

While changes in total stem numbers in Plot 7 show a marked dis-equilibrium, species composition appears comparatively stable. Most species have varied little in abundance and there is a sharp mode at net zero-change. However, this actually reflects longevity and low stem counts. Of the 15 species showing no change, 11 have had no gains or losses, though these are all tiny sample 'populations' of one or two stems (nine n=1, and two n=2, ≥ 20 cm drh). Twenty-five species have increased in abundance and 13 have decreased. Of the six species lost, five were only represented by one stem in 1939. By 1993, 13 species were newly recruited, but of these 10 are represented by only one stem. When other census dates are also considered (1942, '44, '55, '76,' 78 and '92 [when all species were recorded]), 42 additional stems over 20 cm drh were both recruited and lost between 1939 and 1993. These transient stems belong to 13 species of which none are ephemeral: one is a species already observed but subsequently lost and two are species subsequently gained (Sheil 1998). Rare species dominate uncertainties about community change – of the 40 species observed in 1939 mortality *and* recruitment is only recorded for 16 (19 species 'only mortality', 4 'only gained', or including the 13 new species 17 'only gained').

The importance of large trees in determining forest dynamics is underlined by the observation that loss of only seven stems in Plot 7 contributes more than 60% of basal area mortality during the 53 year observation period (Sheil *et al.* 2000). Such change is closely linked to canopy cover and therefore to understorey illumination.

Species diversity
Community level tree species richness is singled out for more detailed evaluation. The unimodal pattern of species-richness in the original comparative plot-series is paralleled by a similar rise-and-fall in stem-densities, but rarefaction confirms that the unimodal pattern in richness is observed for fixed stem-counts (Table 3.2). A similar rise and fall is found with Fisher's α (Table 3.2). The proportion of species occurring in both large and small stem-size-classes increases across the series. As richness declines in later succession, low abundance species occur predominantly in larger stem-sizes (Sheil 2001).

All five time-series show a rise in species richness ranging from 12 to 177 % ha^{-1} (drh ≥ 10 cm, over 50-60 years). The disturbed plots achieved higher tree diversity than was encountered in even the richest dryland sites in the first half of the century. Contrary to expectation a rise was also recorded in the undisturbed late successional plot (in 1940 c. 42 species ≥ 10 cm drh ha^{-1} rising to c. 47 in 1993). The lowest species density observed was a 1940s record of c. 10 species ≥ 10 cm diameter ha^{-1} in monodominant *Cynometra* forest and the highest record (outside of swamp) is a c. 61 ha^{-1} recorded in 1992 in Plot 15 (Table 3.2, and Sheil 2001).

The comparative-series validates the general progression required by Eggeling and Connell's models. The much higher species densities reached in the treated time-series plots support the prediction that disturbance can increase richness. The Plot 7 time-series, by contrast, shows unexpected deviations and increases in richness

despite a predicted decline. Size-based analyses also conform to expectation in the original series, but prove equivocal when applied to the time series. Limited replication and various potential influences make further evaluation more tentative – some are considered in later sections below.

Table 3.2   Plot, species and stem statistics for stems ($\geq$ 10 cm drh).

Plot	Total Area (ha)	Total Stems	Total Species	Fisher's α	Total Genera	Total Families	Estimated species-counts[1] ~sp/ha[a]	n_r=200
1*	1.48	473	35	8.72	32	22	31	26
2*	1.48	556	34	7.98	33	23	30[+]	24
3*	1.48	762	38	8.41	35	23	35	27
4*	1.48	778	58	14.49	50	25	51	33
5*	1.48	752	58	14.65	50	20	52	36
6*	1.48	617	53	13.88	45	20	47[+]	36
7*	1.48	699	49	12.00	40	23	42[+]	29
8*	1.48	548	31	7.11	25	16	26[+]	20
9*	1.48	593	11	1.91	10	8	10[+]	9
10*	1.48	349	25	6.16	22	16	21[+]	19
11*(swamp)	1.48	562	80	25.50	71	29	68	52
2, in 1992	1.86	982	63	15.01	57	30	53	38
5, in 1992	1.86	808	69	18.04	57	22	58	44
6, in 1992	2.12	846	70	18.11	58	24	57	44
7, in 1976	1.86	981	57	13.18	47	27	45	29
7, in 1978	1.86	975	57	13.20	47	27	44	29
7, in 1992	1.86	1090	60	13.66	49	28	47	29
7, in 1993	1.86	1087	60	13.67	49	28	47	29
15, in 1944	1.86	382	25	5.99	21	18	22[+]	22[+]
15, in 1950	1.86	699	35	7.75	30	14	32	28
15, in 1992	1.86	921	74	18.95	61	19	61	45

[a] Estimated according to Hurlbert's (1971) method.

[b] Based on Hurlbert's method and using the stems ha^{-1} as n_r

[c] Data from Eggeling (1947)

[d] In these cases as stems ha^{-1} $\geq (N - N_{max})$ the estimate is provided by a Log[S] versus Log[N] 'linear' interpolation between the highest rarefaction estimate and the total measured plot value.

Traits and trends

There are a number of unpublished analyses looking at how species characters relate to the successional series and to the time series (Sheil 1996a, Sheil & Paterson Unpublished, Paterson 1995). I shall summarise the more interesting and suggestive changes seen in the original data series. There are three reasons why these results are offered here: firstly, they provide a broader picture of what *is observed* (without any theoretical underpinnings); secondly, they may be useful in considering patterns observed elsewhere; and thirdly they serve as a reminder that the changes observed relate to diverse tree species with individual ecological characters.

If each tree species is scored according to its potential maximum adult height the per-stem average increases across the 10 plot series for larger stems (≥60cm drh), but appears to decline in the smaller stem classes (Figure 3.8). The percentage of larger species with buttressing also increases markedly amongst larger diameter stems - this trait is closely associated with adult height. All per-species growth means per plot statistics show a net negative relation with plot number.

Leaf morphology varies across the series with a distinct decline in petiole length, and in the prevalence of deciduousness in larger stems. The proportion of species with compound leaves indicates a 'rise-and-fall' unimodal pattern. There is a decline
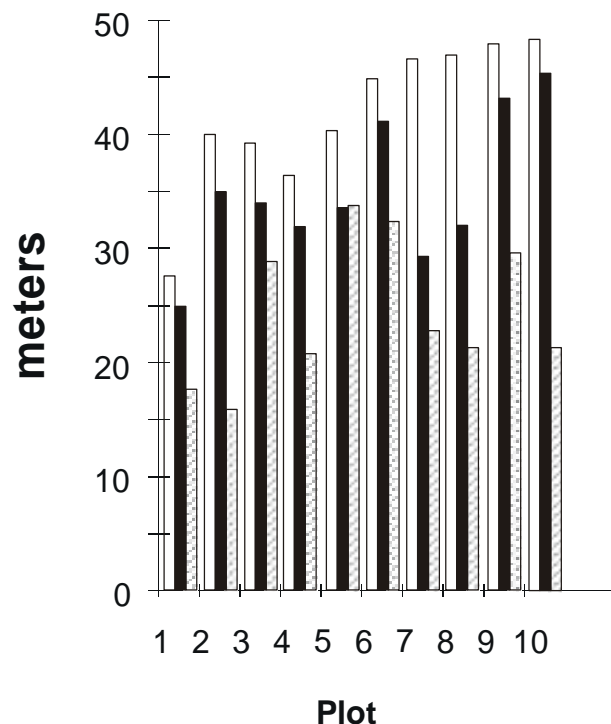

Figure 3.8   The relation between normal adult height and successional stage (evaluations averaged by stems). In this analysis a stem is assigned a height which corresponds not with its actual height but with the normal maximum height for that species.

52

in species with entire leaf margins in the understorey (but not in the over-storey), and a general decline in the prevalence of 'drip-tip' morphology. There are no significant trends with leaf size, though there is a suggestion of an increase in microphyll and a decline in notophyll leaves in larger stems.

Traits have also been noted to change according to species "successional status," determined by assessing the correlation of per-species trait scores with their estimated successional position determined via a reciprocal averaging score based on plot number. The statistically significant correlations extracted from such an analysis imply that as successional status progresses there is an increase in potential maximum adult height of the species (all classes); an increase in species with buttressing (in all stem sizes); a decline in species with spines (marked in the understorey); a decline in bark thickness and increase in smooth barked species (strongest in larger species); an increase in leaf width in the understorey stems; a decline in species with pubescent leaves (both above and below). The flower characters show few clear monotonic trends with succession, but we do observe a reduction in mean blossom (flower or flower group) size in the intermediate stem size class. There is a decline in alleged bird pollinated species, and of syndromes indicating wind pollination especially amongst the smaller stems. Amongst fruit and seed there is a decline in wind dispersal and an increase in seed size.

These evaluations of Eggeling's series should not be confused with changes over real time, which are more complex. The patterns of these data with respect to the real time series changes are too complex and generally inconclusive to detail here. Despite this fact, Plots 15 and 2 appear to develop in accord with the Eggeling's series, while no clear pattern is evident for the other plots. Sheil (1996b) notes the species with increased recruitment rates possess a broad range of pollination and dispersal syndromes implying that reproductive and dispersal strategy is not serving a defining role in these changes.

Finding meaning in these observations should be left until more in-depth evaluations and corroborations can be developed. However, it is notable that several of the general patterns imply a shift from attributes we might generally associate with open woodland tree formations (short trees, wind pollination and dispersal, pollinators using visual cues, more defence against fire and animal browsing, and more ability for leaves to cool in wind) to those associated with denser closed stands (taller trees, still air, adaptations for darker cooler understorey). Whether such patterns apply to other contexts can be determined by assessing other sites, and carrying out more focused studies of tree trait development.

Discussion

Determinants of forest change
I have previously argued the importance of examining what factors might shape forest composition (Sheil 1998). *Post-hoc* interpretation though potentially limitless,

is vital in drawing maximum insight from these unique data. The key issue is that additional hypotheses can be developed and used to clarify the processes involved.

Research has an effect on forest development in monitored tree plots and some changes may thus be artefacts (Sheil 1995b). The older plots can no longer be considered quite as 'representative' of the surrounding vegetation as they once were due to both the direct (paint, trampling) and indirect (visibility, access lines, see Sheil 1995b) impacts of research. Though difficult to examine comprehensively this could be addressed for static properties such as sapling densities by making a large-scale comparison with non-plot areas.

Climate change is a real phenomenon and the recent expansion of the forest (over a century and more) suggests favourable conditions that were not always present. Given the likely longevity of many species it is not clear to what extent we can expect a 'steady state' as temperatures and rainfall vary over the centuries (c.f. Olago *et al.* 2000). Such changes if influential will leave their impression on the successional procession of the forest over time – allowing some compositional imprint over the expanding forest that can be seen in the analysis of age location and composition. It would be valuable if we could find ways to date recruitment episodes in the larger trees found in the forest.

Fluctuations such as mosaic level processes, and the stochastic manner of intrinsic community changes are difficult to distinguish from trends when replication is low. Sampling variance in monitoring tropical forest may be high. Some such effects are inevitable. Even in a hypothetical 'steady-state' forest, large trees will continue to fall peppering any time series with noise. Note, however, that the Budongo time series are uniquely long, and a 1.8 ha plot is larger than most. Yet, older forests have slower overall dynamics and larger trees, implying a successional increase in the 'noise to trend' ratio for any fixed area. The 'tree-fall' explanation does suggest other phenomena that might be used to corroborate this view (developed for Plot 7 below).

Interventions within the forest, and surrounding landscape, have certainly impacted biota, influencing a myriad of ecological processes. Seed rain has certainly changed with the establishment of exotics. There is likely a general shift in seed production associated with forest harvesting, with for example an increased seed rain of pioneers and weedy species from tracks and other disturbed areas. Habitat for seed dispersers (e.g. nest sites for hornbills) will have been influenced as will their food (such as figs, which were controlled in the 1950s). Changes in fauna are most notable amongst the larger herbivores. Elephants no longer have the pronounced effect they once had on understorey vegetation – such an explanation can be examined in greater depth (developed for Plot 7 below).

Frustration with trying to fit this broad milieu of possible causes into a coherent framework, and a careful examination of the Intermediate Disturbance Hypothesis, led to a more realistic and less elegant, viewpoint (Sheil 1998, 1999b). Eggeling (1947a) and Connells' (1978) accounts are both pleasing generalisations that succinctly capture important patterns, but they are both too simple to provide

54

understanding for the real changes observed. An excessive emphasis on theoretical elegance hinders the ability to simultaneously build upon and combine what we already know, the many hard-won facts and principles, into an integrated science. In reality, many environmental changes contribute to both the accumulation and erosion of diversity, at many spatial and temporal scales. Even if artefacts can be removed from the picture, site-histories, contexts, scales, long-term processes, and species-pool dynamics need greater emphasis in our understanding of landscapes, communities and species richness (Sheil 1999b). Such an understanding is necessary to draw appropriate inferences – for example in recognising that under some conditions the Intermediate Disturbance Hypothesis is sufficient to predict that *degradation* of old-growth forest increases tree species richness (c.f. Sheil 1996b, Sheil *et al.* 1999).

Determinants of change in Plot 7

The changes observed in Plot 7 challenge our ability to find and evaluate explanations like those introduced above. Stochastic processes, trends and fluctuations cannot be easily distinguished without adequate plot replication. But there are alternative sources of evidence. When Eggeling (1947a, p. 44) described Plot 7 in the late 1930s he noted 'many gaps in canopy due to recent windfalls of *Khaya* and *Entandrophragma*. The *Cynometra* in the largest diameter class mostly only part grown and tendency for these to spread into gaps'. Observations (1992-1993) show that such tree fall gaps are still evident but these are small, as the heavily buttressed stems generally die standing, dropping most wood before the main trunk collapses (pers. obs.). The fact that a very small number of trees have contributed to the main changes in stand properties, like basal area, further indicates the stochastic processes underlying any trends (Sheil *et al.* 2000). However, a "tree-falls and canopy-opening" hypothesis suggests other responses to the change in light regime within the forest, and some of these can be examined:

1. Recruitment patterns – If there really is a local effect of just a few large trees, we might expect to see regeneration reflecting a spatial 'gap' pattern of recruitment. However, the analytical evidence for clumping in Plot 7 remains subtle (we can detect this for pioneers and recruits across some periods but the implied clumping is nonetheless slight, and likely to be influenced by additional factors such as dispersal, Sheil 1996b, Sheil & Ducey 2002).

2. Basal area –The measured basal area in the plot has remained over 50 m^2 ha^{-1} (Sheil 1998, Sheil *et al.* 2000). This is a high figure and implies the maintenance of dense tree cover.

3. Growth in the residual stems – No general trend is evident in per-stem growth or stand-level basal area growth, although there was a temporary increase in the p95 (95 percentile) fastest diameter-growth stems in the period covering 1950 (Sheil 1997c).

4. Recruitment of less shade-tolerant species – Increases in the total number of pioneer stems are found (Sheil *et al.* 2000) but in relative terms pioneers have decreased as the shade tolerant stems have increased more.

In summary, the overall basal area in Plot 7 remains high and the understorey is dense. The small numbers of pioneer stems are not sufficient to explain the more general changes. The turnover of large trees is a normal backdrop to forest processes and does not appear to have been unduly intense during the observation period. The rise in stem number is not explained indicating that we need consider other possible causes. The loss of large ground-dwelling fauna seems especially plausible. Since the eradication of elephants (*Loxodonta africana*) in the 1960s, a known cause of understorey damage and even larger-tree mortality (Laws *et al.* 1975) has been removed (Sheil 1998, Sheil in prep.).

The 'elephant-loss-hypothesis' provides additional predictions. If elephants were previously responsible for keeping some tree species from higher levels of dominance, we would expect such species to increase in the 'post-elephant' period. To investigate this required a means to estimate species' tolerance and vulnerability to elephants. Seven one ha plots were thus established in the neighbouring Rabongo Forest, an area still subjected to elephant damage (Sheil 1996b, in prep.). These surveys were complemented by a comprehensive general tree species collection. Rabongo, though much smaller (c. 4 km^2), is comparable with Budongo in terms of soil, climate, and general species pool. Recording the species, stem damage and species stand structure allow various analyses. Some exploratory 'persistence indices' were developed based on per-species recorded in Rabongo. Using these indices to weight species compositions per-plot in Budongo indicates an increase in less resilient tree species over time. Not all species are included in the Rabongo observations however. Evaluations indicate that Budongo also shows an above average increase in regeneration of species rare and/or absent in Rabongo, for example neither the *Tetrorchidium* and *Trichilia martineaui* noted above for their recent increases in abundance have been found in Rabongo. These patterns are consistent with an 'elephant-loss-hypothesis' (Sheil 1996b, in prep.). The issue of possible 'elephant-dependent-species' proves harder to examine and there is currently inadequate data to either identify such species or comment on their longer-term persistence (Hawthorne and Parren 2000). If we focus on the destructive side of the herbivores, we can hypothesize that the long-term survival of understorey stems can be reduced by such larger herbivores. This is not felt equally by all species and has a major role in determining forest composition and structure. The widespread loss of such fauna in Africa and elsewhere in the world suggests major changes for forests in the future. The nature of these changes remains hard to predict though some patterns are emerging (Sheil in prep).

Such examples show that in real forest sites a better integration of many mechanisms is needed to predict the diverse relationships between tropical forest diversity, inherent dynamics and external influences (Sheil 1999b). Here the long-term plots have led us to recognise potentially major, yet unanticipated, drivers of forest change.

Conclusions

I have described differences and changes observed in both the original and long-term data. The patterns are not always easy to reconcile, and underline the complexity of forest change. It remains unclear whether the more striking observations such as the increase in stem densities are local or reflect widespread processes. We cannot know without sufficient comparative data from other sites.

The time-series observations reveal the uncertain relationships between short and long term measures of stem turnover (Sheil 1995a,b, Sheil & May 1996), stem growth (Sheil 1995a, 1997b,c) and species richness (Sheil 1998, 2001) - and underline the insufficiency of the numerous tidy hypotheses used to describe forest community change (Sheil 1999b). Such models are useful to illustrate and communicate mechanisms and patterns, but not to integrate the role of the diverse multi-scale processes that operate in reality. There are credible implications that in Budongo many factors, including climate change, stochastic processes, changes in animal populations, and even the presence of researchers, contribute to shaping forest dynamics. The evidence suggests the role of herbivores, particularly elephants, warrants further study.

Many conclusions could be drawn, but I will emphasize two. First, is to acknowledge the general agreement between Eggeling's (1947a) views of Budongo and a more 'sophisticated' re-evaluation of his data. The second is that much of the inherent complexity in real ecosystems nonetheless lies beyond such descriptive models and demands a more process based reasoning. While the first conclusion provides reassurance that a careful observer can gain considerable understanding of a system without access to advanced analysis, the second warns of the difficulties of advancing this understanding into a mechanistic and predictive science. Such a conclusion is both banal and pertinent. Banal, because in retrospect it is an intuitive truism, but pertinent because it calls attention to far subtler patterns and questions the 'truth' we are seeking. There are several aspects to this. One is to note that the value of simple abstract frameworks is in communication not the explanation of the complexity of real forest systems (Sheil 1999b). Another is to reconsider the role of historical knowledge.

Older accounts, such as Eggeling (1947a, see also Richards 1952, Whitmore 1975, Dawkins and Philip 1998), are testament to the understanding and accumulated knowledge available even in the early 20th century. Such accounts, with their emphasis on description and natural history seldom provide the rigorously quantified basis that now pre-occupies so much of the tropical forest literature. However, this does not render them worthless as Connell (1978) illustrated by giving prominence to Eggeling's study. Currently, however, study results are regularly claimed as 'new' when a computationally intensive analyses confirms conventional understanding. An example is a recent paper that demonstrated that tropical trees were spatially aggregated (Condit *et al.* 2000). This otherwise commendable account claims that such aggregation had not been noted until recently: an odd disdain for past understanding. There are few experienced tropical forest ecologists or foresters who

57

would have doubted this were true, and it has been noted in various more specific and more general ways in the literature (e.g. Dawkins 1985). Even Eggeling's (1947a) account by illustrating distinct community associations with limited geographical coverage clearly implies non-random and non-dispersed species patterns at large scales. It is certainly reasonable to challenge and confirm what we know already, and to assess magnitudes and scales. Yet, this should seek to acknowledge and build on past learning and find out when and where we are wrong. For example while Eggeling's views have fared well over time, it is also clear that few of the credible alternatives have yet been addressed. We should highlight the dissenting voices, past and present – what is it that we really don't know? Historical sources remain a rich vein of understanding and insight.

Finally, we need to consider the value of old permanent plots. The analyses from Budongo have either agreed with theory or been problematic. Are such end results really of value? To answer this it is first necessary to recognise some prejudices and misconceptions. Forest scientists are used to a situation where understanding of longer-term forest processes is based not on direct observations but on space-for-time inferences, models calibrated with a few years of data, or just credible propositions. Concepts have replaced empirical observations. Such a predisposition may explain the low regard of the numerous old permanent sample plots scattered around the tropics. Few are now maintained. Justifications are expressed as doubts about data quality, unclear hypotheses (what is the research question?), poor experimental design (replication etc.), and confounding factors (too many influences on the forest).

While old plots indeed pose data problems (Sheil 1995b), this is often misinterpreted. What requires appreciation is that the cycle of crosschecking and verification *allows* the identification and correction of problems that are *considerably* more prevalent, though rarely acknowledged, in short-term studies. Certainly, replication is a problem as surviving plots are often single. The important questions to be asked of such data are not necessarily driven by a simple theory. These plots offer a unique window on long-term change. We have all learnt to place great importance on spatial sampling as this determines many of the choices and assessments we make as researchers. However, opportunities for extending study periods by magnitudes are not part of every-day-experience and the worth of longer-term temporal representation is forgotten. As for the lack of spatial generalisation that comes with poor replication: comparison can and should occur between sites and at the level of meta-analyses (Phillips and Sheil 1997). As to the confounding factors, these occur everywhere in the real world. Even in short-term studies, results will depend on local history – even if this history is unknown. There is an apparent paradox in looking in detail at any site: the deeper we look the more particular and less general the results become. However, it would be odd to conclude we should not look so deeply. Such cases provide the essential building blocks for describing reality.

Science has never been driven by hypotheses alone. A focus on elegant theory must not overshadow the need to observe reality. Many older studies offer many valuable

insights precisely because they were based on experience and insight. Careful observation and description provides the material for which understanding must be developed. Permanent plots should play a central role in our studies of tropical forest but we need to recognise *both* their benefits and limitations.

4 LIFE HISTORY DIVERSITY AND RESPONSE TO DISTURBANCE IN A LOWLAND TROPICAL RAIN FOREST ON KOLOMBANGARA, SOLOMON ISLANDS

David Burslem, Tim Whitmore[1]

Abstract

It has often been stated that life history differences between tropical tree species are important for the maintenance of species richness and forest regeneration after disturbance events. However, the long-term pre- and post-disturbance census data that are needed to characterise the demography and response to disturbance among coexisting tropical tree species are rarely available to test these assertions. In this paper we present data drawn from the long-term (30 year) study of the population dynamics of 12 big tree species in lowland tropical rain forest on Kolombangara in the Solomon Islands, and relate the demographic characteristics of these species to their seedling shade tolerance, adult wood densities, responsiveness to disturbance and size-based growth rates. We demonstrate that the life history characteristics of plants > 4.85 cm dbh define a continuum of successional status among this group that is not a perfect predictor of seedling shade tolerance categories. The most extreme species at one end of this continuum are characterised by high rates of mortality and recruitment over 30 years, low wood density and high potential diameter growth rates. The trade-off between traits conferring persistence over time, and high resistance to disturbance, and traits contributing to high growth rates and resilience to disturbance, contributes to maintenance of a consistent rank hierarchy of relative abundance over time. The differences in the species composition and diversity of primary forest communities across Kolombangara imposes spatial variation in damage and responsiveness in the face of large-scale disturbance events. The more diverse forest communities possess a greater density of early successional tree species and are more susceptible to canopy damage, but their tree populations recover more quickly. Thus spatial variation in diversity is reflected in spatial variation in forest dynamics, and these differences are maintained over time by the life history characteristics of the component species.

Introduction

The existence of inter-specific differences in the functional characteristics of tropical rain forest trees is implicit in models of forest dynamics and response to disturbance (Aubréville 1938, Whitmore 1974, 1975, Grubb 1977, Denslow 1987, Clark & Clark 1992). However, these models are difficult to test because they require long-term demographic as well as life-history data for a large sample of species. The most fundamental distinction lies between tropical tree species that are adapted to establish and grow on in canopy gaps ('pioneers') and species that are not dependent on high resource availability for establishment (Swaine & Whitmore 1988). Shade tolerance characteristics at the seedling stage are associated with other traits, such as wood density and growth responses to high irradiance, and these associations have been used to identify syndromes of co-varying characteristics to underpin functional classifications of tropical tree species (e.g. van Steenis 1958, Budowski 1965, Whitmore 1974). Although it is widely recognised that an absolute dichotomy between pioneers and non-pioneers is a conceptual simplification (Whitmore 1990,

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[1] Sadly, Tim Whitmore died during the preparation of this article. He was associated with ecological research on Kolombangara for nearly forty years, and this article is dedicated to his memory.

Alvarez-Buylla & Martínez-Ramos 1992, Grubb 1996), it is evident that life-history differences reflecting differential seedling responses to resource availability do exist and that they might contribute to maintenance of tree species richness (Kobe 1999, Davies 2001). These functional differences are also key parameters of process models predicting stand-level responses to human-induced large-scale disturbance events such as logging (Vanclay 1994, Alder 1995), and it is important that these models are parameterised using appropriate data.

Interspecific differences in the functional characteristics of plants have evolved in response to heterogeneity in the availability of key limiting resources, and are often characterised as trade-offs or associations between traits. In tropical forests, resource availability varies spatially, in relation to soil conditions, topography and altitude, and temporally, in response to canopy damage induced by disturbances on a variety of scales (Walker *et al.* 1991, Sollins 1998). Most research describing the response of tropical trees to disturbance has focussed on regeneration trajectories in the small canopy gaps created by the death of one or more trees (e.g. Brokaw 1985). However, there is an increasing recognition of the pervasive imprint of large-scale disturbance events on tropical forest composition and diversity (reviewed by Whitmore & Burslem 1998). The impacts of severe wind-storms have been particularly well-documented in the Caribbean (Walker *et al.* 1991), where studies have described the short-term recovery processes in some detail (e.g. Walker 1991, Yih *et al.* 1991, Bellingham *et al.* 1994, Zimmerman *et al.* 1994). The key finding from this work is that the relative abundance of common tree species does not change in response to the impact of severe wind-storms, although long-term post-disturbance data mostly do not exist (Bellingham *et al.* 1995). Validation of this finding by long-term studies would be significant because it would suggest that tropical forest ecosystems might be at equilibrium with respect to their disturbance regime (Burslem *et al.* 2000; ter Steege & Hammond 2001). The mechanisms that determine the response of tropical forest communities to large-scale disturbance are poorly known, but it is highly likely that life history differences among component species play a role in the recovery processes.

In this paper we evaluate the extent to which differences in life history characteristics among the common tree species in a lowland tropical rain forest in the Solomon Islands contribute to long-term maintenance of forest composition and diversity at a site that is subjected to large-scale cyclone-induced disturbance (Whitmore 1974, 1989b, Burslem & Whitmore 1999, Burslem *et al.* 2000). A number of recent authors have pointed out that a complete characterisation of life history diversity among tropical trees requires long-term measurements of growth and mortality through ontogeny and across the range of micro-sites available to forest plants (Clark & Clark 1992, Burslem *et al.* 1998, Davies 2001). In this study we use data derived from a thirty-year study of censused tree populations to address the following specific questions:

1.   How does inter-specific diversity in functional characteristics contribute to community-level responses to disturbance?

2.   Do functional groups, defined on the basis of seedling shade tolerance, provide robust classifications for larger size classes?
3.   Is there evidence of a shift in species relative abundance in response to large-scale disturbance?
4.   What mechanisms are responsible for shifts or stasis in species composition and diversity over time?

Study site and species

The study sites were located in tropical lowland evergreen rain forest on Kolombangara Island in the western Solomon Islands (8° S, 157° E). Kolombangara is an extinct Pleistocene volcano rising from sea level to a crater rim at 1420 – 1580 m a.s.l. A general description of the topography and soils is given by Hansell and Wall (1975). Most of the island and all the plots are underlain by olivine basalt breccias and lavas (Anon. 1984). Twenty-four topsoil samples (mostly in the range 0-31 cm depth) taken from 22 lowland forest plots had a mean $pH_{H_2 0}$ of 4.6 (range 4.1-5.3) and a mean total N concentration of 4.1 mg g^{-1} (range 1.5-15.5 mg g^{-1}). In a separate study of two lowland (< 305 m a.s.l.) soil profiles on Kolombangara, Lee (1969) found much more acidic soils ($pH_{H_2 0}$ 3.5 at 0-10 and 0-25 cm) with a lower concentration of total N (0.7 mg g^{-1} at 0-25 cm) and very high concentrations of total P (0.5 and 0.6 mg g^{-1} at 0-10 and 0-25 cm respectively for different profiles). Soil characteristics vary with altitude on Kolombangara, particularly in relation to humus type and related properties (Lee 1969).

The climate is extremely wet with no regular dry season. For a coastal station on the west coast, mean annual rainfall over the period 1965-1993 was 3196 mm (range 2571-4012 mm), with monthly averages varying from 173 mm (June) to 395 mm (February). Similar figures were found for two coastal stations on the north coast over a shorter measurement period (Neumann 1986 and unpublished data). Periods of up to two weeks without rain occur occasionally and longer dry periods of up to five or six weeks perhaps once a decade (W. Wooff, personal communication). Rainfall probably increases considerably with altitude on Kolombangara (Brookfield 1969), but data are not available. Temperature records are not available for Kolombangara, but at nearby Munda, New Georgia Island, mean daily temperature varied between 23.4 °C (August) and 26.1 °C (December) over the period 1962-1985 (Neumann 1986).

The tree flora of Kolombangara contains at least 192 species which reach 10 cm diameter at breast height ('dbh'). The species richness of small plots tends to be low (Whitmore 1974, Figure 2.7), reflecting the geological history of the Solomon Islands (Whitmore 1969). In other respects, however, lowland forest on Kolombangara is typical of tropical rain forest found in similar climates elsewhere: maximum canopy height is 40-50 m, climbing plants and epiphytes are abundant and buttressed trees are common (Whitmore 1974). The lowland forest on Kolombangara shows floristic variation in relation to geographical location, altitude
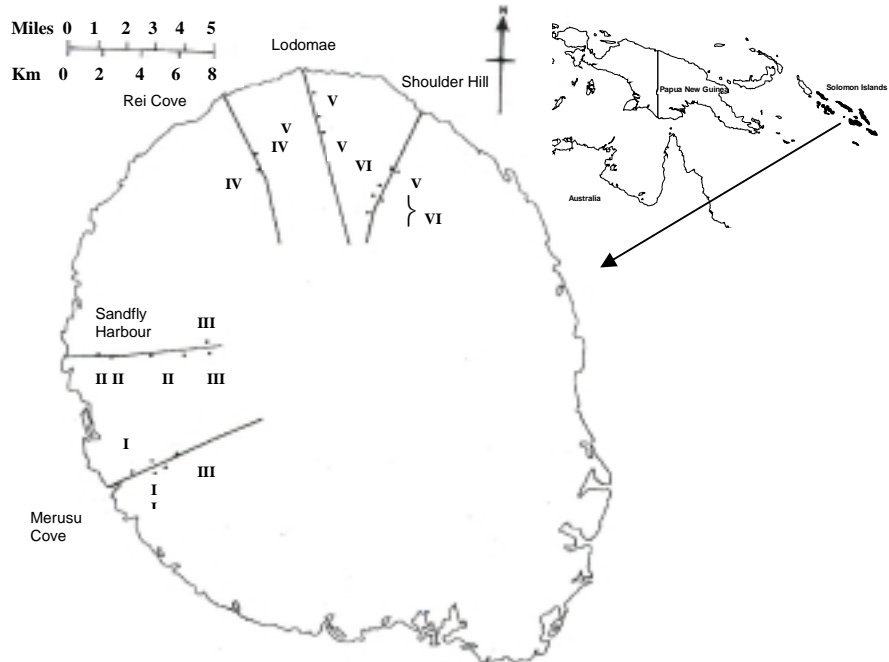
Figure 4.1   Map of Kolombangara showing the location of the 22 permanent sample plots. Roman numerals represent forest type sensu Greig-Smith *et al*. (1967) and Whitmore (1974).

and topography, decreasing in that sequence (Greig-Smith *et al.* 1967). Association analysis of the stands considered in this paper identified six floristically distinct 'forest types' divided between those on the west coast (forest types I, II and III on Figure 4.1) containing *Teysmanniodendron ahernianum* and *Dillenia salomonensis,* and those on the north coast (Forest types IV, V and VI) lacking these two species. In addition, plots of Forest type VI, on the north coast, possessed a greater abundance of species with seedlings requiring large canopy gaps for establishment and onward growth, and with size class distributions suggesting that they were not regenerating in situ (Whitmore 1974). There are also ruins of human settlements close to the plots of this forest type and a local oral tradition confirming the existence of villages in this area until the late 19th century, when a civil war and then increased missionary activity led to an emigration of inland human populations to the coast. We have argued elsewhere that the plots of Forest type VI are probably located in old secondary forests that have grown up on abandoned swiddens linked to these settlements (Burslem & Whitmore 1999, Burslem *et al*. 2000) and these plots will not be included in the discussion of variation in primary forest composition, diversity and dynamics in this paper.

The species studied in long-term plots on Kolombangara are described in Table 4.1. In this paper, species will be identified by their genus names, except in the case of the two *Calophyllum* species. All species are capable of reaching the canopy, but only one, *Terminalia*, can become an emergent (Whitmore 1974). These 12 are the

Table 4.1 Characteristics of the 12 species studied since 1964 in lowland tropical rain forest on Kolombangara, Solomon Islands. The four species groups among the 12 common timber tree species are classified according to the conditions required for seedling establishment and onward growth and are based on observations over 6.6 years over the interval 1964-1971 (Whitmore 1974).

Shade-tolerance class	Species	Conditions to establish	Condition to grow up	Wood density (kg m^{-3})[1]
1	*Dillenia salomonensis* (C.T. White) Hoogl. (Ds)	High forest	High forest	550
	Maranthes corymbosa Bl. (Mc)	High forest	High forest	720
	Parinari papuana ssp. *salomonensis* (C.T.White) Prance (Ps)	High forest	High forest	660
	Schizomeria serrata (Hochr.) Hochr. (Ss)	High forest	High forest	490
2	*Calophyllum neo-ebudicum* Guillaumin[5] (Cn)	High forest or small gaps	High forest/gaps	500
	Calophyllum peekelii Lauterb. (Cp)	High forest	High forest/gaps	480
	Pometia pinnata Forst. (Pp)	High forest or disturbed	High forest or ? small gaps	590
3	*Campnosperma brevipetiolatum* Volkens (Cb)	High forest or gaps	Gaps	330
	Elaeocarpus angustifolius Bl. (Ea)	High forest	Gaps	350
4	*Endospermum medullosum* L.S. Smith (Em)	Mostly gaps	Gaps	370
	Gmelina moluccana (Bl.) Backer (Gm)	Mostly gaps	Gaps	410
	Terminalia calamansanai (Blco.) Rolfe (Tc)	High forest, soon dying except in gaps	Gaps	460

[1] data from Anon. (1976) and Anon. (1979).

most common tree species in lowland forest on Kolombangara and are equally common elsewhere in the western Solomon Islands. They collectively account for 13-69 % (mean 42 %) of the basal area of all trees > 30.5 cm dbh and 23-100 % (mean 72 %) of the basal area of all trees > 70 cm dbh. For further details on the ecology and silviculture of these species see Whitmore (1966, 1974, 1989b) and Burslem and Whitmore (1996).

Methods

Plot establishment
In 1964 five points were selected at random on the north (three points) and west (two points) coasts of Kolombangara (Figure 4.1). Access lines were laid out along the top of the nearest ridge ascending to the crater rim from each point. Twenty-two rectangular plots of 0.6 ha each were chosen along transects normal to these lines to reflect the full range of variation in altitude, topography and species composition for

primary lowland forest on Kolombangara, based on data collected during an earlier pre-harvesting inventory of timber trees (see Whitmore 1974, 1989b for further details and a map).

Tree assessments
In mid 1964 an enumeration was made of all trees over 1 ft girth at breast height (9.7 cm dbh) on the plots. In addition, all individuals greater than 6 in girth (4.9 cm dbh) of the 12 species described in Table 4.1 were measured, mapped, permanently marked and numbered. The plots have been enumerated a further 14 times since 1964, but the number of plots has declined over time as a result of cyclone- and logging damage. One plot was never re-located after a cyclone in 1967, six were logged between 1975 and 1979, a further three between 1979 and 1985 and three plots were deliberately abandoned after 1985 (Whitmore 1974, 1989b; Whitmore & Chaplin 1987). Therefore nine plots, totalling 5.4 ha in area, have records extending over 30 years. Enumerations were carried out in October 1965, March and August 1966, February and August 1967, February and August 1968, February 1971, September/October 1975, February/March 1979, November 1985, April/May 1989, June/July 1991 and February 1994. On each occasion, surviving marked individuals of the 12 focal species were relocated and remeasured, and unmarked individuals above the minimum size for inclusion ('new recruits') were measured and marked. Maps were drawn to facilitate plot and tree location, but they are not sufficiently precise to enable us to superimpose tree position on the forest phase (sensu Whitmore 1975) maps also drawn on six occasions (Whitmore 1974, 1989b).

Analysis
Mean annual rates of mortality (m) and recruitment (r) were estimated by species, plot or forest type according to the equations presented by Sheil *et al*. (1995) and Sheil (1998) respectively.

$$m = 1-(1-(N_0-N_1)/N_0)^{1/t}$$

and

$$r = 1-(1-n_r/N_1)^{1/t}$$

where N_0 and N_1 are the total numbers of stems at the beginning and end of interval t, and n_r the number of new recruits during that interval. Turnover is defined as the mean of m and r over a given interval. In order to minimise the analytical problems associated with comparing mortality and recruitment estimates over intervals of unequal length (Sheil 1996, Sheil & May 1996), we collapsed the five intervals prior to the first cyclone (i.e. August 1964- August 1967) into a single 3-year period. The remaining intervals are all in the range 2.2 - 4.6 years except the 6-month intervals August 1967 - February 1968 and February 1968 - August 1968, and the 6.7 years between 1979 and 1985.

An analogous formulation was used for estimating mean annual rates of canopy disturbance, d, during interval t.

$$d = 1-(1-(N'_0-N'_1)/N'_1)^{1/t}$$

where N'_0 is the number of sample units per plot and N'_1 the number of sample units which were not disturbed during the interval. These formulae assume constant probabilities of stem loss, stem gain or disturbance during the interval.

Species diversity per plot was expressed as values of Fisher's α (Fisher *et al.* 1943). In a recent evaluation of tropical forest data-sets this diversity index has been shown to be less sensitive to sample size than other commonly-used indices (Condit *et al.* 1996b, 1998). Values of Fisher's α were estimated from stem and species number per plot using the programme presented by Condit *et al.* (1998). Across the range of values of stem number in this study (193 - 352 stems per plot) there was no significant relationship between stem number and Fisher's α (F = 0.67, *P* = 0.422, n = 22 plots) or between log N and log α (F = 0.70, *P* = 0.412, n = 22 plots), so we have not corrected values of α to a common sample size as recommended by Condit *et al.* (1998) for samples of this size.

Values of m, r, d and Fisher's α were computed for each plot over various intervals or censuses as described below, and mean values compared between the six forest types identified for these 22 plots (n = 3 or 4 plots per forest type). All correlation coefficients reported are Pearson product-moment correlation coefficients.

Results

Disturbance history
Four cyclones passed close to or crossed Kolombangara between November 1967 (cyclone Annie) and April 1970 (cyclone Isa, Figure 4.2). Because of the patterns of assessment of forest phase on plots, it is not possible to separate the individual effects of the first three cyclones, although the rates of canopy disturbance were much greater during this period than at any time since April 1970 (Figure 4.2). The timing of plot assessments does allow the impacts of the fourth cyclone to be isolated and quantified, and plot-level rates of reversion through the forest growth cycle in response to this cyclone ('canopy disturbance') will be used as an index of susceptibility to cyclone damage for comparisons among Forest Types.

Responses to disturbance
Mean or median annual mortality rates of all stems censused on surviving plots increased from low values before the impact of the first cyclone (median across all plots of 0.00 % yr^{-1}) to a 30-year maximum (median 10.9 % yr^{-1}) during the six months spanning the first cyclone. In subsequent intervals, including those spanning the three other cyclones, median values of mean annual mortality rates were much
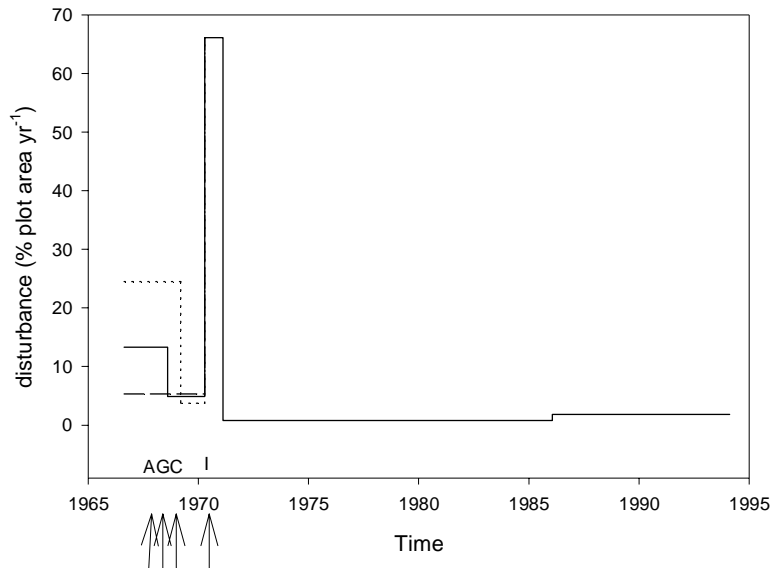
Figure 4.2   Mean annual disturbance rate (% plot area yr^{-1}) in plots on Kolombangara between all assessments of canopy structure from 1966 to 1994 measured as percentage of plot area which reverted to earlier phases of the forest growth cycle between successive assessments. The sampling strategy and the number of plots assessed changed over time as discussed in the text. The three lines for the intervals between August 1966 and April 1970 record the different pattern of assessments made for groups of plots over this interval; three plots (dashed line) were only visited in 1966 and 1970, five plots (dotted line) were also visited in March 1969 and 13 plots (solid line) were also visited in August 1968 but not March 1969. Arrows and letters indicate the approximate timing of cyclones Annie (A), Gisela (G), Colleen (C) and Isa (I).

lower (in the range 1.0 – 3.8 % yr^{-1}), so mortality rates during the interval spanning the first cyclone will be used as an index of potential susceptibility to cyclone-induced mortality for comparisons between species.

Mortality during the interval spanning the first cyclone ranged from 0.0 % (*Endospermum*) to 18.6 % (*Elaeocarpus*) of stems alive at the beginning of the interval (Table 4.2). Although there was not a significant relationship between mortality rates during the cyclone and wood density, the two species with the lowest density wood (*Campnosperma* and *Elaeocarpus*) were the first and third most susceptible to cyclone-induced mortality respectively. Mean annual mortality rates computed across all intervals that did not span a cyclone (i.e. August 1964-August 1967 and all intervals between February 1971 and February 1994) were negatively related to wood density (Figure 4.3a).

Mean annual recruitment rates for stems of all 12 species pooled were very low (median values across plots of 0.0 % yr^{-1}) for all intervals between August 1964 and

68

Table 4.2   Stem numbers and mortality (%) of 12 big tree species and all stems of those species (bold) on Kolombangara during the interval spanning the impact of cyclone Annie (August 1967 - February 1968), with 95 % confidence intervals in parentheses.

Species	Stem number before cyclone	Mortality in response to Cyclone Annie	
		Stems dying during period	Mortality (%)
Endospermum	23	0	0.00 (0.00-14.51)
C. neo-ebudicum	78	2	2.56 (0.71-9.43)
Dillenia	178	5	2.81 (1.26-6.65)
Terminalia	72	2	2.78 (0.67-9.84)
Gmelina	28	1	3.57 (0.19-17.48)
Parinari	153	8	5.23 (2.47-9.67)
Schizomeria	46	3	6.52 (2.29-18.86)
C. peekelii	137	11	8.03 (4.40-13.90)
Pometia	93	10	10.75 (5.79-19.17)
Campnosperma	136	15	11.03 (6.56-17.45)
Maranthes	34	5	14.71 (6.90-32.71)
Elaeocarpus	43	8	18.60 (10.80-35.43)
All stems	**1021**	**70**	**6.86 (5.54-8.78)**

February 1971. Between 1971 and 1994 annual recruitment rates varied from 0.94 to 4.64 % yr^{-1} and were significantly greater than annual recruitment rates before the impact of the first cyclone in all cases (P < 0.05, Wilcoxon matched-pairs signed rank tests).

At the species level, mean annual recruitment rates estimated over the full 30 years of the study fell in the range 0.33 – 2.16 % yr^{-1} except for one outlier (*Elaeocarpus*, 5.07 % yr^{-1}) and correlated positively with mean annual mortality rates (Figure 4.3b). Recruitment rates were not strongly correlated with wood density.

Differences among functional groups defined by seedling shade tolerance
The 12 common big tree species for which population dynamics data over 30 years are available were classified into four functional groups on the basis of their seedling shade tolerance characteristics by Whitmore (1974 and Table 4.1). They include species with strongly shade-tolerant seedlings that require high forest conditions for establishment and onward growth, such as *Dillenia salomonensis*, through to light demanders such as *Endospermum medullosum* whose seedlings require large canopy gaps for both establishment and onward growth. Median wood density for large timber size trees was greater in species with more shade-tolerant seedlings (H = 9.06, P = 0.029), although the two species with the least dense wood were *Elaeocarpus* and *Campnosperma*, rather than the three species with the most light demanding seedlings (Tables 4.1 and 4.3). Mean annual mortality rate estimated across all intervals lacking cyclone disturbance and mean annual recruitment rates over 30 years were also greater for the functional group containing *Elaeocarpus* and *Campnosperma* than the other three functional groups (Table 4.3).
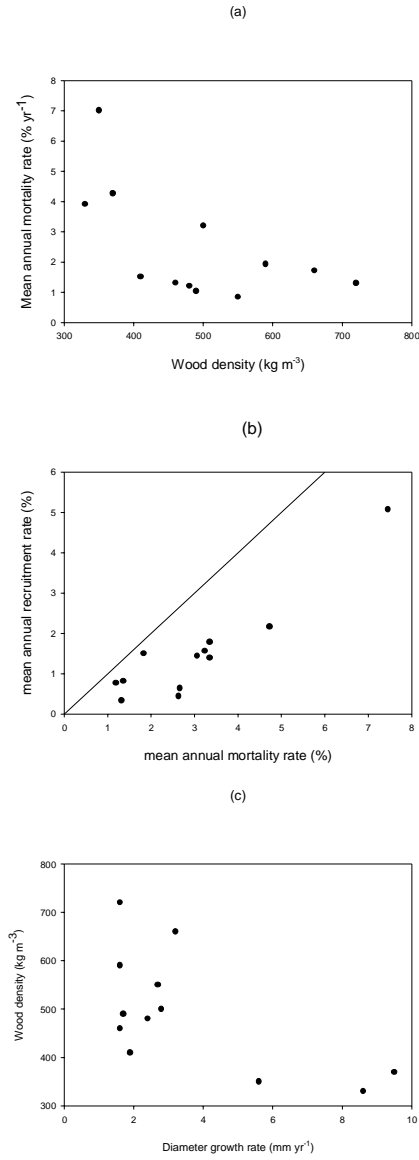
69

(a)

(b)

(c)

Figure 4.3   Inter-relationships between demographic characteristics, wood density and diameter growth among 12 tree species of lowland tropical rain forest on Kolombangara, Solomon Islands: (a) wood density (kg m^{-3}) and mean annual mortality rates (% yr^{-1}) estimated over all intervals that did not include a cyclone, (b) mean annual mortality and recruitment rates over 30 years (% yr^{-1}), with the 1:1 mortality = recruitment line also shown and (c) median diameter growth rate for stems >10-20 cm dbh at the start of an interval (mm yr^{-1}) and wood density (kg m^{-3}).

70

Table 4.3 Median wood density (kg m^{-3}) and mean (± standard error) annual mortality rates estimated across all intervals lacking cyclone disturbance (% yr^{-1}) and annual recruitment rates estimated over 30 years (% yr^{-1}) for the four functional groups defined on the basis of seedling shade tolerance (Table 4.1), with the Kruskal-Wallis statistic (H) or variance ratio (F) and degree of significance (*, P < 0.05) for comparisons between functional groups. Within a column, means with different superscript are significantly different (Tukey's test, P < 0.05).

Functional group	Wood density (kg m^{-3})	Mean annual mortality (% yr^{-1})	Mean annual recruitment (% yr^{-1})
1	605	1.2 ± 0.19[a]	1.1 ± 0.21[a]
2	500	2.1 ± 0.58[ab]	1.2 ± 0.40[ab]
3	340	5.5 ± 1.55[b]	3.6 ± 1.46[b]
4	410	2.4 ± 0.96[ab]	0.9 ± 0.36[a]
	H = 9.06 *	F = 5.12 *	F = 4.5 *

Median and maximum growth rates were highly variable among species and size classes, with median and maximum values frequently differing by an order of magnitude. All species except for *Schizomeria* showed an increase in median diameter growth rates with diameter for trees 4.9-10 cm dbh to >20-30 cm dbh. In all species other than *Campnosperma* the increase continued into the >30-50 cm diameter size class. *Calophyllum peekelii* and *Maranthes* showed further increases with tree size up to the largest, while all other species had a maximum rate at an intermediate size. *Endospermum* peaked in the >10-20 cm dbh size class (although the sample is very small), *Campnosperma* at >20-30 cm dbh, *Elaeocarpus* and *Terminalia* at >30-50 cm dbh and the remaining species at >50-70 cm dbh. *Elaeocarpus* showed a bimodal relation between growth rate and tree size, with median growth rates peaking at both >30-40 cm dbh and >70 cm dbh. Median growth rate was non-linearly related to wood density in the smaller stem size classes (Figure 4.3c). Comparison of median and maximum growth rates between functional groups are constrained by the small number of species in our samples, but suggests that contrasts are more likely to be significant for stems of intermediate size (Table 4.4). In two cases the maximum growth rate of the functional group containing *Elaeocarpus* and *Campnosperma* is significantly greater than that of the functional group containing the species with the most shade-tolerant seedlings.

Disturbance and community diversity

Species richness and diversity (estimated as Fishers α) of stems > 9.7 cm dbh in 1964 varied significantly between the five primary forest types on Kolombangara (Table 4.5). Two forest types on the West Coast (I and III) had a particularly low species richness and diversity and are characterised by a high abundance of the shade-tolerant species *Dillenia salomonensis* (means of 50 % and 11 % of all stems > 9.7 cm dbh on these two forest types respectively). Forest type II, also on the West Coast, had the highest species richness and diversity and the highest abundance among the five primary forest types of species with relatively gap-demanding seedlings, such as *Campnosperma brevipetiolatum*. The three North Coast forest

Table 4.4   Median and maximum annual diameter growth rates (mm yr^{-1}) for four functional groups of tropical tree species defined on the basis of seedling shade tolerance characteristics (Table 4.1). The number of species-level median or maximum values contributing to each functional group value of median or maximum growth rate is indicated by N. Kruskal-Wallis H and associated probability values (*, P < 0.05, otherwise non-significant) are indicated.

Functional Group	4.9 – 10 cm			> 10 – 20 cm			> 20 – 30 cm			> 30 – 50 cm			> 50 – 70 cm			> 70 cm		
	Med.	Max.	N	Med.	Max.	N	Med.	Max.	N	Med.	Max.	N	Med.	Max.	N	Med.	Max.	N
1	1.6	12.4	4	2.2	11.6	4	4.1	13.7	4	5.2	18.6	4	6.1	14.1	4	6.2	17.4	4
2	1.7	16.0	3	2.4	18.8	3	4.8	22.2	3	5.8	20.1	3	8.8	19.5	3	8.0	17.0	3
3	2.8	25.6	2	7.1	25.2	2	16.2	31.8	2	14.1	34.5	2	4.6	23.5	2	6.1	27.9	2
4	0.9	5.4	3	1.9	13.3	3	2.6	17.9	2/3	4.8	16.1	3	4.4	20.0	3	3.9	15.2	3
Kruskal-Wallis H	0.71	5.97		3.11	4.85		6.14	8.32*		4.85	4.01		4.27	8.22*		2.37	1.79	

types (IV, V and VI) were intermediate in their species richness and diversity at the 1964 census (Table 4.5).

Mean canopy disturbance in response to cyclone Isa in 1970 correlated positively with mean species richness of stems > 9.7 cm dbh (r = 0.959, P < 0.01) and diversity (r = 0.881, P < 0.05) per plot at the 1964 census for the five primary forest types on Kolombangara (Forest type VI was excluded as described above). The percentage canopy disturbance for the most heavily impacted Forest type (II) was almost twice that of the least damaged Forest types (I and III), despite their geographical proximity on the west coast of Kolombangara (Figure 4.1). Species richness and diversity of the primary forest types in 1964 were also significantly positively associated with mean annual recruitment rates during 1971-1975 and turnover rates over the interval 1964-1975 (for details see Burslem & Whitmore 1999). In

Table 4.5   Mean (and standard error) number and diversity (Fisher's α) of tree species >9.7 cm dbh on 0.6 ha plots in 1964, rates of canopy disturbance (% plot area yr^{-1}) between April 1970 and February 1971, mean annual recruitment rates 1971-1975 (% yr^{-1}) and turnover 1964-1975 for five primary forest types on Kolombangara, Solomon Islands. The number of replicate plots within each forest type is indicated by n, and degree of significance (variance ratios following analysis of variance) as follows: *, P < 0.05; ***, P < 0.001. Within a column, means that do not share a superscript letter differ significantly (P < 0.05, Tukey test).

Forest type	n	Species number 1964	Fisher's α 1964	Canopy disturbance 1970	Recruitment 1971-1975	Turnover 1964-1975
I	4	42.5 (0.96)[a]	14.9 (0.28)[a]	53.4 (5.04)	1.56 (0.41)[ab]	0.90 (0.20)
II	3	61.7 (0.88)[b]	27.9 (2.39)[b]	91.2 (6.02)	7.70 (2.20)[b]	2.84 (0.51)
III	4	43.3 (4.09)[a]	14.6 (2.11)[a]	53.6 (17.9)	1.12 (0.47)[a]	1.33 (0.36)
IV	3	55.3 (5.81)[ab]	19.8 (2.93)[ab]	79.5 (9.39)	4.72 (2.53)[ab]	2.18 (0.94)
V	3	51.0 (2.80)[ab]	18.3 (1.24)[a]	80.9 (7.49)	2.48 (1.58)[ab]	1.77 (0.79)
F		5.73**	7.87**	2.37	3.34*	1.84

summary, species rich forest stands in 1964 were relatively more heavily impacted by a cyclone in 1970 than stands that were species poor in 1964, but the recruitment of new stems was also significantly faster in these species rich stands in the post-cyclone recovery interval.

Long-term changes in species relative abundance
The relative abundance of the 12 common big tree species did not change significantly when compared between plots or Forest types and when relative abundance was measured in terms of stem number or basal area (e.g. Figure 4.4). Although there were reductions in the mean density of many species in response to the cyclone impacts in the late 1960s, the autocorrelation between mortality and recruitment rates over time (Figure 4.3b) resulted in very little change in relative abundance after a period of 3.5 – 8 years had elapsed since the last cyclone.

(a)

(b)
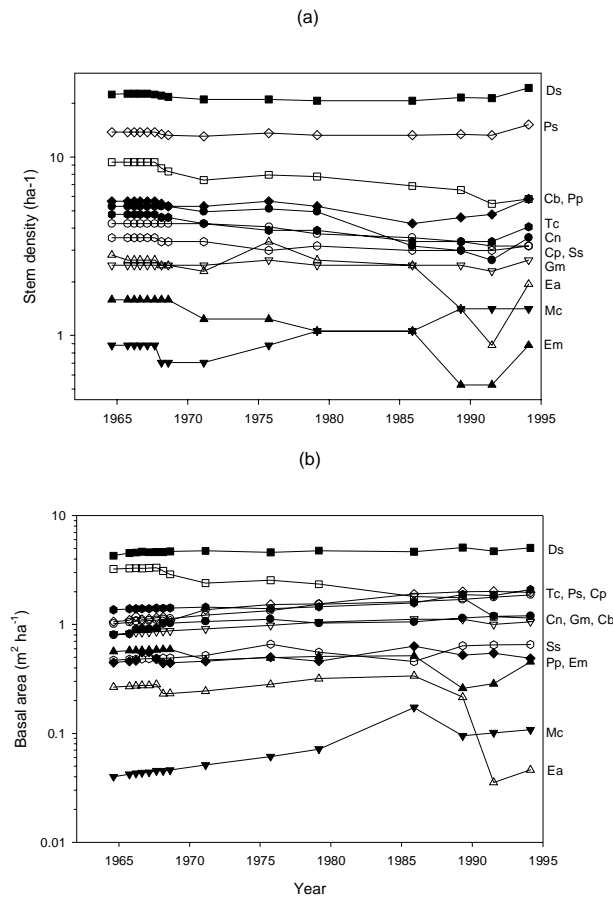
Figure 4.4 Log mean stem density and log mean basal area of 12 tree species in lowland tropical rain forest on Kolombangara, Solomon Islands, comparing all nine plots over 1964-1994. Two letter codes correspond to the species listed in Table 4.1.

73

Discussion

Interspecific diversity in functional characteristics

The 12 species studied in detail on Kolombangara were arrayed along a spectrum of seedling shade tolerance on the basis of their distributions in relation to canopy openness (Whitmore 1974). The sample includes species that have strongly shade-tolerant seedlings, such as *Dillenia salomonensis*, as well as species with light-demanding seedlings, such as *Endospermum medullosum* (Table 4.1). The four functional groups defined on the basis of seedling shade tolerance differed significantly in terms of adult wood density, growth rates, mortality rates in non-cyclone intervals and recruitment rates (Table 4.3), as well as other factors not presented here such as crown exposure and growth responses to a small increase in light (Burslem & Whitmore, unpublished data). These traits are inter-correlated among species and define a continuum of life history characteristics that is reflected in differential rates of population turnover between species. Other studies of tropical forest trees have suggested that mortality rates are correlated positively with growth rates and inversely with wood density across species (Manokaran & Kochummen 1987, Swaine *et al.* 1987, Swaine & Whitmore 1988), but these relationships are rarely quantified. A summary of the general characteristics of representatives of the extremes of this continuum is given in Table 4.6.

Two conclusions emerge from the summary of life history diversity among the common tree species of Kolombangara presented here. First, there is not a perfect correspondence between seedling shade tolerance classes (Table 4.1) and the life history continuum defined on the basis of the characteristics of saplings and trees > 4.85 cm dbh (Table 4.6). For example, *Campnosperma* and *Elaeocarpus* possessed the highest mortality rates overall yet were found by Whitmore (1974) to possess seedlings with a greater degree of shade tolerance than *Endospermum*, *Gmelina* and *Terminalia*, and seedling shade tolerance class was also a poor predictor of

Table 4.6   Life-history correlates of demographic parameters among 12 big tree species on Kolombangara, Solomon Islands

	'High turnover' species	**'Low turnover' species**
Mortality rates	High	Low
Recruitment rates	High	Low
Diameter growth rates[1]	High (5-20 mm yr^{-1})	Low (2-7 mm yr^{-1})
Diameter growth rates[2]	Low (3-7 mm yr^{-1})	Low (3-9 mm yr^{-1})
Crown Exposure Index (1-5)	3	1 – 4
Diameter growth	Low or High	Low
in shade (stems 5-10 cm dbh)	(1-6 mm yr^{-1})	(1-2 mm yr^{-1})
Growth response[3]	High	Low
Mortality in shade (all stems)	High (6 - 12 % yr^{-1})	Low (< 2 % yr^{-1})
Wood density	Low (330-350 kg m^{-3})	High (550-660 kg m^{-3})
Example species	*Campnosperma brevipetiolatum*	*Dillenia salomonensis*
	Elaeocarpus angustifolius	*Parinari papuana*

[1]stems 10-50 cm dbh; [2] stems >50 cm dbh; [3] to increase in light.

differences in mean annual recruitment rates, growth rates and wood densities for trees >4.9 cm dbh (Table 4.3). Clark & Clark (1992) have proposed that the life history characteristics of tropical tree species may change through ontogeny, a conclusion that is supported by this study and elaborated by us elsewhere (Burslem *et al*. 1998).

Secondly, it is clear that the common tree species also differed in their susceptibility to mortality during the first cyclone (Table 4.2), as found in other studies (Wadsworth & Englerth 1959, Lugo *et al*. 1983, Foster 1988, Basnet *et al*. 1992, Zimmerman *et al*. 1994). Although mortality during the cyclone was not correlated with mortality rates estimated from non-cyclone intervals or with wood density, it is clear that some of the species with a high proportional mortality during the cyclone (*Campnosperma* and *Elaeocarpus*) possess a low wood density and other characteristics typical of pioneer species (Table 4.3). The high percentage mortality of *Maranthes* is anomalous in this context, and may be a chance outcome of an indirect cause, as most stems killed were small in size and were probably killed by other trees falling on top of them (Whitmore 1974, Bellingham *et al*. 1995). Architectural properties may also account for low mortality in some species. For example, *Dillenia salomonensis* is characterised by a lower height/diameter quotient for a given diameter than all the other species (personal observations), while big trees of *Terminalia calamansanai* have huge buttresses (Whitmore 1966).

Despite the lack of a significant relationship between mortality rates induced by the first cyclone and mortality rates during other intervals, mortality rates estimated over the full 30 years of the study correlate positively with recruitment rates estimated over the 30 year interval (Figure 4.3b). Interspecific differences in these rates of population turnover are in turn associated with differences in the demographic and life history characteristics listed in Tables 4.3 and 4.6. Thus, the long-term nature of this study has allowed us to distinguish short-term noise determined by the stochastic impact of the cyclone from the long-term demographic signal imposed by the inherent properties of the species. Since relative abundance is determined by the balance between mortality and recruitment, and these are strongly inter-correlated in our sample, the life-history continuum described above may also be regarded as a demographic continuum, ranging from species that have high population turnover rates in the community to species with low rates of population turnover. The consequences of these differential population dynamics will be discussed below.

Diversity and species composition
In comparisons among the five primary forest types on Kolombangara, species richness and diversity were positively related to rates of canopy disturbance during a cyclone and to the rates of recovery by recruitment subsequently (Table 4.5 and see Burslem & Whitmore 1999). The differences in the resistance and resilience of forest types to cyclone impact were determined by the characteristics of the species that were abundant in the contrasting forest types. The common species with low density timber (such as *Campnosperma*, *Elaeocarpus* and *Endospermum*) reach their greatest abundance in the forests that were most species rich and diverse in 1964 (forest types II and IV), while the forests that were species poor in 1964 were

heavily dominated by the dense-wooded species *Dillenia*. Since the 'high turnover' species were inherently susceptible to the impact of disturbance, the forests where they were abundant were most heavily disturbed during the cyclone. However, the ability of these species to grow fast and recruit quickly contributes to the greater resilience of these forest types. Conversely, the characteristics of *Dillenia* contribute both to the high resistance and the low resilience of the species-poor forest types in response to disturbance. Thus, responses to disturbance at the community level are influenced strongly by the life history characteristics of key abundant species in the community, and were associated with differences in community diversity. In this community, as in many others tropical forests (Phillips *et al*. 1994), diversity, disturbance and dynamism were all positively inter-related.

The lack of a significant change in the relative abundance of the 12 most common species over the 30-year interval provides an independent illustration of the importance of fundamental demographic characteristics to community composition (Figure 4.4). Our data suggest that the trade-off between survival and recruitment illustrated in Figure 4.3b is a potential cause of the maintenance of a stable rank hierarchy of species relative abundance over time. Although a positive relationship between mortality and recruitment rates across species has been noted by previous authors (e.g. Okuda *et al*. 1997), its significance for maintenance of rank relative abundance hierarchies over time has not been noted.

Conclusions

We interpret these findings as evidence of processes operating to maintain equilibrium species relative abundance among the common tree species on Kolombangara. The life history characteristics that determine differential mortality and recruitment rates between species are also key determinants of a species' position along the demographic continuum and therefore their resistance and resilience in response to disturbance. These characteristics centre on the fundamental trade-off between allocation of resources to traits that determine persistence (high density wood, slow growth rates and low mortality) and those that enhance growth and reproduction (manifested as high recruitment rates). The Kolombangara data-set illustrates the significance of this trade-off for long-term community dynamics in a tropical forest subjected to one type of large scale disturbance.

Elements of Connell's (1978) Intermediate Disturbance Hypothesis (IDH) receive support from our research on Kolombangara. For example, by invoking the relationship between timber density and susceptibility to damage during severe wind storms (Putz et al. 1983, Zimmerman et al. 1994), it is possible to interpret the positive relationship between diversity and canopy disturbance during the April 1970 cyclone as a prediction of the IDH (Table 4.5, see also Burslem & Whitmore 1999). As we emphasise above, the positive relationships between Forest Types in their diversity in 1964, susceptibility to disturbance in 1970 and post-cyclone recruitment rates are determined by trade-offs in the life history characteristics of the common species present, as reflected in their demographic rates. It is evident that

76

these trade-offs have contributed to the maintenance of a consistent hierarchy of species' relative abundance over a thirty-year interval, but confirmation of the relationships between demography, forest dynamics and long-term changes in forest diversity remains to be determined by future research.

5 LONG-TERM EFFECT OF TIMBER HARVESTING IN MAPANE – NORTH SURINAME

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Abstract

We present a comparison of tree inventories and results of permanent sample plots in north central Suriname. Two harvests in this relatively rich forest did not lead to large changes in species composition and tree diversity. This suggests that the forest is rather resilient to a few of such interventions. The best prediction of a species abundance in 1997 was its abundance in 1981. However, a number of fast growing species from the genera *Cecropia, Pourouma* and *Inga* profited more than average from the disturbances. Tree α-diversity decreased slightly with increased activities (silvicultural treatments) but species richness decreased more significantly. Rare species were more likely to disappear from plots than common one and run a risk of disappearance from the forest under a continuous regime of harvesting and liberations.

Introduction

Much of Suriname's forest is still quite intact. Although logging has had a relatively long history in Suriname much of this took place in the forestry belt, more or less parallel to the coast, mainly due to the inaccessibility of the interior (de Graaf 1986, Jonkers 1987). As a result, most of the interior forests remained untouched to date.

Whereas the earliest logging records date back to the 1600's (*Brosimum guianense*, Jonkers 1987), the first silvicultural experiments were started in 1904, after the formation of the Forestry Department (Gonggrijp & Burger 1948). For later experiments see Schulz 1960, Boerboom 1965, Vink 1970, de Graaf 1986, Jonkers 1987 and Hendrison 1990.

CELOS (Centre for Agricultural Research in Surinam) research has played a central role in the development of silvicultural systems in Suriname. The CELOS Silvicultural System (CSS) was initially developed from small-scale experiments and finally tested at semi-practical scale (de Graaf 1986). The aim of the CSS was to produce good quality timber in relatively short cycles in lightly exploited and unexploited 'mesophytic forest' in Suriname. To restore the proportion of commercial species after harvest, non-commercial trees are removed by either refinement (de Graaf 1986) or liberation (Jonkers 1987). The purpose of these treatments is to reduce stand level basal area to c. $12m^2$. Three treatments are planned between harvests at 0, 8 and 16 years after harvest. The refinements are not meant to eradicate non-commercial species but to reduce their proportion in the stand (de Graaf 1986). Due to the reduced competition, individuals of commercial species were expected to show higher growth rates (De Graaf *et al*. 1999). It was expected that a regrowth of c. 40 m^3 of commercial species could be realised in 20 to 25 years, of which 25 m^3 could be harvested again after 25 years (de Graaf 1986).

The main aim of the CELOS Harvesting System (CHS, Hendrison 1990) was to introduce planning in a forest operation and to improve the quality of the residual

stand by minimising felling and skidding damage. Results showed that higher input (planning) costs could be earned back due to higher efficiency of stem removal (Hendrison 1990). Together the CSS and CHS form the CELOS Management System (CMS).

Conceptually, a few potential problems exist with regard to the long-term effect of the CSS (ter Steege & Hammond 1996). As treatments increase the 'disturbance', they may have a side effect in further promoting the abundance of short-lived pioneers. Secondly, the CSS significantly affects the tree-diversity in its process of 'domestication' (de Graaf 1986, de Graaf *et al.* 1999), including the diversity of commercial species. It can be expected that especially rare non-commercial species will finally be removed from the stand by continuous refinement or liberation treatments. Although it is generally understood that 'domestication of the forest" (sensu de Graaf) will lead to a change in composition and loss of species we have no information as to how large these changes are in Suriname. Another problem is that selective pressure on tree form and quality is high, leading to impoverished genetical composition. A last problem relates to the market situation: trees considered non-commercial may become commercial at a latter stage, a potential problem in all silvicultural systems that use liberation or refinement as standard procedures. In the Mapane plots studied here the presence of very large dead *Couratari* individuals evidently shows that at the time of intervention this species was non-commercial. At present, however, the species is well marketable. The treatments, carried out to improve the commercial value of the forest, have thus also inadvertently led to an unforeseen destruction of future capital.

Whereas the effects of the CSS have been studied with regard to the re-growth of volume and basal area of the commercial stock (e.g. De Graaf *et al.* 1999), less attention has been paid to changes in population sizes (but see Dekker & de Graaf 2003), forest composition and tree diversity. Personal observations in the Mapane area suggest that especially pioneers of the genera *Cecropia* and *Pourouma* have become overabundant.

With data from 1981 and 1997 of 15 one-ha plots in the centre of the Mapane area, and data of a larger area from 1954, before any extraction, we here describe the effects of two light commercial harvesting operations and silvicultural treatments, following one another, on species composition and tree diversity. Much of the expected changes in tree composition after logging are to be expected from fast growing species with relatively low wood density and relatively small seeds (Swaine & Whitmore 1988, Chapter 1). By classifying species into functional groups based on wood density and seed mass, two characters which we consider to be 'disturbance sensitive' (ter Steege & Hammond 2001, Chapters 1, 8), we try to assess if such properties are related to success or failure in recruitment over the years. In other words whether or not we can predict the success of species in this system based on characters used to classify species into functional groups (Chapters 1, 8). We furthermore assess the success of commercial recruitment on a population basis and success of the silvicultural treatment that are central to thinking in the CELOS silvicultural system.
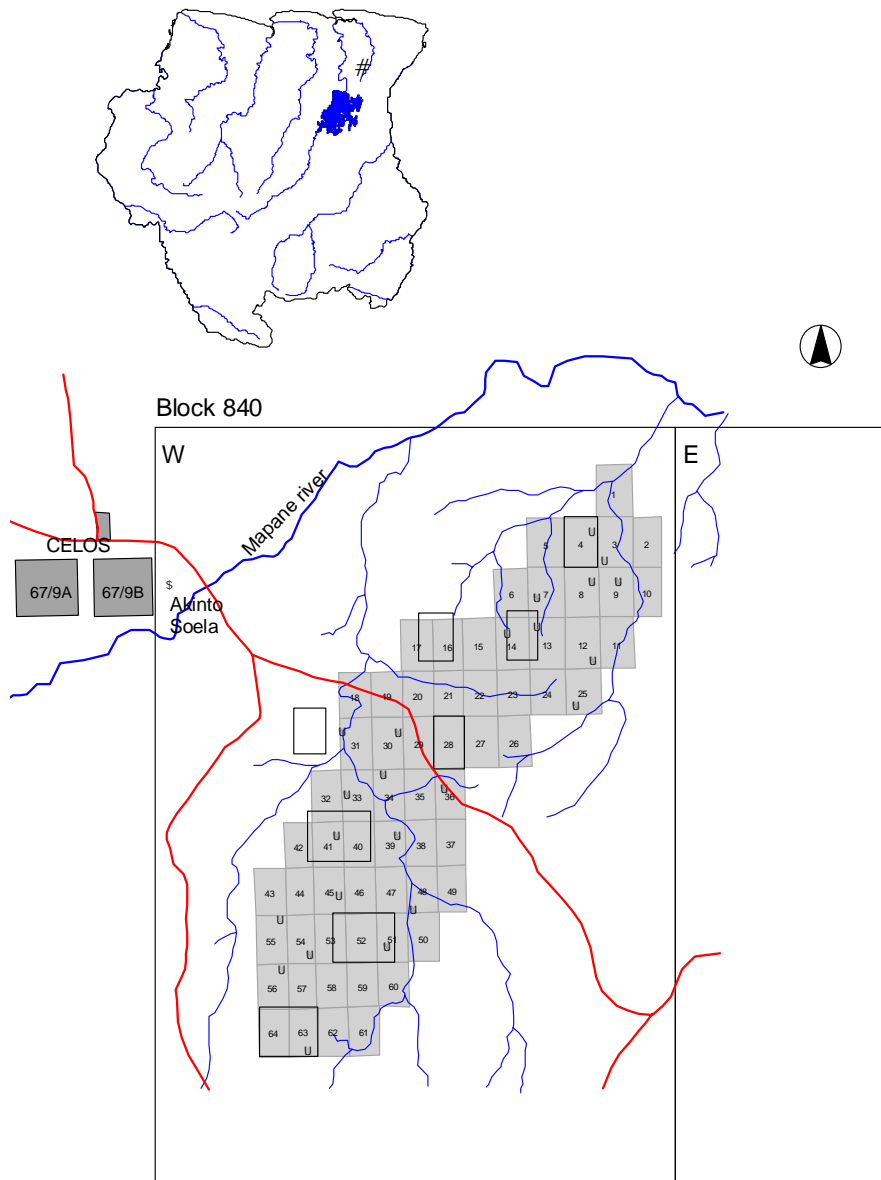
Figure 5.1   Location and lay-out of the plots used in the Mapane study area. The 1954 inventory block 840 is only partially visible. The grey blocks numbers are the 64 LBB blocks. Small grey squares indicate the 1-ha 'de Vletter' plots. The larger (10 & 20 ha) rectangles are the 8 treatment blocks of Hendrison (1990). De Graaf's plots (Expt 67/9A & 67/9B; de Graaf 1986, de Graaf *et al*. 1998) are located just outside block 840. Further information of the plots can be found in the text.

Study site and methods

Site description

Mapane is located approximately 100 km south of the capital Paramaribo, between the Suriname and Commewijne Rivers (Figure 5.1). Mapane is one of the five management zones in the forestry belt of Suriname. Most of the area has been exploited lightly and some 4000 ha of plantations of *Pinus caribbea* have been established (Hendrison 1990). Forest activities in the area started in the 1950's (Hendrison 1990). Very importantly, the Mapane area has been a major focus for forest research in Suriname (Schulz 1960, Boerboom 1964, de Graaf 1986, Hendrison 1990).

The soils of Mapane are part of the Zanderij formation (comparable to Berbice formation in Guyana and the 'sables blancs' of French Guiana), and in Mapane these soils consist mainly of Ferralsols and some Leptosols. They are poor in nutrients and covered by mixed rain forest (47,000 ha). Some high savannah forest (analogous to Wallaba forest in Guyana) is present, mainly on bleached white sands (albic Arenosol, 5,000 ha). Along creeks marsh forest (11,000 ha) is found (Hendrison 1990).

Forest inventories 1953 - 1954

The first forest inventory in Mapane was carried out by the state forest service (LBB) from 1953-1954. Some 25 blocks were demarcated between the Commewijne and Suriname Rivers. Trees over 35 cm diameter at breast height (dbh) (Vink 1983) were inventoried on 10 m wide strips that were cut in E-W direction at 500 m intervals, resulting in a 2% sample (Schulz 1960). The inventory blocks were 8.3 by 8.3 km (6889 ha) and included 17 lines. They were subdivided into a western and eastern compartment. Blocks 836 and 840 are situated in the area where most of the silvicultural work has been carried out. Plots of Schulz (1960) and the Graaf (1986) are located within block 836 and the plots of Hendrison (1990), which will be used here, are located within the western section of Block 840 (Figure 5.1). Although most of the original field data has been lost, copies of field data for some blocks were still present at the National Herbarium Netherlands, Utrecht Branch, among which the two Mapane blocks. For purpose of comparison, the data of Block 840-W is used here, as the Permanent Sampling Plots, established later (see below), are all located in this block section.

First harvesting

Harvesting started in 1957. Over the forestry belt, approximately 30 concessions varying from 1600 to 6400 ha were granted. From 1957 to 1970 only 8 species were harvested. Official log production was low, approximately 8-10 m^3 ha^{-1}. In 1970 most of the concessions had been worked once with this highly selective system (Hendrison 1990). In 1981 the highest felling intensity was 8 trees ha^{-1} (Blocks 21, 22, 23, Fig. 5.1). Forty percent of the blocks had a felling intensity of 4-6 tree/ha, 30% were very lightly logged, whereas another 30% of the blocks were untouched (Hendrison 1990). Hence the exploitation can be considered relatively light but varying by location. Damage was reported to be difficult to assess, as old felling

gaps were difficult to distinguish from natural gaps. Total gap area (natural and man-made) was 6%. Skid trails were easily recognized because of their distinct vegetation. In spite of the low harvesting level, the loss of certain commercial trees was considerable: *Goupia glabra*, *Dicorynia guianensis*, *Nectandra rubra* and *Ocotea* spp. were harvested in quantities of 6 m^3 ha^{-1} each. In 1981 the area still had as much as 35.4 m^3 ha^{-1} (North) and 32.9 m^3 ha^{-1} of commercial and potentially commercial species, enough for a viable economic extraction (Hendrison 1990), notably for *Vouacapoua americana* and *Tetragastris altissima*.

CELOS harvesting studies 1981 (after Hendrison 1990)
In 1980 an experiment was set up to test reduced impact harvesting (CHS) in the Mapane area. The study was carried out in a part of the area that had been logged with chainsaw and skidder some 10 years before the start of the experiment. An inventory was carried out to assess forest tree composition in the remaining stand. Plots were located just east of the bridge at Akinto Soela (Figure 5.1). The research site was divided into 64 rectangular inventory units of 250 x 400 m (10 ha). These blocks are visible in Figure 5.1 as the slightly slanting grid. Corners of the plots were marked with aluminium labels on wooden pickets. Commercial trees were enumerated by LBB (The Surinamese State Forest Service) in a strip of 40 x 250 m in each inventory unit (details in Hendrison 1990). As only the commercial trees were enumerated this information is not used here. For the damage study 8 logging compartments were established (Figure 5.1).

The 'de Vletter' plots
In the framework of the research project "Natural Regeneration" 23 one-ha permanent sample plots (PSP) were established in the Akinto Soela research area in 1981 (de Vletter 1980, Bus & Laumans 1997). These 23 plots are known locally as the 'de Vletter plots'. All trees with DBH ≥ 15 cm were enumerated and marked on PSP's of 100 x 100 m, subdivided into 25 sub-plots of 20 x 20 m. Within each PSP trees between 5-15 cm were recorded from 3 subplots (0.12 ha), together forming a Permanent Central Quadrant (PCK).

Further plot establishment
In 1982 Hendrison established 8 plots of 10/ 20 ha to study the effect of low impact harvesting (Hendrison 1990). The plots and surrounding area were logged from 1982 to 1984, at an intensity of c. 15 m^3 ha^{-1} (Bus & Laumans 1997). It was intended that all plots would receive a uniform refinement (sensu de Graaf) but this did not happen. From 1984 to 1986 Mallants added a number of plots and changed treatments on other plots. His plots were situated so that sets of three plots existed over the area with one plot untreated; one plot selectively refined (S treatment); and one plot uniformly refined (D treatment). The D treatment consisted of frilling all trees above a certain dbh to reduce BA uniformly to 12.5 m^2. This treatment was carried out in the plot and a buffer zone of 25, or sometimes 50, meter around the plot (Bus & Laumans 1997). The uniform treatment was always carried out on a 'de Vletter' plot, the other two on new 'Mallants' plots. Finally in 1997, Bus and Laumans reinventoried 15 of the 23 de Vletter plots, some of which had been treated by Mallants. To compare the effects of uniform treatments on forest composition

and diversity we can thus use the D-plots and the control plots. These plots were relocated and re-established to match the situation of 1981. Great care was taken to relocate all trees. Those trees dead or not relocated were considered dead and new trees were considered recruits. If the tree still carried a number, the name was checked from a list. DBH was measured at the same height/location as in 1984, unless buttresses or callus made this impossible. If the name of 1981 and 1997 did not agree the name given in 1981 was taken (Bus & Laumans 1997).

The 15 plots can be divided into three sets of five plots each:

1.   NTS (Not Treated South): Plots logged in 1983 and not further treated. The plots are all located in the southern half of the area.
2.   TS (Treated South): Plots logged in 1983 and uniformly treated in 1994/5 in the southern half.
3.   TN (Treated North): Plots logged in 1983 and uniformly treated in 1994 in the northern half.

Functional groups
For this study we defined three groups of species based on life history characteristics that are thought to be important for the successional status of species (see Finegan 1996, Favrichon 1994, ter Steege & Hammond 1996, ter Steege & Hammond, 2001). Based on: 1) the fact that all pioneers cited in the above references had an air-dry wood density below 700 kg m^{-3} and 2) the fact that among the pioneers, the so-called short lived pioneers tend to have the smallest seeds (Chapter 1, 8), we classified species on the basis of their wood density and seed mass (logarithmic classes sensu Hammond & Brown 1995, data from ter Steege & Hammond 2001). The three 'plant functional types' thus derived can be summarised as (Chapter 1, 8):

1.   Small seeded softwoods (SSW) : wood density < 0.7 g cm^{-3}, seed mass < 0.1 g
2.   Large seeded softwoods (LSW) : wood density < 0.7 g cm^{-3}, seed mass $\geq$ 0.1 g
3.   HWD (hardwoods)   : wood density $\geq$ 0.7 g cm^{-3},

Analysis of the data
Based on the data from 1954, 1981 and 1997 we compare the forest's original (1954) tree composition and that after one (1981) and two (1997) light harvests. We do not analyse these data statistically, as the inventory methods are too dissimilar.

The plot data of 1981 and 1997 (de Vletter plots) are repeated measures from an ANOVA point of view. However, due to spatial autocorrelation in the data the plots are not necessarily independent data sources. Hendrison (1990) showed that the plots from the northern half occur on a slightly different soil type than those of the south and differ slightly in species composition. As we have only treated plots from the north they can therefore not be used for comparison, as we are unsure if differences arise due to location or treatment. Thus, for the statistical analyses only the ten plots from the south are used.

We used Detrended Correspondence Analysis (DCA) and Principal Component Analysis (PCA) for a descriptive analysis of tree composition for both the PCK's (trees under 15 cm) and of the PSP's (trees over 15 cm) based on abundances. Even here a conceptual problem exists. As many trees will remain in each plot ($N_{97} = N_{81}$ − $N_{mortality}$ − $N_{treated}$ + $N_{recruitment}$), the repeated data for each plot will be temporally autocorrelated. While the rule in the repeated measures ANOVA below, in the DCA and PCA this is a bit of a conceptual problem but useful to make out point later.

To detect differences in the plots as caused by the treatments we used ANOVA with repeated measures. We tested tree density, species richness, tree diversity, commercial stock and non-commercial stock and densities of the functional groups.

In order to see if species with low or high wood density and low or high seed mass recruit differently, we first tested their relationship with growth of the most common species. After this we tested if growth, wood density, or seed mass conferred an advantage for recruitment in the plots. This analysis was carried out on the data of all the 15 plots, mainly with standard regression analysis.

Results

Compositional changes
A total of 6130 trees (182 species) were recorded on the 11 recovered lines of block 840 (total area 91 ha). In 1954 the most abundant taxa in block 840 were (in order of abundance): *Eperua falcata, Tetragastris altissima, Eschweilera subglandulosa, Lecythis corrugata, Protium* spp., *Couratari stellata, Dicorynia guianensis, Inga* spp., *Licania* spp., and *Carapa procera*, together amounting to some 39% of all trees. (See Figure 5.2 for a list of most common genera). The forest in Mapane has a high percentage of pioneers (SSW + LSW). The soft woods are separated into the small seeded ones (3.3% of all ind.) and the large seeded ones (30.2%! of all ind.). The hardwoods of Functional Group 3 (HWD) are the most important ones with 62.7%.

General composition in 1981 was not very much different from 1954 (see also Figure 5.2). The most abundant species were (in order of abundance in the plots): *Tetragastris altissima, Eperua falcata, Eschweilera coriacea, Inga bourgoni, Couratari stellata, Pseudopiptadenia suaveolens, Carapa procera, Eschweilera subglandulosa, Lecythis corrugata, Protium polybotryum*, which together amounted to 50% of all trees ≥ 25cm.

Overall composition in 1997 was again not very much different from the previous censuses. The ten most abundant species were: *Tetragastris altissima, Inga bourgoni, Eperua falcata, Eschweilera coriacea, Lecythis corrugata, Cecropia obtusa, Pseudopiptadenia suaveolens, Carapa procera, Eschweilera subglandulosa, Cecropia sciadophylla*. Despite the small change, note the twice-increased position of *Inga* (since 1954) and the inclusion of two *Cecropia* sp. in the top ten! Two *Pourouma* spp. also increased substantially and ranked 11 and 15 in 1997.
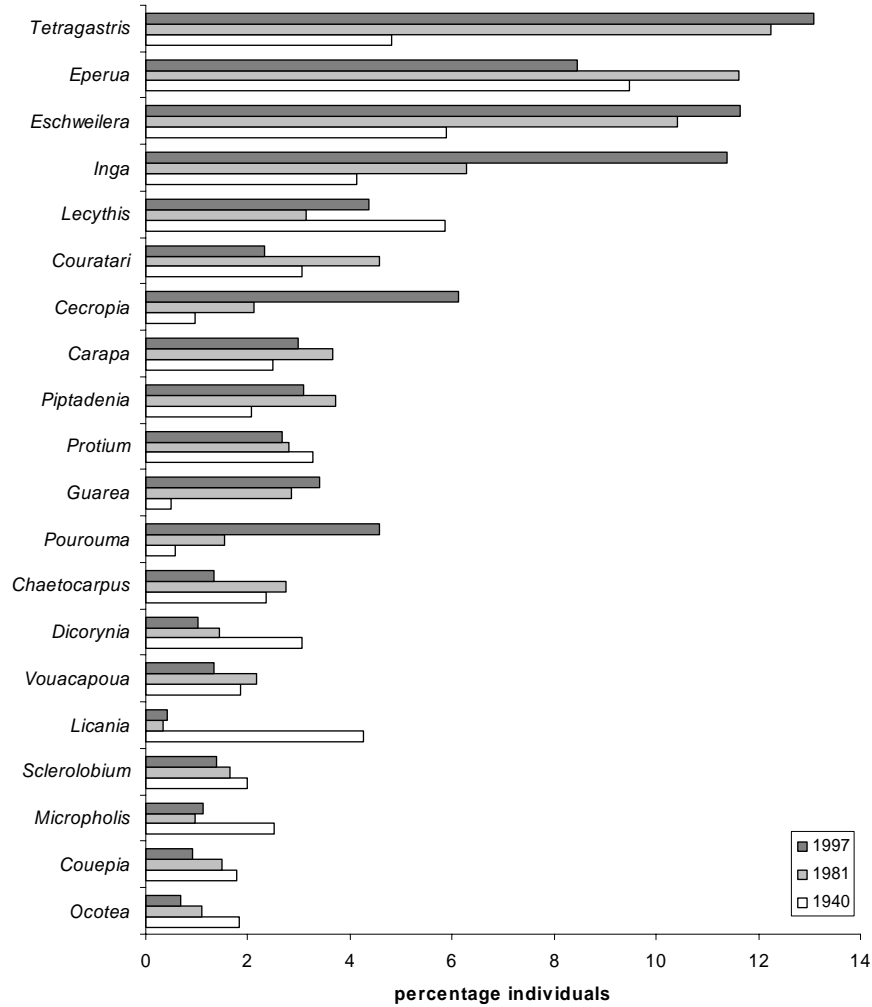
85

Figure 5.2   Abundance of the 20 most common genera expressed by the percentage they make up of all individuals inventories in 1954 (lowest bar), 1981 (middle bar) and 1997 (upper bar). The large differences in abundance of *Licania* and *Eschweilera* in 1954 on the one hand and 1981 and 1997 are most likely partially 'block effects'. Many least common genera show a consistent decrease, whereas pioneers such as *Cecropia, Pourouma* and *Inga* show a consistent increase.

Both the tree composition of the PSP's (trees over 15 cm) and of the PCK's (under 15 cm) remained relatively constant from 1981 onwards. In both DCA (Figure 5.3) and PCA (data not shown) analysis the repeated measurements of the plots were always very close together. DCA and PCA also gave very similar results as to the relative position of the plot-pair data in the bi-plot. This suggests that the original composition dominated the analysis and was relatively robust with regard to analysis technique.
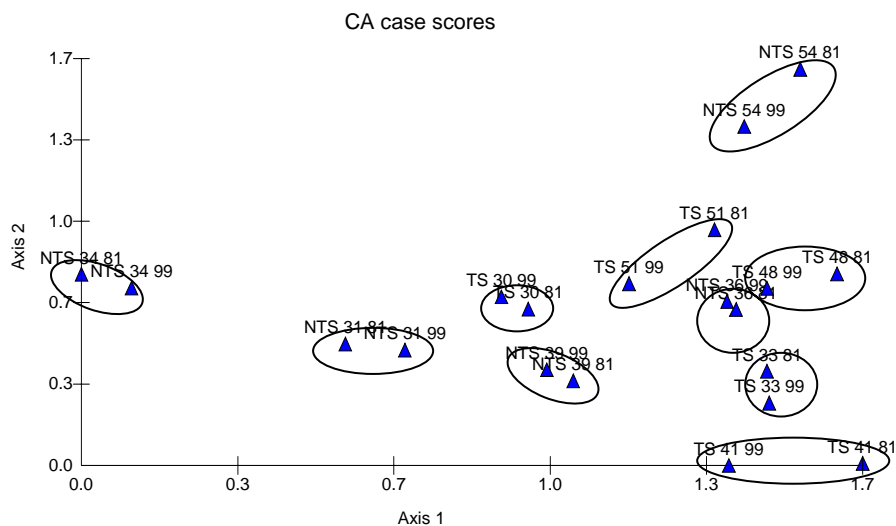
Figure 5.3   DCA bi-plot for PCK's (trees smaller than 15 cm). The circles connect repeated measurements of the same plots in 1981 and 1999. NTS: not treated south; TS: treated south; first number: plot nr; second number year of measurement.

A comparison of the locations of the plots in the DCA-bi-plot (Figure 5.3) with the location of the plots (Figure 5.1) suggested that plots were ordered by the DCA in a north to south direction. Location of the plots in a north south direction, as indicated by the row numbers of the blocks (lowest row being row 1), shows a trend with Axis 1 scores for the plot data of 1981 (i.e. before the treatments took place, $R^2 = 0.29$, P = 0.11). Constraining the DCA with the row numbers of the blocks (CCA = Canonical Correspondence Analysis) resulted in a new ordination sequence, in which row number had a correlation with Axis 1 score of -0.914. Because most of the non-treated plots are located (by chance) in the northern part of the southern section, in 1981 they are nearly significantly different in their Axis score from the treated plots (t-test, t = -1.85, P = 0.069). This suggests that the plots were not well distributed over the treatment classes with respect to their composition.

Functional Groups
Overall density of large trees was not different between treatments due to high variation (Table 5.1). Density of smaller trees increased significantly from 1981 to 1997 (Table 5.1), most likely due to increased space and light levels. SSW increased significantly from 1981 to 1997 and the nearly significant interaction suggests that this was mainly caused by an increase of SSW in the treated plots. There was no change in LSW but HWD decreased significantly in both treatments from 1981 to 1997. In the small trees SSW did not change significantly but LSW increased significantly in both treatments, concurrent with a significant decrease in HWD.

Table 5.1   Results for the PSP plots (trees ≥ 15 cm dbh) and PCK plots (trees < 15 cm dbh) of the southern part of the research area (TS and NTS) of tree densities for all trees, commercials and non-commercials; diversity indices; and percentages by functional groups. Only P values for ANOVA with repeated measures are given. Significant P values are in bold italic. If only the treatment effect is significant this can be caused by differences in the plots before or after treatments. If only year is significant changes are similar on all plots between the years – silvicultural treatments have no additional effect. A significant interaction indicates that the treatment effects are not of the same magnitude or direction over the years. Hence, this signifies a temporal effect of the treatments, which is the main effect of interest.

	Non-treated		Treated		ANOVA, repeated measures		
	1981	**1997**	**1981**	**1997**	**Treatm.**	**Year**	**Int.**
Large trees (>15 cm)							
Trees (# ha^{-1})	143.0	147.4	136.4	128.8	0.097	0.689	0.158
Species (S)	50.0	51.2	46.8	40.0	0.077	0.068	*0.017*
Fisher's alpha	27.3	28.1	25.7	20.3	0.164	0.092	*0.034*
Shannon index	3.38	3.4	3.3	3.1	0.073	*0.013*	*0.004*
Commercials/ha	35.6	33.6	45.0	42.6	0.111	0.284	0.919
Non-commercials/ha	107.4	113.8	91.4	86.2	*0.048*	0.848	0.093
SSW (%)	9.7	10.9	5.5	13.9	0.840	*0.015*	*0.051*
LSW (%)	37.1	39.9	35.2	34.4	0.335	0.464	0.201
HWD (%)	53.0	48.9	59.0	51.6	0.396	*0.003*	0.253
Small trees (<15 cm)							
Trees (# ha^{-1})	124.60	134.20	135.80	160.60	0.117	*0.002*	0.087
Species (S)	45.60	49.40	51.20	51.60	0.268	0.061	0.115
Fisher's alpha	26.37	28.56	30.02	26.54	0.753	0.532	*0.021*
Shannon index	3.32	3.42	3.48	3.41	0.536	0.700	0.062
Commercials/ha	22.4	22.0	30.2	28.4	0.359	0.601	0.738
Non-commercials/ha	102.2	111.8	105.4	132.2	0.216	*0.003*	0.087
SSW (%)	8.3	11.3	10.7	10.8	0.634	0.181	0.209
LSW (%)	33.0	37.7	32.9	42.6	0.601	*0.001*	0.133
HWD (%)	57.9	50.1	55.4	46.2	0.580	*0.001*	0.677

Diversity and species richness

In terms of diversity there are slight but significant differences through time (Table 5.1). In 1954 Fisher's α (average of the lines in the inventory block) was 33.7 (data not shown). In 1981 the average for 5 one-ha plots was 27.3 for NTS plots and 25.7 for the TS plots.

While there were no differences in diversity between the treatments in 1981, as was to be expected, there were significant differences in 1997, as indicated by a significant interaction. This difference is caused by a decrease in Fisher's α in the treated plots. By comparison, Fisher's α hardly decreased in the unused TN plots, however (data not shown). On the average a plot treatment cost ca. one species/ha (of large trees) in the north (data not shown) and ca. 7/ha in the south (Table 5.1). In the mean time in the untreated plots the number of species had increased by 1 sp/ha.

The net number of species lost is in fact a balance between species lost and species gained. Most logged plots gained some species and thus lost more in most cases. Most of the species that had a marked increase in abundance (as expressed as (Number of individuals in 1997 +1)/ (Number of individuals in 1981 +1) also showed an increase in the number of plots they were found. Common species never disappeared nor entered, which is logical since they were already common. Species that increased much in abundance (trees >15cm ha^{-1}) and frequency were *Pourouma mollis* (newly appeared among the larger trees in 9 out of 15 plots); *Cecropia obtusa* (7), and *Miconia* spp. (5). Among the smaller trees the most prominent 'invaders' were *Tapirira guianensis* (6), *Pourouma mollis* (6), *Jacaranda copaia* (5), *Cecropia sciadophylla* (5), *Annona montana* (5), *Drypetes variabilis* (5), *Miconia* spp. (5). These species entered either from established smaller seedlings, seed bank, or seed rain from adjacent areas.

Of the species that disappeared from plots, the most striking were *Sloanea garckeana* (lost from 7 plots out of 15), *Diospyros guianensis* (6), *Inga alba* (6), and *Sclerolobium melinonii* (5) among the large trees. None of these are commercial species. Among the smaller trees (<15 cm) no species disappeared from 5 plots or more.

Wood density and growth
For the common species (>5 ind in the PSP's), annual growth showed a significant negative correlation with wood density (R^2 = 0.37, Figure 5.4). The average growth in diameter over the whole 16-year period is ca. 2 cm for the species with wood of 1.2 g cm^{-3} compared to 13 cm for those with light wood (0.4 g cm^{-3}).
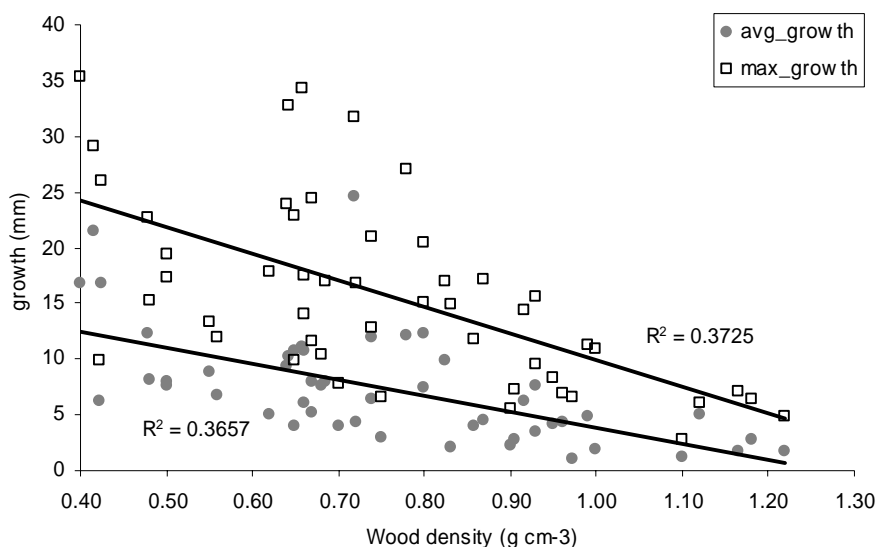

Figure 5.4   Average and maximum growth (mm) over the entire period of common species (> 5 ind.) as a function of wood density (g cm^{-3}).

Recruitment

Faster growth of individuals of a species did not necessarily lead to an increase in the population of that species. The faster growing species in this study are indeed somewhat faster recruiters (R^2 between growth and percentage recruitment = 0.13) than the slow growers, but they also died a little faster (R^2 between growth and percentage mortality = 0.04). As a consequence, the correlation between maximum or average growth and population increase of species (N97/N81) is very small (R^2 = 0.05 and 0.06); for wood density this correlation is equally low (R^2 = 0.08). Growth of small individuals (trees < 15 cm) is expected to be related to initial seed mass (chapters 1, 2) but here too maximum growth, average growth, wood density and seed mass have very little effect on population changes (R^2 : 0.05; 0.04; 0.10; 0.05 respectively). Hence, the main 'functional' life history characteristics that were used to classify the species into the functional groups were poor predictors of the population increase or decrease of species.

We can assume that recruitment from 1981 to 1997 into the >15 cm size class was mainly dependent on the number of individuals that were present in the <15 cm size class in 1981. Secondly, recruitment into the smaller classes (< 15 cm) can be thought to depend on the seed sources from large adults for large trees but also on the smaller trees that do not reach over 15 cm. As all recruits into the smaller classes are new individuals they are statistically independent of all the trees present in 1981. Both relationships are shown in Figure 5.5. From 1981 to 1997 individuals of 111 species recruited into the > 15 cm class. Ten species make up 63% of that amount. Four of these species, *Inga bourgoni, Cecropia obtusa, Pourouma mollis, Cecropia sciadophylla* do so in much higher percentage than the other species, as shown by their high positive residual value (Figure 5.5). Only *Inga bourgoni* recruited much more than expected from the expected average (regression line in 5.5).
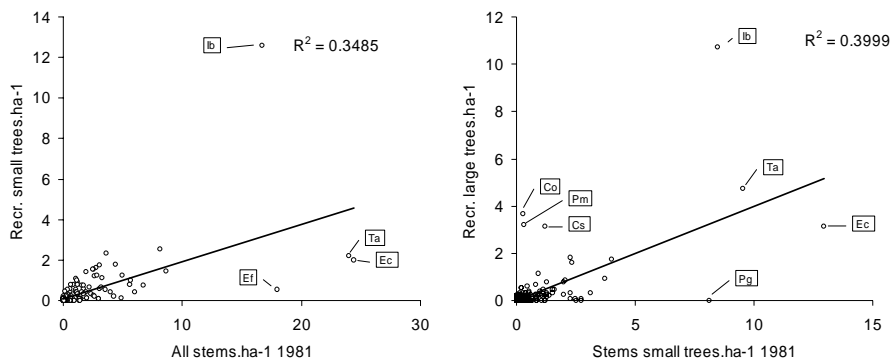

Figure 5.5   Recruitment of new trees (period 1981 to 1997). Left: recruitment into the smaller tree size class (< 15 cm) as a function of all trees present in 1981. Right: recruitment into the larger tree size class (>15 cm) from the smaller size class and as a function of the number of individuals in that class in 1981. Abbreviations : Ib *Inga bourginoni*, Ef *Eperua falcata*, Ta *Tetragastris altissima*, Ec *Eschweilera coriacea*, Co *Cecropia obtusa*, Cs *C. sciadophylla*, Pm *Pourouma mollis*, Pg *Paypayrola guianensis.*

There are also species that recruited less than expected from their initial numbers, *Tetragastris panamensis, Eschweilera coriacea* and *Eperua falcata* recruited less into the smaller trees than expected from their numbers among the larger trees. The lack of recruitment of *Paypayrola guianensis* into the larger size classes, despite its abundance in the smaller classes, is simply caused by its relatively small adult size as an understorey tree and thus not unexpected.

Except for these exceptions it would appear that abundance in 1981 gives a good prediction for recruitment from 1981 through 1997.

Discussion

Two logging cycles in the forest of Mapane have not yet led to an appreciable loss of tree diversity. The changes in composition are indeed so small that plot censuses of 1981 and 1997 are so similar that in an ordination the two repeated measures are always close very together (Figure 5.2). Although changes in composition are small, there is a pronounced increase in the numbers of *Cecropia, Pourouma* and *Inga*. In the long run this may affect the sustainability of the CMS. However, we must realise that the 2nd and 3rd treatment, which should have reduced the numbers of these species (de Graaf 1986, pers. com.), were never carried out.

How do species increase in numbers?
The strong increase of pioneers, such as *Cecropia* and *Pourouma*, is in stark contrast with the results of 75 years of logging in central Guyana, where these species hardly profited (ter Steege *et al.* 2002, Chapter 4). Perhaps the answer lies in the initial seed sources that are available prior to logging. In Mapane SSW amounted to 3.3% of the initial stand (1954). In central Guyana that number was just 1.3% (1924, Chapter 4). The LSW amounted to 30.3% in Mapane but only to 11.1% in central Guyana. Consequently the proportion of HWD species (read climax species) is much lower in Mapane (62.7%) than in central Guyana (87.5%). Perhaps the higher abundance of pioneers in the Mapane forest has created a sizeable seedbank (cf. Holthuijzen & Boerboom 1982) whereas this seedbank may be much less important in the nearly pioneer-free forest (ter Steege & Hammond 2001) of central Guyana. Also in the Tonka-Kabo plots (Dekker & de Graaf 2003) the pioneers did not increase disproportionately after logging using CSS. However, in Bolivia, Fredericksen & Mostacedo (2000) found that light-seeded, shade-intolerant tree species strongly increased after logging activities, and that lianas were quickly invading the logging gaps.

Species that increased most in numbers (e.g. *Cecropia* and *Pourouma*) also increased in the frequency in which they occurred on plots. Such new occurrences are either the result of establishment from the seed bank or from seed rain from adjacent places and confirm that these species gain much of their presence from new establishments. Although the seed bank for these species may be substantial in Suriname (Holthuijzen & Boerboom 1982), other work in Mexico suggest that

91

newly established individuals of *Cecropia* are most often from newly dispersed seeds (Alvares-Buylla & Martinez-Ramos 1992).

There is a significant correlation between the increase in abundance of species and their increase in frequency (large trees, $R^2 = 0.55$, small trees, $R^2 = 0.35$). The large increase of other species such as *Inga* is unrelated to their increase in frequency as they were already present on all plots.

How do species decrease in numbers or disappear?
None of the species that disappeared from the plots were commercial species, which suggest that at least some regeneration potential for these species existed. Most species that disappeared from the plots were already low in abundance and they disappeared almost all from plots were they were present with only one individual in 1981. In total 19 species among the large trees disappeared from the 15 one-ha plots and 18 species among the small trees. Among the larger trees, only two of these were commercial species (*Virola surinamensis, Vochysia guianensis*). Hence, trees have a high chance of disappearing from plots when they are rare and in most cases this will be the result of logging damage or refinements. As only few species that disappeared from the plots were commercial, harvesting in the strict sense was not a main cause of species loss.

Refinements can ask a high toll of abundant non-commercial species, e.g. *Couratari stellata* of which the emergent status makes it a likely candidate for competition with commercial species. This species decreased from 84 to 42 individuals (large trees) and this is for a large part attributable to refinements. Prospects are not bad for this species though, as in the small trees class it increased from 47 to 59 individuals over the 15 plots. Because of its new commercial status it may face different challenges in the future.

If mainly rare species suffer from harvesting and subsequent liberations, how well will these rare species cope with continuous liberations? We suspect that many of those will eventually disappear from production forest, either because of direct human action or due to decreased and unsustainable population sizes. We suggest to put such species on special-attention-lists to avoid their complete eradication from production forest. An alternative, and perhaps better, solution is that a small percentage of production forest will be conserved in each concession area.

Are the changes in biodiversity predictable?
The second harvesting had a relatively small, but significant, effect on the tree diversity of the plots (Table 5.1). As several of the harvested species are among the common species (especially true for *Tetragastris altissima*), this result is to be expected from the way we have expressed diversity with one number: Fisher's α or the Shannon index. In other words by harvesting the (co-) dominant species we increase diversity as expressed by these 'information statistics' and by loosing species this number decreases. The actual effect of species loss may thus be larger than expected from the small change in these statistics. The number of species on the plots (another way of expressing diversity) significantly reflects this change in the

92

large trees but in the small trees the number of species actually increases, due to an increase in the number of stems. Here, correcting for the number of stems, however, results in a still lower diversity (Fisher's α). This shows how difficult it is to objectively report on changes in diversity in managed (or perhaps many dynamic) systems with single number statistics.

The total gross decrease of species among the large trees was larger that suggested by the net change as new species are also added. On average (for all 15 plots) 12 species of large trees disappeared from the plots, whereas on average 8 appeared, i.e. a net loss of 4 (cf. Table 5.1). In the smaller trees a gross average loss of 8 species was more than compensated for by an addition of 12 species, i.e. a net total of 4 additions. On the total number of species of 50 this is a considerable turn-over. Because most of these species are rare, the total effect on composition is small, as shown by the DCA results (Figure 5.3).

Were the treatments effective?
Treatments in the CSS are a measure to instantly restore/enhance the original proportion of commercial species, and in the long run to enhance the growth and re-establishment of commercial species. In the large trees a small (non-significant) effect is found among the non-commercials, which decreased as a result of the treatments. This, probably, reflects the immediate effects of liberation, in which many individuals of these species are killed. The commercials, however, did not increase in numbers.

Among the smaller trees the reverse is true. Non-commercials increased significantly in all plots and, in addition to that, significantly more in treated plots. Non-commercials, and especially the pioneers (SSW, LSW) profited more from the opened canopy than did the many slower growing commercials. Here we need to make the observation that the 2nd and 3rd treatment were never carried out, due to unforeseen circumstances. However, as ter Steege & Hammond (1996) suggested further treatments may even favour pioneers more, resulting in an increasingly difficult situation. This, however, depends on the species that are being eliminated. This agrees with our initial ideas (and perhaps common sense) that species like *Cecropia* and *Pourouma* may benefit most from the heavier canopy openings. As the contribution of the seed bank for the establishment of such pioneers may be smaller than previously appreciated (Alvares-Buylla & Martinez-Ramos 1992), controlling seed sources in logging areas and their surrounding may be beneficial.

We may need to investigate those species that benefit disproportionately from the harvesting more closely. We know that *Cecropia* and *Pourouma* germinate well in disturbed soil and less well under litter. Hendrison (1990) suggests at least that skidding has been far more intense than initially planned and this may well be an additional cause of the high recruitment of species among the smaller trees.

The reports of the foresters of the CELOS experiments are generally positive - treatments lead to enhanced productivity of commercial species. Many of these claims are perhaps based on increases of basal area rather than populations of

commercial species. BA can in fact increase if only two or three healthy, liberated, individuals increase a lot in BA, even if the population decreases. De Graaf *et al*. (1998) also show an increase in number of individuals of commercial species in a variety of treatments. However, due to the high variability of the used treatments, statistical analysis may be problematic and the same must be said for a proper comparison. However, again, In Tonka-Kabo these species did not increase at extreme levels of intervention (Dekker & de Graaf 2003).

For the results of this area to be conclusive a proper comparison of the large number of experiments may be necessary. Such an analysis will be hampered by the high variability (and hence low repetition) of treatments, long periods of non-measurements and the absence of planned treatments.

Functional groups do not assist yet in better prediction of changes
Although lower wood density generally led to higher maximum growth, neither low wood-density nor high maximum growth resulted in higher population increases from 1981 to 1997. Similarly, although small seeded species tend to grow faster in high light (Rose 2001, Rose & Poorter Chapter 2), low seed mass was not advantageous for recruitment into the smaller tree class.

The best prediction for total tree abundance of a species in 1997 is given by the abundance in 1981 before felling (R^2 = 0.8775, data not shown here but see Chapter 10). A huge number of trees present in 1997 are in fact the same individuals that were present in 1981 (70% of the smaller trees; 60% of the larger trees) but it does show that changes in composition are likely to take quite some time. However, this is due to the relatively low harvesting intensities in the present study, and most probably will not be true for forests where the larger part of stems is removed.

A long term perspective?
Forest changes are slow. Two harvests in relatively rich forest in Mapane have not led to large changes in species composition and tree diversity. Similar results were found in experiments in Amazonas, Brazil (Magnusson et al. 1999). Although species richness and density was higher in logged forest, the changes were small in relation to the natural variation in the forest. Pélissier *et al*. (1998) showed that in the Western Ghats, India, selective logging had no immediate drastic consequences for forest structure and composition. These results suggest that the forest is rather resilient to a few of such interventions, at least in the short term. What will happen in the longer term is more difficult to predict. De Graaf *et al*. (2003), however showed that the land-intensive option of CSS is compared favourably to less intensive options.

Grouping species into functional groups did, as yet, not add much insight. What is obvious is that rare species will suffer most from continuous liberation treatments (and perhaps unacceptably so from refinements). As the CSS was designed for relatively rich forest, in terms of commercial stock, this warrants protection of such species in non-logged forest and in biodiversity reserves that perhaps need to be established at concession level in commercial forest as well.

6 RESPONSES OF TREE POPULATIONS AND FOREST COMPOSITION TO SELECTIVE LOGGING IN GUYANA

Eric Arets, Peter van der Hout, Roderick Zagt

Abstract

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

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

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

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

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

Introduction

In tropical rain forests there is a continuous, dynamical pattern of small and larger disturbances caused by falling trees and branches. Consequently the forest is a mosaic of patches with different environmental conditions. Different tree species are assumed to possess life history traits that are adapted to different degrees and different phases of disturbance. Traditionally, tree species can be grouped, according to their adaptations, into two functional groups, namely pioneers and climax species (Swaine & Whitmore 1988, Whitmore 1989a, Chapter 1), while in other classifications also an intermediate group (e.g. long-lived pioneers, late secondary species) is distinguished (Finegan 1996, Peña-Claros 2001). These classifications are based on differences in combinations of plant morphological and physiological traits, such as seed size, dispersal syndrome, size at maturity, and photosynthetic capacity. The inter-specific differences in traits and trade-offs among traits

(Veneklaas & Poorter 1998, Brown *et al.* 1999) result in differences in light requirements for processes such as germination, growth and mortality in the various life stages and affect the population dynamical rates of these processes.

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

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

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

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

We do this by analysing recruitment, growth and survival patterns of trees classified into three life history strategies (pioneer, long-lived pioneer and climax). We used functional groups because in tropical forests most tree species are rare and just a few are abundant enough to measure population dynamics at the species level. Our classification is based on two morphological parameters, wood density and seed

mass, which we believe are predictors of species' responses to disturbance in terms of recruitment, survival and growth. Wood density and seed mass have an advantage over population dynamical characteristics, as they are instantaneous and relatively easy to obtain.

Seed mass is correlated with recruitment success and early survival of a species. Climax species are characterised by large and heavy seeds, while pioneer species generally have many small and light seeds (Foster & Janson 1985, Hammond & Brown 1995, Boot 1996, Rose and Poorter Chapter 2, ter Steege Chapter 1, but see Grubb 1996). Wood density is used as a proxy for maximum potential diameter growth rate (Chapter 1). The large differences in wood density between species is mainly due to differences in wood porosity (Winstead 1972, Barajas-Morales 1987, Suzuki 1999). As a consequence, per unit of assimilated carbohydrates, species with a relatively low wood density will be able to grow faster in diameter than species with a high wood density. Although the relation between wood density and or diameter growth rate seems to be quite obvious and is often assumed (Swaine & Whitmore 1988, Köhler *et al.* 2000, ter Steege & Hammond 2001) it is hardly demonstrated (but see Chapters 5 and 7). We test the relation between maximum potential growth rate and the wood density of tree species for which we expect a negative relationship.

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

Methods

To test our hypotheses we used permanent sample plot (PSP) data from two different areas in Guyana. The first set comes from the Barama Company Ltd.'s (BCL) timber concession in the Northwest district of Guyana (henceforth referred to as Northwest-data) around Port Kaituma (7?44' N, 59?52' W). The second data set originates from 12 permanent experimental plots in the West-Pibiri compartment (henceforth referred to as Pibiri data) of Demerara Timbers Ltd. 's concession approximately 50 km south of Mabura Hill (5?02' N, 58?37' W) (van der Hout 1999). An important difference between the two areas is that the plots in the Northwest have been selectively logged without special precautions to reduce the impact of the logging operation, while the Pibiri plots have been logged with reduced impact logging

techniques. Possible differences between these two methods are no direct subject for this study, but may be relevant.

Northwest plots
In the Northwest, PSPs were established and inventoried in advance of the logging operations of BCL (ECTF 1994). Thereafter the area, along with the plots, was logged within one year after the plots were set up and inventoried. Some of these plots were "missed" by the harvesting operation and will be used as (unplanned) non-harvested control plots. The trees in these plots were re-measured on a yearly basis starting from approximately 1 year after logging (ECTF 1994). We used 56 PSPs that were re-censused during 2-6 years after logging for growth analyses, while the results on the diversity and composition are based only on those 37 (7 unlogged and 30 logged) PSPs for which 6 years of data were available. In table 6.1 the measurement thresholds and sampling intensities are shown.

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

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

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

Pibiri plots
The Pibiri experimental plots were set up in 1993, considering 4 different intensities of reduced impact logging (see van der Hout 1999, 2000); low intensity reduced impact logging (4 trees ha^{-1}); moderate intensity (8 trees ha^{-1}); high intensity (16 trees ha^{-1}); and a control without intervention. The experiment was set up as randomised block design in three blocks with 4 treatments. Reduced impact logging was carried out in 1994. The trees in the plots were re-censused at one (1995), three (1997) and six years (2000) after logging. In table 6.1 the measurement thresholds and sampling intensities are summarised.

The plots are situated in mixed Greenheart forest (Ek 1997, van der Hout 1999), dominated by *Tapura guianensis* (Waiaballi, 10.4%), *Oxandra asbeckii* (Karishiri, 7.8%), *Catostemma fragrans* (Sand Baromalli, 6.5%), *Chlorocardium rodiei* (Greenheart, 6.3%), *Lecythis confertiflora* (Wirimiri Kakaralli, 5.8%), *Mora gonggrijpii* (Morabukea, 3.6%), *Eschweilera sagotiana* (Black Kakaralli, 3.3%) and

Table 6.1   Minimum measurement limits for trees, number and size of subplots and total sampled area
              per, plot for each size class in the Northwest and Pibiri experiment.

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

Licania heteromorpha var. *perplexans* (Kairiballi, 3.2%). Together these 8 species account for just over 45% of the individuals larger than 5 cm DBH.

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

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

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

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

on the relationship between wood density and growth rate and the effects of logging on functional group composition and diversity we used the data from both areas.

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

A 3-means cluster analysis with wood density and seed mass class, of all tree species in Guyana with known values for these two parameters, resulted in the classification as shown in Table 6.2. Except for one species, all species classified as climax species have seed mass = 0.1 g.
In the Pibiri data, we were able to classify 161 out of 189 (85.2 %) species, while in the Barama data this was 134 out of 147 (91.2 %) species. These represented 1501 out of 1682 saplings (89.2 %) and 2988 of 3188 poles (93.7 %) in Pibiri and 4719 out of 5351 saplings (88.2 %) and 6796 out of 7075 poles (96.1 %) in the Northwest (in 37 plots with 7 censuses). The species that could not be classified were left out from all analyses, except for the calculation of the effects of logging on relative abundances of the functional groups.

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

Tree growth
For individual trees with at least two DBH measurements available, we regressed DBH on date of measurement to obtain an estimator for the annual DBH growth

Table 6.2   Limits for wood density (g cm^{-3}) and seed mass (g) for the three functional groups.

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

rate. We omitted individual trees with conditions that may have had an influence on growth (i.e. trees that died in the course of the period, trees with rotten bark, trees with damaged bark, stem or crown, and so forth) and species with fluted stems (3 species). Additionally, we rejected data of trees with aberrant growth trends that were obviously caused by measuring or recording errors.

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

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

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

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

section Pibiri plots in methods) are used for replication of the mortality, recruitment and net gain rates.

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

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

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

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

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

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

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

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

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

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

Diversity

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

We did all statistical analyses, except the χ^2, G and Dunn post hoc tests, using the SPSS 11.0 (2001) statistical software package. Dunn post hoc tests for Kruskal-Wallis tests and G tests were carried out using a spreadsheet.

Results

Light availability and logging

In Pibiri, 6 years after logging, the proportions of individuals in higher light climates (i.e. higher CII values) increased with increasing harvest intensity (Figure 6.1). The frequency distributions of poles and saplings over CII classes were significantly different between most harvest intensities (Figure 6.1, χ^2 tests at P<0.005 for all
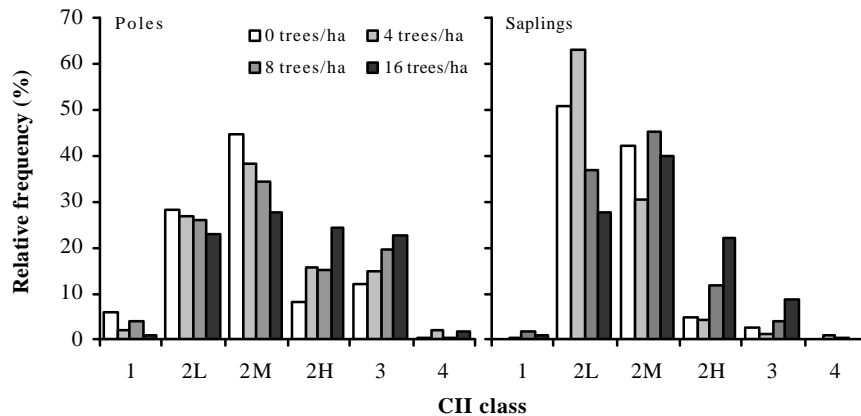
Figure 6.1   The relative frequency distribution of Crown Illumination Index (CII) for poles and saplings in plots with different logging intensities (0, 4, 8 and 16 trees ha^{-1} - see legend in poles figure) in Pibiri, 6 years after logging. With increasing logging intensities the frequency distributions for poles and sapling shifted significantly to lighter CII classes (χ^2-tests, P<0.001).

differences), except between plots with 4 and 8 trees ha^{-1} logged for the poles and between the control and 4 trees ha^{-1} logged plots for the saplings.

Tree growth

The maximum potential growth rate of species was significantly negatively correlated with the specific wood density (Figure 6.2; Northwest; R^2=0.23, n=74, P<0.001 and Pibiri; R^2=0.10 n=66, P<0.01; based on 90 percentile of growth). When we only used individuals with CII > 3 (i.e. individuals that grow in high light conditions), the amount of explained variance more than doubled to 25 percent (Figure 6.2; R^2=0.25, n=23, P<0.05; Pibiri plots only).

Mean growth rates, not adjusted for differences in CII, of pioneer poles and saplings were much higher than for long-lived pioneer and climax species, but were accompanied by high standard errors and based on small numbers of individuals (Table 6.3). Only the mean growth rates of long-lived pioneer and climax poles (Dunn-test, Q=4.64, P<0.01) and pioneer and climax saplings were significantly different (Dunn-test, Q=2.81, P<0.05).

The mean growth rates of poles and saplings of all functional groups increased with increasing CII class (Table 6.4). Pioneer poles with CII 2 grew significantly faster
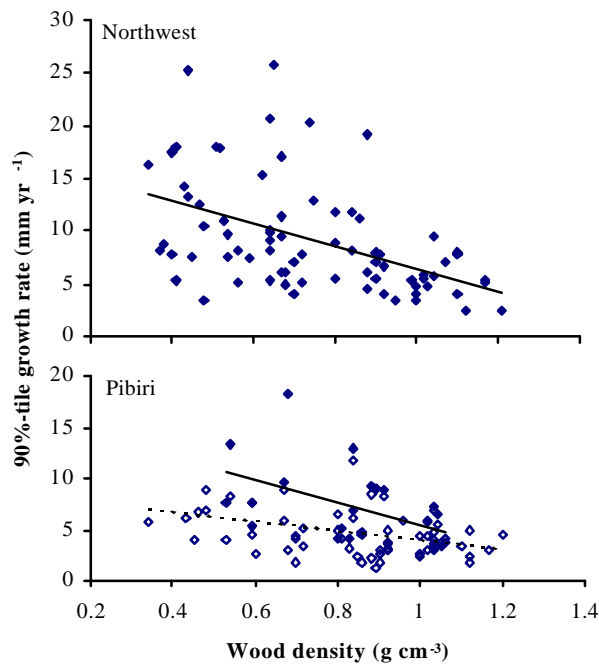
Figure 6.2 The relation between wood density (g cm^{-3}) and 90-percentile growth rates of tree species in the Northwest and Pibiri plots. The Northwest figure is based on all species with more than 10 individuals (R^2=0.23, n=74, P<0.001). In the Pibiri figure, open symbols with dashed trend-line are all species with more than 10 individuals (Fig. 2b; R^2=0.10 n=66, P<0.01), the closed symbols with solid trend-line are based on individuals with CII > 3 for species with more than 10 individuals (R^2=0.25, n=23, P<0.05).

104

Table 6.3 Mean diameter growth rates ± standard error (s.e.) (mm yr^{-1}) and sample sizes (N) per size class, per functional group in all Pibiri plots. Within each size class, values of mean growth rate with different letters are significantly different (Dunn test at P<0.01 for poles and P<0.05 for saplings).

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

than those with CII 3 (Mann Whitney U=6, P<0.05) but there were no significant differences within the pioneer saplings. For both long-lived pioneer and climax poles and saplings, the growth rates were significantly different between all CII classes, except between CII 1 and CII 2 for the poles of both groups (Kruskal-Wallis tests, all P<0.001, see table 6.5 for comparisons with Dunn test).

For poles with CII 1, long-lived pioneers grew significantly faster than climax species (Mann-Whitney, U=285, P<0.05), but there were no significant differences for the saplings. The multiple comparisons at CII 2 and CII3 between the functional groups, including the pioneers, showed that growth rates of pioneer poles and saplings at CII 2 were significantly higher than those of the climax poles (Dunn test, Q=4.36, P<0.001) and saplings (Dunn test, Q=3.01, P<0.001). There were no significant differences for CII 4.

Table 6.4 Mean diameter growth rates ± standard error (s.e.) (mm yr^{-1}) and sample sizes (N) per size class per functional group among individuals with different Crown Illumination Index (CII) classes in Pibiri. Growth rates based on less than three individuals are not used for the analyses.

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

105

Table 6.5   Significance levels (*: P<0.05, **: P<0.01 and n.s: not significant) of differences in mean growth rates (see table 6.4) between CII classes within each functional group. Pioneers only have sufficient individuals for CII 2 and CII 3. Comparisons within the pioneers were done with Mann-Whitney tests and within the other groups with Dunn post-hoc tests.

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

Mortality and recruitment patterns
For the saplings in Pibiri, there was a significant effect of functional group (F=6.85, df=2 and P<0.01) and CII (F=3.86, df=2 and P<0.05) on recruitment rates but not mortality rates (Figure 6.3). Pioneers had a significantly higher recruitment rate (SNK, P<0.05) than the other two groups, and subplots with CII 3 had significantly higher recruitment rates than subplots with lower CII values.

The ANOVA for net gain rate of the saplings (Figure 6.3) showed a significant interaction between functional group and CII values (F=4.69, df=4 and P<0.05). From this we can conclude that the effect of CII of the subplot is different for the different functional groups. Net gain rate was significantly higher (P<0.05) for the pioneers in subplots with CII 3 than for any other combination of functional group and CII (SNK, P<0.05).

The recruitment and mortality patterns of the poles were less clear (Figure 6.3). There were no pioneer and only few long-lived pioneer and climax poles that had a CII value of 1 or 4. Recruitment and death of a few individuals will in that case have relatively large effects on the rates. For recruitment and net gain rates there were significant interactions between functional group and CII values (recruitment; F=2.80, df=6, P<0.05 and net gain rate; F=3.92, df=6, P<0.01). We found no significant differences in mortality rates. Pioneer poles with CII 2 had a significantly higher recruitment rate (SNK, P<0.05) than any other combination of functional group and CII. Pioneer poles with CII 2 and 3 had significantly higher net gain rates (SNK, P<0.005) and long-lived pioneer and climax poles at CII value 1 had significantly lower (negative) net gain rates than the other combinations of functional group and CII.

Functional group distributions
The distributions of both poles and saplings over CII classes were significantly more towards higher CII values for pioneers than for long-lived pioneers (Figure 6.4,
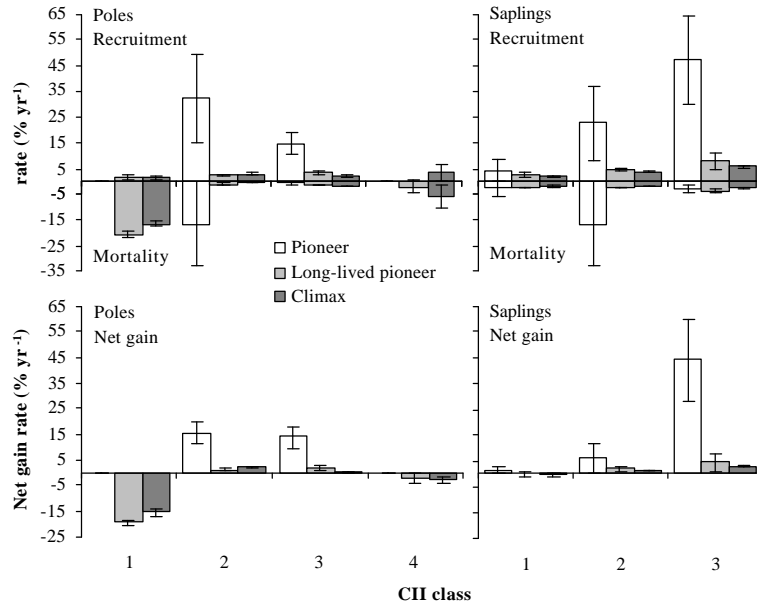
Figure 6.3   Mean mortality, recruitment and net gain rates (% yr^{-1}) for pioneer, long-lived pioneer and
climax poles and saplings at different CII classes. Error bars are standard errors. Mortality
rates are represented as negative values. The net gain rate is the sum of the recruitment and
(negative) mortality rates.

poles: χ^2=15.7,P<0.005 and saplings: χ^2=15.25, P<0.005) and climax species (Figure
6.4 poles: χ^2=17.7, P<0.001 and saplings: χ^2=16.11, P<0.005). The distributions for
long-lived pioneers and climax species were almost identical.
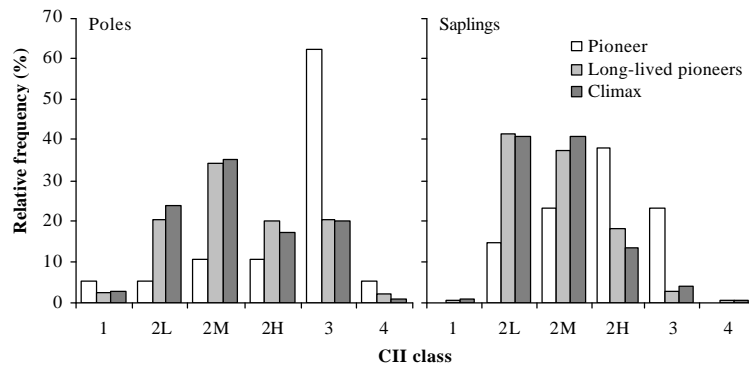
Figure 6.4   The relative frequency distributions of CII for pioneer, long-lived pioneer and climax poles
and saplings in Pibiri. In both size classes the distributions of the pioneers significantly
differed from that of the long-lived pioneers (poles: χ^2=15.7, P<0.005 and saplings:
χ^2=15.25, P<0.005) and climax species (poles: χ^2=17.7, P<0.001 and saplings: χ^2=16.11,
P<0.005).

Shift in functional group composition

In the Northwest plots, the relative abundance of saplings of pioneer species significantly increased over the first three years after logging from 1% to 7%, at the expense of the relative abundance of saplings of climax species, which decreased in the same period from 51% to 47% (G-test on absolute abundances; G=454.7, df=9, P<0.001; Figure 6.5). After three years, the relative abundance of pioneer saplings decreased again (Figure 6.5), which was due to outgrowth to the poles size class (compare with the saplings in Figure 6.5). The relative abundances of saplings of the three functional groups did not shift in the non-logged plots (Figure 6.5). Delayed by one year, a similar trend was found for the poles, where the relative abundance of pioneers increased from 2% to 8% and that of the climax species decreased from 61% to 58% (G-test on absolute abundances; G=245.9, df=9, P<0.001; Figure 6.5). This increase was caused by in-growth from the sapling size class (see above).

In the Pibiri plots the relative abundance of the pioneer saplings in the plots that had a harvest intensity of 16 trees ha^{-1} significantly increased at the expense of that of climax species (G-test on absolute distributions; G= 41.1, df=9, P<0.001; Figure 6.6). In these plots, within 6 years after logging the relative abundance of pioneer saplings increased from 0% to 6.2% and the relative abundance of saplings of climax species decreased from 61.5% to 57%. For the saplings in the other logged
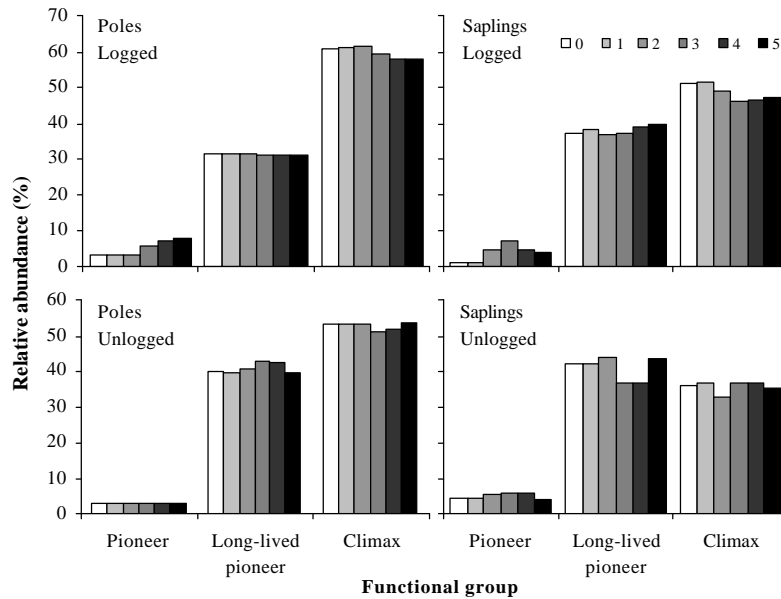
Figure 6.5   Time series of relative abundances of pioneer, long-lived pioneer and climax poles and saplings since logging (see legend in figure; 0: initial inventory and 1-5: one to five years after set-up) for logged and unlogged plots in the Northwest. Logged plots have been harvested just after the initial inventory. In the logged plots the abundance of the pioneers increased significantly at the expense of the climax species (G-tests, all P<0.001) while in the unlogged plots there were no significant shifts in abundance between the functional groups.
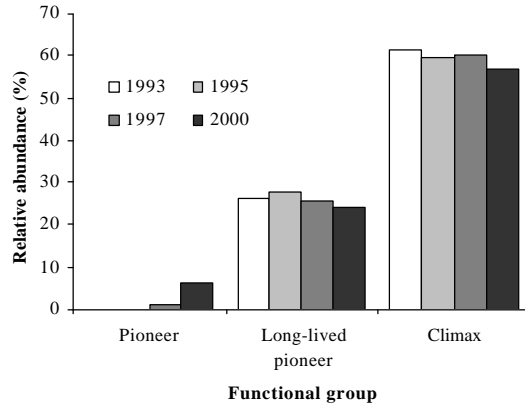
Figure 6.6   The relative abundances of pioneer, long-lived pioneer and climax saplings over years (see
            legend: 1993: before logging; 1995: just after logging) in Pibiri PSPs with a harvest intensity
            of 16 trees ha^{-1}.

PSPs the relative abundances of pioneers slightly increased from 0.4% to 1.2% in
plots with harvest intensity 4 and from 0.6% to 1.9% in plots with harvest intensity
8, but these shifts were not statistically significant. Functional group composition for
saplings in the unlogged plots and for poles in all treatments remained more or less
constant over years.

Diversity
The ranges in $FA_{(0)}$ and $FA_{(al)}$ for poles and saplings in 37 plots in the Northwest and
the Pibiri plots are presented in Table 6.6. In both the Northwest and Pibiri plots the
$FA_{(al)}/FA_{(0)}$ ratio for the saplings was positively related to logging intensity (Figure
6.7; Northwest; N=37, R^2=0.28, and Pibiri; N=12, R^2=0.79, both at P<001, logging
intensity expressed as %basal area lost). There was also a weak positive relation
between logging intensity and $FA_{(al)}/FA_{(0)}$ ratio for the poles in the Northwest
(Figure 6.7; N=37, R^2=0.16 at P<0.05) and a weak negative relation for the poles in
Pibiri (Figure 6.7; N=12, R^2=0.34, P<0.05). In both areas the $FA_{(al)}/FA_{(0)}$ for trees
were not related to percentage basal area lost (data not shown).

Table 6.6   Ranges in $FA_{(0)}$ and $FA_{(al)}$ for poles and saplings in 37 plots in the Northwest and the Pibiri
            plots.

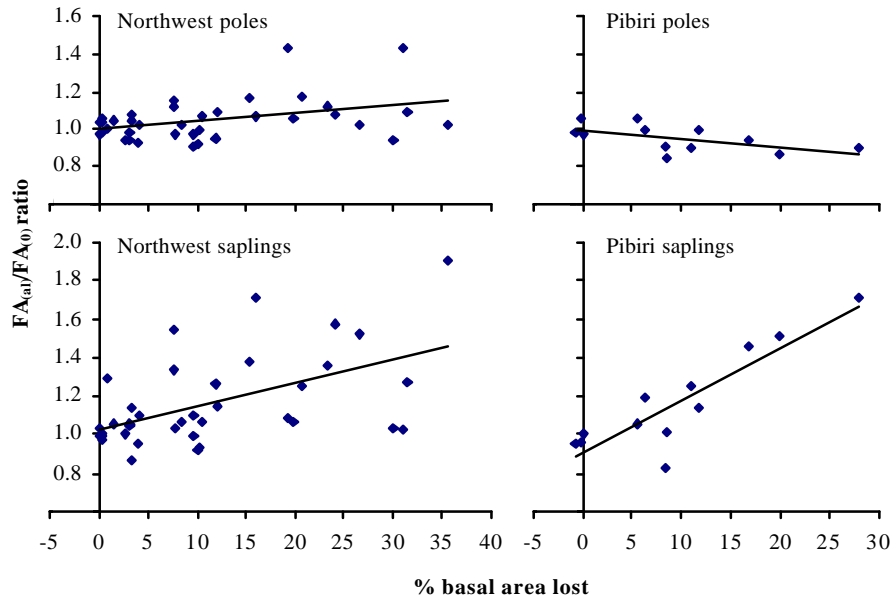| Area	Poles		Saplings	
	$FA_{(0)}$	$FA_{(al)}$	$FA_{(0)}$	$FA_{(al)}$
Northwest	6.4 - 15.9	7.0 - 15.9	5.6 - 13.8	6.0 - 16.6
Pibiri	15.8 - 29.7	14.2 - 31.4	11.2 - 29.2	11.35 - 28.0

109

Figure 6.7   Relation between $FA_{(al)}/FA_{(0)}$ and the percentage basal area lost after logging, for poles and saplings in PSPs in the Northwest and Pibiri. $FA_{(0)}$ is Fisher's alpha before logging and $FA_{(al)}$ is Fisher's alpha at the last available post-logging census, i.e. five years in the Northwest and six years in Pibiri. In the Northwest, % basal area lost explained 16% of the variance in the ratio for poles ($N=37$, $R^2=0.16$ at $P<0.05$) and 28% of the variance in the ratio of saplings ($N=37$, $R^2=0.28$ at $P<0.001$). In Pibiri it explained 34% of the variance in the ratio for poles ($N=12$, $R^2=0.34$ at $P<0.05$) and 79% of the variance in the ratio for saplings ($N=12$, $R^2=0.79$ at $P<0.001$).

Discussion

Population dynamics
The tree-communities that we studied appear to be adapted to low intensity and infrequent disturbance events and contain many species that are able to establish, survive and grow (slowly) in small gaps and the shaded forest understorey**.** As expected, light availability in the forest increased with increasing logging intensity. From the differences in the CII distributions of poles and saplings between the various treatments in Pibiri we can conclude that six years after logging there are still significant effects of logging on light availability in the forest. In general the growth rates of all three functional groups increased with increasing light availability, suggesting a positive effect of logging on growth rates of all species, conform our hypothesis. Increased light availability showed a clear positive effect on the recruitment (in-growth) rates of the pioneer saplings. This may be explained by the faster growth at higher light availabilities, enabling new recruits to reach the minimum sapling size-class limit faster. The relative frequency distributions of CII classes of poles and saplings (Figure 6.3) showed that pioneers occur relatively more often in high light conditions than individuals of the other two groups.

110

Brokaw (1985) found that pioneers need gaps larger than 150 m^2 for successful regeneration in Panama, while others (Ek 1997, van der Hout 1999 and Rose 2000) suggest that no major pioneer proliferation occurs in gaps below 300-400 m^2, based on data in Guyana. In a review, Rose & Poorter (Chapter 2) show that large seed mass is associated with high survival in shade and slower relative growth rate in high light conditions. Only in large gaps (high light) where pioneers are able to germinate and realise higher growth and survival rates they are able to outcompete seedlings of large seeded species that are already present before gap creation. (Rose & Poorter Chapter 2, Boot 1996, ter Steege & Hammond 1996, Chapter 1).

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

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

Functional groups
At both sites, the 90-percentile growth rate was significantly related to wood density, with high growth rates associated with low wood density. In the Northwest, wood density of species accounted for 23% of the variation in 90-percentile growth rate and in Pibiri the wood density explained 25% of the variation in 90-percentile growth rates of individuals growing in high light conditions. The amount of explained variance is in the same order as found by ter Steege *et al.* in chapter 5 and Verburg & van Eijk-Bos (2003, chapter 7). Based on these results we conclude that species-specific wood density can be used as a predictor of a species potential growth rate. Other studies (Williamson 1975, Augspurger 1984) show that wood density is positively related with other measures for the shade tolerance of tree species.

Species that we classified a-priori into three functional groups based on differences in two plant traits, wood density and seed mass, could indeed be distinguished in their functional response to light availability as generally (e.g. Brokaw 1985, Brokaw 1987, Clark & Clark 1992, Poorter 1999, Poorter & Arets 2003) found for

111

pioneer, long-lived pioneer and climax species. For another study in Guyana (ter Steege *et al*. 2002) that used an almost identical classification of species into functional groups (only subdivision of wood density at 0.7 vs. 0.8 in this study) was found that all species cited in literature as pioneers had wood densities < 0.7 g cm^{-3}. Hence our classification is comparable with more subjective classifications used in other studies.

Functional groups composition
In Pibiri the relative abundance of pioneer saplings increased with increasing harvest intensity. In the Northwest there was an effect of logging on relative abundance of pioneer saplings and poles. Because we pooled all logged plots in the Northwest, the changes in relative abundance are based on an average response across the whole range of harvest intensities. The results from both areas are consistent with our expectations and other studies on effects of logging on composition (Silva *et al*. 1995, Verburg & van Eijk-Bos 2003, chapter 7).

The timing and magnitude of the changes in functional group composition after logging differed between the two study areas. In the Northwest, there was already a notable increase in abundance of pioneer saplings within 2 to 3 years after logging, while in Pibiri this was seen after 4 to 6 years. Further, the relative abundance of pioneer poles in the Northwest increased within 5 years since logging, but in Pibiri this was not as yet the case within 6 years since logging. These differences are associated with a difference in mean pioneer growth rates between the two areas (data not shown, but compare the two graphs in Figure 6.2), which will probably also be the case for the saplings. Furthermore, the minimum size limit of saplings was lower in the Northwest plots than in Pibiri (Table 6.1). Hence in the Northwest recruits of the pioneer species would have been able to achieve sapling size more quickly than in Pibiri. Differences in growth rates are most likely due to differences in nutrient availability between the soil types in the two areas (Gross-Braun *et al*. 1965).

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

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

Increased diversity after disturbance is consistent with the predictions of the IDH with respect to effects of disturbance on diversity in forests with a few dominant species and low intensity natural disturbance regimes. We did not find, however, the humpbacked relationship between disturbance and diversity (Figure 6.7) as predicted by the IDH (Connell 1978 and see Chapter 1) that was found in a forest with similar compositional and disturbance properties (ter Steege *et al.* 2000a) in French-Guiana (Molino & Sabatier 2001). In this study in French-Guiana, Molino & Sabatier (2001) found that diversity was highest in logged forests with an intermediate abundance of pioneers (around 30%), which was used as an estimator for disturbance regime. The cumulative basal area lost for trees > 10 cm DBH over a 8 years period (including logging) at that site varied from 0 to 24.6 m^2 ha^{-1}. Since the highest pioneer abundance found in our study was not higher than 8% and the cumulative basal area lost (during 7 years period in Pibiri) did not exceed 11 m^2 ha^{-1}, the disturbance levels in our study appear to be too low to find an optimum effect of disturbance on diversity. The change in diversity after increased disturbance in our case would then still be in the ascending trajectory (arrow C1 in Figure 1.2, Chapter 1) towards optimum diversity. If logging increases disturbance beyond this point, diversity would be expected to decrease again.

Some studies that determine the effect of large-scale disturbance events (of which logging is an important example) on tree species diversity only take into account trees with large DBHs (i.e. typically 10-20 cm DBH and larger) combined with relatively short monitoring periods since logging (Cannon *et al.* 1998, Webb & Peralta 1998). Based on 90-percentile growth rates from functional groups in this study (Table 6.7) we calculated that the minimum number of years for a sapling of 2 cm DBH to reach 20 cm DBH is approximately 20 years (Table 6.7), while the times needed by species of the other two groups are even longer. Hence, effects of recruitment of new species after disturbance cannot be found in the composition and diversity of trees larger than 20 cm DBH until more than 20 years after disturbance. Studies that find no effect of disturbance on diversity may not be long enough in relation to the size classes that are considered. Although Cannon *et al.* (1998) found that diversity of trees >20 cm DBH increased within 8 years since selective logging on Borneo it appeared that these results were most likely caused by older disturbance events (Sheil *et al.* 1999).

Table 6.7   90-percentile annual DBH growth rates (mm yr^{-1}) for pioneer, long-lived pioneer and climax poles and saplings. For the pioneer saplings the sample size was insufficiently large for calculation of 90-percentile annual growth rates, therefore we used for these the maximum growth rate. The amount of years needed to grow from 2 to 20 cm DBH was estimated using the 90-percentile annual growth rates, assuming that these stay constant over time and within a size class.

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

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

Long-term effects
Although in this study we report on effects over relatively short periods after disturbance the results and trends we found can be used to make predictions about future developments in composition and diversity. We propose that pioneers will further increase their relative abundance if logging will be repeated in the same area within the lifespan of the pioneers that have recruited after the first logging (estimates of the maximum life spans of typical pioneer species are e.g. 54 yrs for *Cecropia sciadophylla* and 69 yrs for *Miconia punctata*, Korning & Balslev 1994). In that case the distances from pioneer seed sources (i.e. the new recruits from the past logging event) to newly formed gaps will become smaller and may result in more effective colonisation of the area. If this happens repeatedly over long time, the proportion of pioneers within the forest will gradually increase while the abundance of the climax species that are typical for the primary forest as it is now, will further decline due to their inferior colonisation of the large number of large gaps in relation to pioneers. As a consequence, we expect that tree diversity in these forests will decrease towards low diversity at the high intensity disturbance end of the disturbance range (i.e. arrows A and C3 in Figure 1.2 Chapter 1). If logging is only limited to this one occasion, or the time till the next disturbance event is longer than the lifespan of the newly recruited pioneers, we expect that the tree community will completely recover from this single perturbation of the disturbance regime and will return to its previous state.

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

7 TEMPORAL CHANGES IN SPECIES DIVERSITY, COMPOSITION, AND PLANT FUNCTIONAL TYPES AFTER LOGGING IN A BORNEAN RAIN FOREST

René Verburg, Clara van Eijk-Bos

Abstract

In tropical rain forests long-term studies on species composition and replacement using permanent sample plots are scarce. This study describes the changes in the tree community in selectively logged forests, during a monitoring program of more than 20 years. The effects of selective logging on tree diversity, changes in tree species composition and plant functional types was studied with the use of 7 permanent sample plots in virgin and 7 permanent sample plots in logged forest. All plots were located in a lowland Dipterocarp rain forest in East Kalimantan on the island of Borneo. Just after logging and during the following 20 years tree diversity measured as Fishers' a was not significantly lower in logged forest plots. Temporal shifts in tree species composition were analysed with a size-structured data set and the use of Principal Component Analysis (PCA). Logged forest plots showed much larger changes in time than virgin forest plots. Only in the smallest diameter class some logged forest plots showed a distinct trajectory from virgin forest plots, while in larger diameter classes movement of logged plots in PCA space was in a random manner. The latter result suggests that there is no pre-determined community to which logged forest plots tend to shift after logging. A significant negative correlation was found between the 20 years of measurements on diameter increments and the species-specific wood densities of tree species. Species-specific wood density and potential tree height was used to assign species into 5 Plant Functional Types. As expected, logging increased the fraction of softwood stems in small diameter classes. In the largest diameter classes (from 50 cm DBH onwards) a strong decrease of softwood emergent stems was found in logged forest plots. Some trees with this property belong to the important commercial timber trees in Southeast Asia. After more than 20 years no recruitment in the smallest diameter class was found of softwood emergent stems in selectively logged forest. This result suggests that it may take a long time before previously logged forest can fully recover from logging.

Introduction

Long-term studies in tropical rain forests on species composition and replacement using permanent sample plots are scarce. They are time consuming, difficult to maintain, due to logistical reasons, and therefore very expensive (e.g., Sheil 1998). Furthermore, the long-term effects of large-scale disturbances such as commercial logging have rarely been studied in the tropics (e.g., Finegan 1996). Recently Cannon *et al.* (1998) described the effects of commercial logging on tree diversity in Borneo by the use of a comparative, chronosequence study. They found an increased species-by-stem ratio in 8 years old logged forest. Likewise, chronosequences of secondary forests after slash and burn and fallow in the Neotropics also showed an increased number of species up to respectively ca. 30 and 80 years of secondary succession (Peña-Claros 2001, Saldarriaga *et al.* 1988). In chronosequence studies comparisons of plots with a different successional status, such as logged forest plots with a different logging history are made. However, the assumption that the initial conditions of all plots in the chronosequence are equal (e.g., Plumptre 1996) is a major disadvantage of such a study design. This assumption may hardly be met in tropical systems that have high levels of beta-diversity. By using a permanent plot design this disadvantage can be circumvented. However, a major drawback of a

permanent plot design is that the time scale of the process studied is often much shorter than in a chronosequence.

The study of selectively logged forests with the use of permanent sample plots over such time scale has hardly been carried out in the tropics (Sheil 1998), and the results may be of vital importance to the conservation of logged forests. In the present study permanent sample plots are laid out both in mature (virgin) forest and in selectively logged forests. During a monitoring program of more than 20 years the changes in tree diversity, changes in species composition of the tree community, and distribution and changes in the abundance of plant functional types (PFT) are studied as affected by logging.

Logging can be seen as a (man-made) disturbance to the forest. Hence hypotheses dealing with the response of forests to natural disturbance may also apply to forests disturbed by logging. The intermediate disturbance hypothesis (IDH) proposed by Connell (1978) describes an unimodal relationship of species diversity to disturbance. The interpretation and implications of this hypothesis has been thoroughly discussed (e.g., Sheil, 1998, Sheil 1999a, Sheil & Burslem 2003), while the model has been subjected to various adaptations (e.g., Huston 1994). Niche-assembly hypotheses that deal with the maintenance of diversity assume that species are able to co-exist through adaptation to their 'own' ecological niche (e.g., Hubbell 1998). The concept of pioneer and mature-phase tree species is one of the well-studied ecological niches in tropical rain forests (e.g., Swaine & Whitmore 1988). The gap-phase regeneration hypothesis (GRH, Brokaw 1985, Denslow 1995) stems from this concept. The GRH can be seen as an extension to IDH in which small-scale (single tree-fall) or large-scale (hurricanes and landslides) disturbances provide ephemeral niches in which a subset of species, other than those occupying undisturbed mature forest, can grow. Such disturbance may lead to higher levels of diversity than in a forest lacking such short-term environments. Tree-fall caused by selective logging provides gaps that might enable light depending, pioneer species to become established. Thus, according to both IDH and GRH we expect that selective logging causes a temporarily increase in species diversity, but only in forests with 'low dynamics' (i.e., forests found on the right-hand-side of the 'hump' in the IDH).

The enormous amount of tree species in tropical rain forests, even on one hectare, has put serious limitations on the analysis of compositional differences among forest plots. This holds particularly for the majority of species that have a very low abundance (one or two trees per hectare). Multivariate techniques, such as ordination, correspondence analysis, and principal component analysis (PCA) have been used to study species composition in the tropics (e.g., Austin & Greig-Smith 1968, Austin 1977, Newbery *et al.* 1996) but often have a low discriminating power. Hence the amount of explained variation of each axis is usually small. Time series in tropical rain forests have seldom been analysed with multivariate methods. In temperate zones Austin (1977) described a lawn (grassland) succession by ordination of sample plots through time and Anand & Heil (2000) used PCA to unravel the recovery of a heathland ecosystem after a large-scale disturbance. Sheil (1999b) studied primary forest succession in Uganda by using a detrended

118

correspondence analysis. Instead of analysing all trees together at once, Sheil (1999b) divided his data set of tree species into different stem diameter classes in order to unravel changes in the tree community during forest succession. Logging may strongly promote growth of pioneer species into the smallest diameter classes. As the vegetation recovers from disturbance the cohort of pioneers will move into larger size classes. In addition some non-pioneer tree species at larger diameter classes might benefit from the temporary higher light levels by increasing their growth. Enhanced growth of different species to the changed light levels can lead to a different tree composition in the different diameter classes. During the pre-logging phase of the forest species composition may differ largely among forest plots. However when only a subset of species can take advantage of the ephemeral high light levels, we can expect that previously logged forest plots recover in time towards a more common and similar tree community.

The wealth of species in tropical rain forests has forced researchers to assemble species into collections, guilds or plant functional types (PFT) (e.g., Condit *et al.* 1996a, Köhler *et al.* 2000). The classification derived from the pioneer versus climax species dichotomy of Swaine & Whitmore (1988) is often being used. However, this concept is regularly used in a rather loose way and based on the notion whether a species is found in virgin- or secondary forests. Only recently PFTs are derived from more objective approaches using, for example, cluster analysis on measured plant traits (e.g., Gitay *et al.* 1999). Wood density has been proposed as a measure for the potential growth rate of a tree species (Brown & Lugo 1990, ter Steege & Hammond 2001). The species-specific growth rate can be interpreted as a species-specific response to disturbance. Usually pioneer species have low wood densities and a high (species-specific) growth rate. As a result they can respond quickly to gap formation. In contrast, slow growing canopy species usually have hard wood and do not respond quickly, in terms of DBH growth, to a sudden increase in light availability after gap formation. In the study presented here, all tree species are classified into different PFT by their species-specific wood density. We expect an increase of the fraction of softwood species after logging. An increase of this fraction must be at the expense of another PFT. Therefore, we also describe changes in the fractions of other PFT.

Material and methods

Site description and plot layout

The International Timber Company Indonesia (ITCI) concession area is located in the Indonesian province of East Kalimantan, approximately at 0°15' S, 116°45' E (Figure 7.1). It covers an area of ca. 600,000 ha (van Eijk-Bos 1996). The elevation in the concession ranges from 0 to 500 m asl. Mean monthly temperature in the area is 27° C, while mean annual rainfall ranges between 2000 mm and 2500 mm (van Eijk-Bos 1996). The area does not have a particular dry season (mean precipitation in driest month is more than 60 mm) but has two rainfall maxima (April-May and December-January) (van Eijk-Bos 1996). The forest covering this area is identified as mixed Dipterocarp forest. In some small areas within the concession *Agathis*
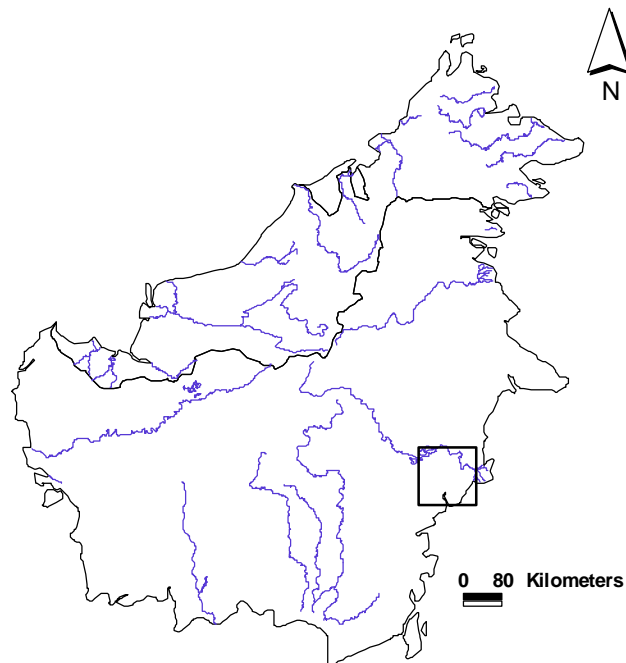
Figure 7.1   Map of Borneo. The ITCI concession in East Kalimantan is located within the square.

borneenis (Araucariaceae) partly replaces the large emergent Dipterocarpaceae (van Eijk-Bos 1996).

From 1971 to 1977, 7 plots in virgin forest and 7 plots in selectively logged forest were laid out (Table 7.1). The plot area in virgin forest ranges from 0.25 to 2.0 ha, in selectively logged forest from 0.35 to 0.84 ha (van Bremen *et al.* 1990, van Eijk-Bos 1996). The first full census that is available for data analysis was carried out in 1976, although some plots in virgin forest were established before that year. From 1976 on complete inventories of virgin forest plots were carried out after 1, 2, 4, 5, 11, 13, and 16 years. The selectively logged plots were subdivided into two logging regimes, i.e., 4 plots designated as low-intensity logging (LI-logged), and 3 plots as moderate-intensity logging (MI-logged) (Table 7.1). There are no pre-logging measurements available for any plot in selectively logged forest. For LI-logged plots full enumeration's were carried out after 2, 3-4, 12, 13-14, and 16-17 years after logging. For MI-logged plots full enumeration's were carried out after 5, 6, 7, 8-9, 10, 16-17, 18-19, and 21-22 years after logging. For further information on the data collected by various researchers see van Eijk-Bos (1996).

120

Table 7.1   Forest type (virgin, low intensity logged (LI-log), moderate intensity logged (MI-log)), total area and between brackets average ± SD area of plots in the different forest types, average basal area before logging (BA, * = estimated for logged forest plots), the number of stems, basal area (BA, m²/ha) and percentage basal area (%BA) removed by logging, and the total damage of all stems > 10 cm DBH caused by logging (including logged stems) on the number of stems, basal area (BA, m²/ha) and percentage basal area (%BA).

Forest type	Area (ha)	BA* (m²/ha)	removed			Total damage		
			stems	BA	%BA	stems	BA	%BA
Virgin	6.54 (0.93 ± 0.69)	36.9 ± 9.4	-	-				
LI-log	3.35 (0.84 ± 0.40)	35.1 ± 6.2	4.5	2.4	7.6	76.5	13	38.3
MI-log	1.66 (0.55 ± 0.09)	31.7 ± 19.6	8.5	9.1	26.5	58.3	18.7	51.3

At each census in all plots all trees larger than 10 cm DBH were enumerated and identified to the species level. In total the 14 plots in the ITCI concession contained ca. 800 (morpho-) species. Enumeration of trees from 10 to 15 cm DBH was not carried out consistently during the first 4 censuses. As a result the minimum tree size used for all calculations is 15 cm DBH.

Species diversity
Alpha diversity of the plots at each census was calculated with Fishers' a (Fisher *et al.* 1943, Taylor *et al.* 1976, Rosenzweig 1995), using all individuals and species larger than 15 cm DBH. To test for statistical differences in values of Fishers' a amongst different forest types over time, two-way ANOVA with repeated measurements (SPSS 1997) was used. Main factors were forest type (virgin, LI-logged, MI-logged forest) and time (years after first measurement for plots in virgin forest and years after logging for plots in selectively logged forest).

Species composition
Principal component analysis (PCA) is used to summarise compositional dynamics. PCA is a widely applied technique in which the multivariate correlations amongst species are used to describe vegetation patterns (e.g., Austin 1977, Anand & Heil 2000). The full data set, comprising frequencies of species, is split up into 6 diameter classes (15-20 cm, 20-30 cm, 30-40 cm, 40-50 cm, 50-60cm, > 60 cm DBH) for each temporal measurement. Separate PCA were applied for each diameter class including all plots in virgin and selectively logged forests and all temporal measurements. Dynamics in the species composition (i.e., the recovery of forest after logging) can be observed by following the trajectories of each plot in PCA space. The average travelled Euclidian distance of each plot is calculated as a measure of displacement in PCA space. This is a measure of both changes in abundance and changes in species composition. Euclidian distance is calculated between successive temporal measurements within each plot. One-way ANOVA with Sidàk post hoc tests are performed to test for differences among forest types (SPSS 1997).
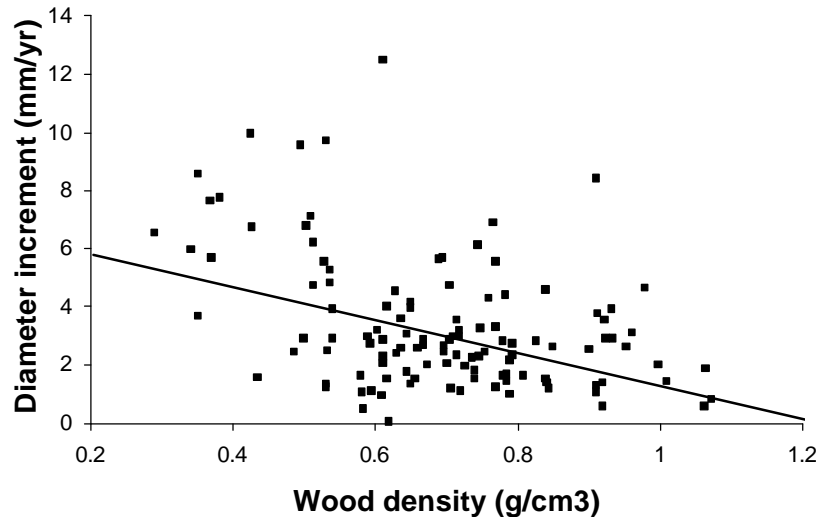
Figure 7.2 The relationship between the species-specific wood density (derived from Burgess 1966, Reyes *et al*. 1992, Soerianegara & Lemmens 1993, Lemmens *et al*. 1995, Sosef *et al*. 1998, and Suzuki 1999) and the measured diameter increments of tree species in the 7 virgin forest plots over 16 years time period. ($R^2 = 0.1872$, $P < 0.0001$)

Plant functional types

To study the relationship between growth rate and wood density of Bornean tree species diameter increments of all trees and species in the 14 plots were calculated. Wood density properties for tree species are derived from Burgess (1966), Reyes *et al*. (1992), Soerianegara & Lemmens (1993), Lemmens *et al*. (1995), Sosef *et al*. (1998), and Suzuki (1999). A significant, negative relation is found between wood density and diameter increment (Figure 7.2). Species-specific wood density is used as a measure of potential, species-specific growth rate to subdivide species into 3 wood density classes. These classes are derived from the frequency distribution of wood density classes of Asian tree species (Reyes *et al*. 1992). The classes consist of softwoods (from 0.2 to 0.49 g/cm^3), medium-hardwoods (from 0.5 to 0.79 g/cm^3), and hardwoods (from 0.8 to 1.2 g/cm^3). About 10% of the species could not be classified into a wood density class since the wood properties of those species or its genus is unknown. Because the fraction of unknown classified species is rather constant amongst the different forest types and diameter classes, these species are left out of the analysis and considered a constant measuring error. A first analysis of the frequencies of the 3 functional types revealed that the softwood class comprised both 'true' pioneer species, such as *Macaranga* spp. (Euphorbiaceae), as well as potentially tall growing climax species, such as *Shorea parvifolia* (Dipterocarpaceae). These two species groups may be interpreted as short- and long-lived pioneers. To make a distinction between these different plant-types a second division was made based upon potential maximum tree height (not actual tree height), derived from the *Flora Malesiana*. Within this subdivision 3 subgroups are recognised; an understorey class (maximum tree height of 15 meter), a sub-canopy class (maximum tree height from 15 to 40 m), and a canopy or emergent class

(maximum tree height larger than 40 m). In total 5 different PFT are identified; L1, L2, L3-types (softwoods with height classes 1 to 3), M-type (medium-hardwoods), H-type (hardwoods, see Table 7.2). Frequencies of plant functional types were calculated for each temporal measurement and averaged for virgin forest plots and selectively logged plots. Repeated measures ANOVA and Dunett post-hoc tests (SPSS 1997) were performed for each forest type to test for significant changes in the abundance of plant functional types in relation to time per diameter class. Prior to the statistical analysis all frequency data were Arcsine transformed. Statistical tests among the forest types for each temporal measurement could not be carried out because the time intervals of the different forest types differed.

Table 7.2   Wood density (g/cm^3), maximum potential tree height (m), and number of species for the five plant functional types. For wood density the range and average is given (data derived from Burgess 1966, Reyes *et al.* 1992, Soerianegara & Lemmens 1993, Lemmens *et al.* 1995, Sosef *et al.* 1998, Suzuki 1999), for maximum tree height the range is given (tree height derived from the *Flora Malesiana*).

PFT	Description	Wood density (range)	Wood density (mean)	Tree height (range)	Nr. species
L1	Softwood understorey	(0.2 – 0.49)	0.343	(0 – 15)	3
L2	Softwood sub-canopy	(0.2 – 0.49)	0.423	(15 – 40)	18
L3	Softwood emergent	(0.2 – 0.49)	0.413	(40 – 80)	4
M	Medium-hardwoods	(0.5 – 0.79)	0.667	–	259
H	Hardwoods	(0.8 – 1.20)	0.905	–	156

Results

Alpha diversity
Alpha diversity, calculated as Fishers' a, did not differ significantly amongst forest types (i.e., virgin forest and the two types of selectively logged forests) (ANOVA F = 1.23[ns], Figure 7.3). Furthermore, Fishers' a did not change significantly over time (ANOVA F = 0.075[ns]) in the different forest types, nor was the interaction between forest type and time significant (ANOVA F = 0.087[ns], Figure 7.3).

Species composition
Figures 7.4a to 7.4f display the first two axes of the Principal Component Analyses (PCA) of different diameter classes. The cumulatively explained variation of the first two principal components ranges from 33.1% (diameter class 30 – 40 cm DBH) to 54.7% (diameter class > 60 cm DBH). In Figures 7.4a to 7.4f the multi-temporal points of each plot are interconnected with lines to illustrate the trajectories in PCA space. The general patterns found for virgin and selectively logged plots are very similar with respect to the different diameter classes. Each plot, regardless of being in virgin or logged forest, followed its own trajectory. At most diameter classes plots in selectively logged forests did not move to a distinct area in PCA space. From diameter class 15-20 cm DBH to 40-50 cm DBH logged forest plots had significantly larger travelling distances in PCA space (Table 7.3). This indicates
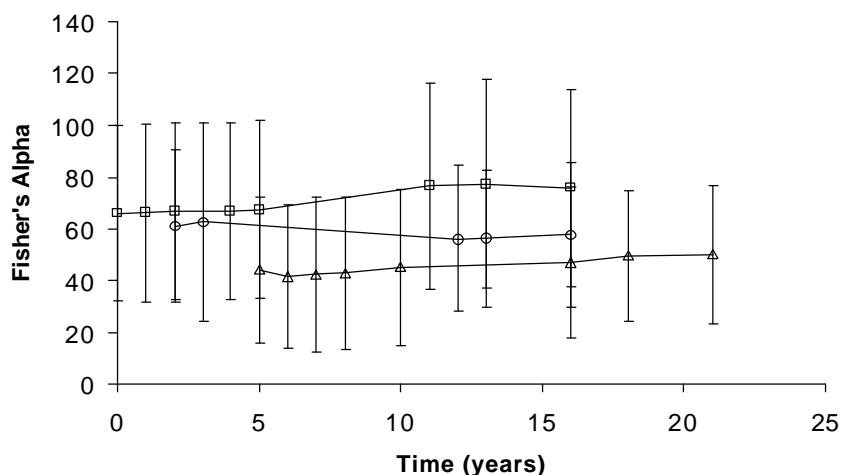
Figure 7.3   Mean values ± SD of Fishers' a of virgin forest plots (?, n=7), LI-logged plots (O, n=4) and MI-logged plots (?, n=3). Time refers to time since first measurement in virgin forest plots, and time since logging in logged forest plots.

larger changes in composition than in virgin forest plots, which is in accordance to expectation. In contrast, some virgin forest plots do not show any temporal dynamics in species composition indicated by the multi-temporal points that are more or less stacked onto each other.

Table 7.4 summarises all species that have the highest or lowest ranking along the first or second principal component. This ranking is calculated separately for each diameter class by using the factor loadings of the PCA of species. The majority of the species have only low to moderate contributions to the first two principal components relative to the contribution of the highest ranked species. This is caused by the low abundance of these species in the different plots. Furthermore, species with high factor loadings only have this in a few diameter classes (Table 7.4). Ironwood (*Eusideroxylon zwageri*, Lauraceae) is an exception to this, since it has a high ranking on the fist two principal components in all diameter classes (Table 7.4).

Table 7.3   Displacement of forest plots in PCA space, calculated as Euclidian distances (D) in the different diameter classes (given in cm DBH). Means with the same letter were not significantly different (ANOVA, Sidàk Post-hoc test P < 0.05).

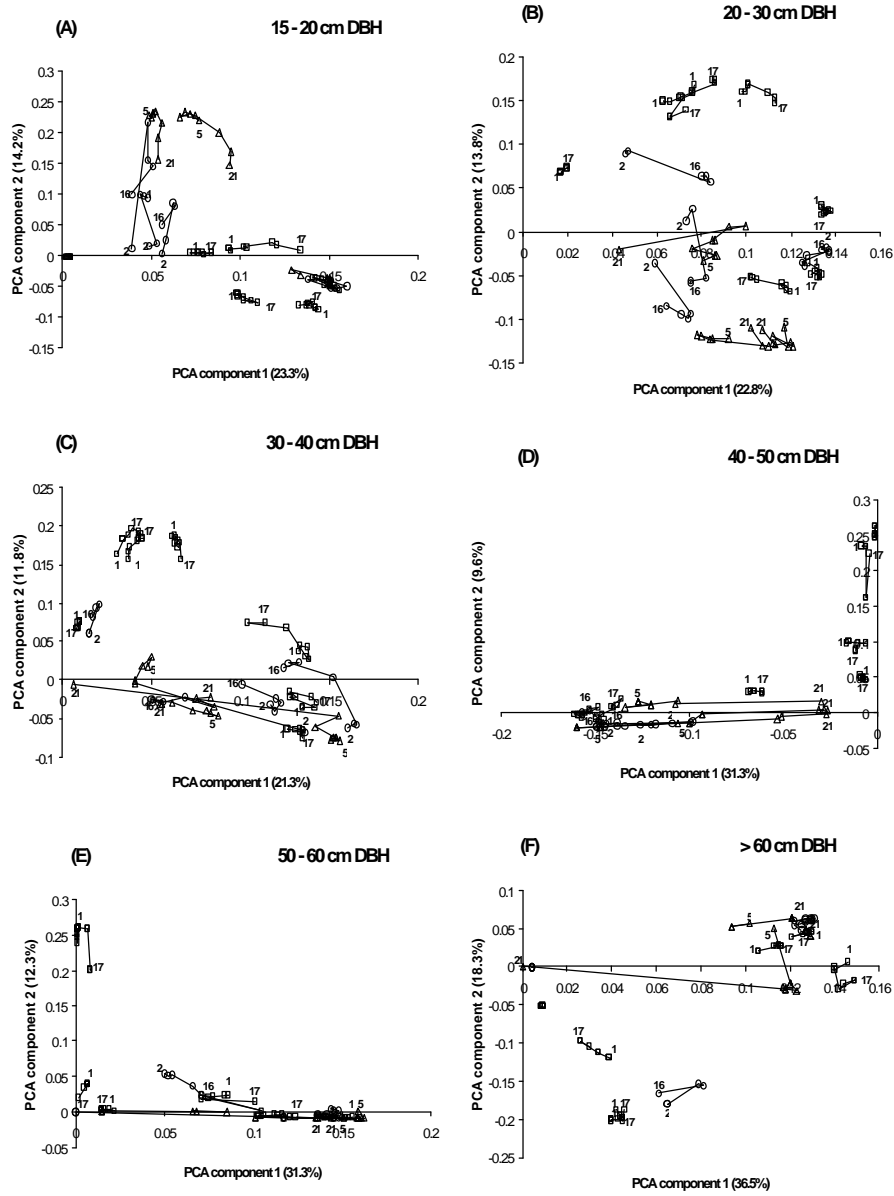| Forest type	Size class (cm DBH)					
	15-20	20-30	30-40	40-50	50-60	> 60
Virgin	0.48a	0.47a	0.66a	0.64a	0.75a	0.34a
LI-logged	3.63b	2.23b	2.52b	2.08b	1.76a	1.36a
MI-logged	1.63ab	1.87b	2.93b	2.67b	1.88a	1.58a

124

Figure 7.4   The first two principal components of the PCA carried out for all trees between 15-20 cm DBH (**A**), 20-30 cm DBH (**B**), 30-40 cm DBH (**C**), 40-50 cm DBH (**D**), 50-60 cm DBH (**E**), and > 60 cm DBH (**F**). Symbols represent: **?** - virgin forest plots, **O** - LI-logged plots, **?** - MI-logged plots. The numbers near the symbols indicate the year of measurement. Year refers to time since first measurement in virgin forest plots, and time since logging in logged forest plots.

Table 7.4 List of species that have the highest ranking along the first or the second principal component (1 and 2) in the different diameter classes (given in cm DBH). Ranking is calculated for each diameter class separately. + Indicates a positive loading and – indicates a negative loading on a principal component.

Size class (cm DBH)	15-20		20-30		30-40		40-50		50-60		>60	
Component	1	2	1	2	1	2	1	2	1	2	1	2
Species												
Vatica oblongifolia	+											
Madhuca sericea	+											
Macaranga pearsonii		+	+	-								
Anthocephalus chinensis		+		-								
Shorea morpho-species1	+		+	+		+						
Eusideroxylon zwageri	+		+	-	+	-	-		+		+	+
Shorea parvistipulata			+		+			+	+			
Hopea mengerawan			+		+							
Shorea leavis			+		+					+	+	
Agathis borneensis					+			+	+			-
Dacryodes puberula					+							
Durio excelus					+							-
Eugenia dyeriana					+							
Shorea johorensis									+			
Shorea parvifolia											+	

This species is found in high abundance in all diameter classes. As expected, in diameter class 15-20 cm DBH only two species, notably the pioneers *Anthocephalus chinensis* (Rubiaceae) and *Macaranga pearsonii* (Euphorbiaceae) had a high ranking on the second principal component.

Plant Functional Types (PFT)
Two years after logging the fraction of softwood, understorey and sub-canopy stems (PFT types L1 and L2, Table 7.2) was on average already twice as high in the smallest diameter class, compared to virgin forest (Figure 7.5a). Ten to 12 years after logging the L1 and L2 fraction decreased in number in both types of logged forest. Up to a diameter of 50cm DBH a clear, but delayed ingrowth of the L2 type was found (Figures 7.5a to 7.5d). In the diameter class of 60cm DBH and more softwood species were almost completely absent in the logged forests (Figure 7.5f). As expected, the fraction and number of softwood stems in virgin forest was modest and rather constant (ca. 10%) in the diameter classes from 15cm to 50cm DBH (Figure 7.5a and Figure 7.6). In contrast to the logged forests, softwoods in the virgin forest were mainly canopy/emergent species (L3 type, Table 7.2). The L3 type consisted almost entirely of *Shorea parvifolia* and *Agathis borneensis* stems. In the largest two diameter classes of virgin forest ca. 25% of the stems belonged to the L3 type (Figures 7.5e and 7.5f). However, without the contribution of the locally abundant *A. borneensis*, the L3 fraction of virgin forest plots comprised only 7%.
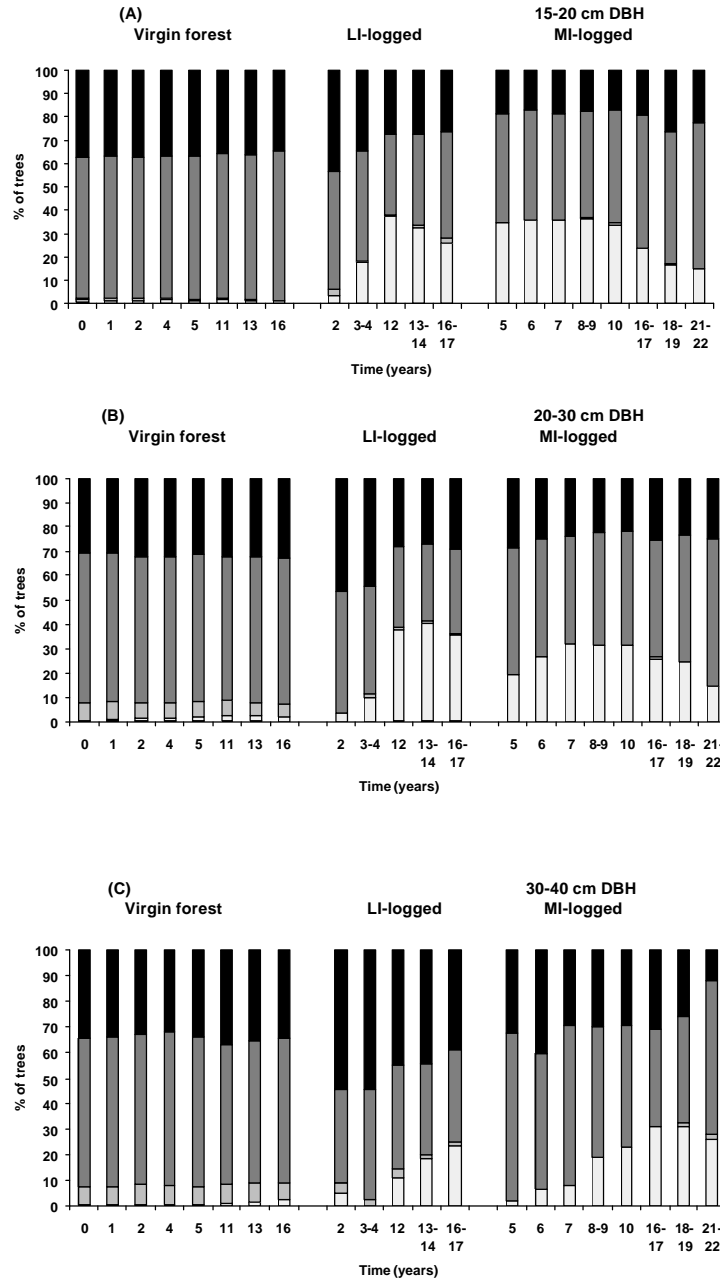
Figure 7.5   The fraction of Plant Functional types L1, L2, L3, M, and H (see table 4 for abbreviations of PFTs) of trees between 15-20 cm DBH (A), 20-30 cm DBH (B), 30-40 cm DBH (C), 40-50 cm DBH (D), 50-60 cm DBH (E), and > 60 cm DBH (F). Time refers to time since first measurement in virgin forest plots, and time since logging in logged forest plots.
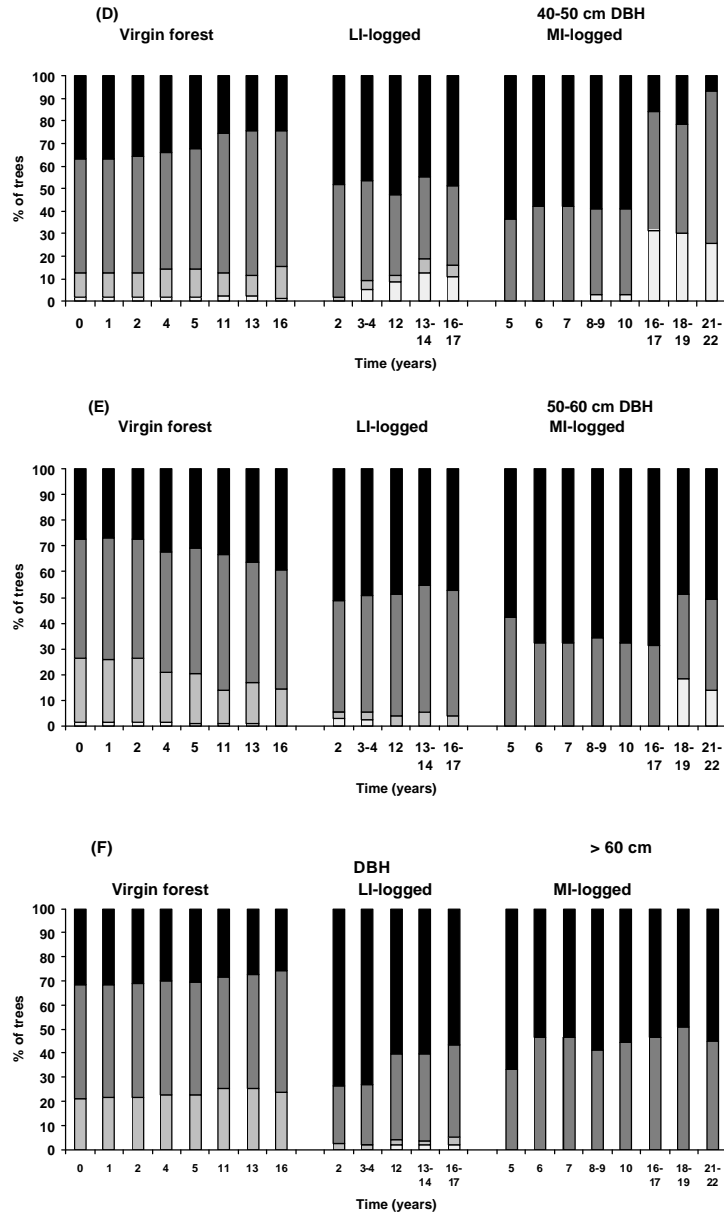
(D)

Virgin forest   LI-logged   40-50 cm DBH
                                           MI-logged

(E)

Virgin forest   LI-logged   50-60 cm DBH
                                           MI-logged

(F)

                              DBH   > 60 cm
Virgin forest   LI-logged   MI-logged

Figure 7.5   (continued).

Although in logged forest plots the fractions of PFTs tended to differ among sequential temporal measurements and a clear 'wave' of the L2 type can be observed over time, none of these differences were significant. In addition, also logging intensity did not seem to affect the partitioning of stems among PFTs. Only in the 40-50 cm diameter class MI-logged forest had a twofold higher fraction of L2 stems than LI-logged forests, sixteen years after logging. This increase in MI-logged plots was at the expense of hardwood stems. The amount of L1 and L2 stems was clearly affected by logging intensity. LI-logged plots had twice as many L1 and L2 stems per hectare than MI-logged plots (Figure 7.6).

Changes in the population structure of medium-hardwood (M) and hardwood (H) stems due to logging were analysed by studying a number of Dipterocarpaceae species. The Dipterocarpaceae genera *Dipterocarpus*, *Dryobalanops* and *Shorea* contain a large number of valuable timber species. As expected, the number of large M and H-type stems (> 60 cm DBH) was lower in selectively logged forest plots (Figures 7.7 and 7.8). This difference was most pronounced for the H-type species (Figure 7.8). In LI-logged forest a growing stock of small stems in both wood density classes was found (Figures 7.7 and 7.8). Twelve years after logging the number of stems within the 15-20 cm diameter class is increased in the LI-logged plots. The MI-logged plots show a different pattern. The number of small-sized, medium hardwoods has already increased 5 years after logging. However, the H-type Dipterocarpaceae were almost completely absent in the MI-logged forest (Figure 7.8). It is not clear if Dipterocarpaceae were already absent before logging of these plots or if logging destroyed almost all of them. However, the recruitment of new stems into the smallest diameter class 18 years after logging does suggest some removal of adult stems in these plots.
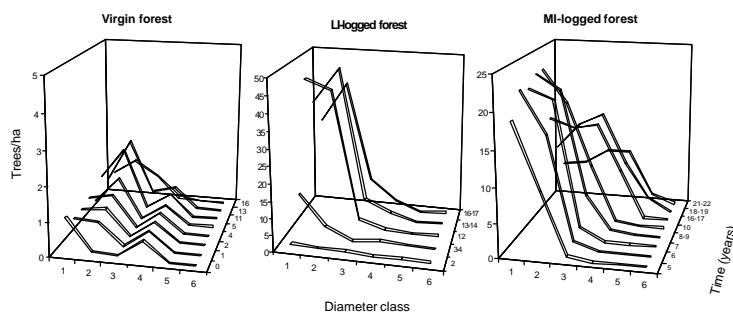

Figure 7.6   Changes in the population structure in time of trees of plant functional types L1 and L2 in virgin forest plots, LI-logged, and MI-logged plots. Time refers to time since first measurement in virgin forest plots, and time since logging in logged forest plots. Please note the difference in density scales between the forest types.
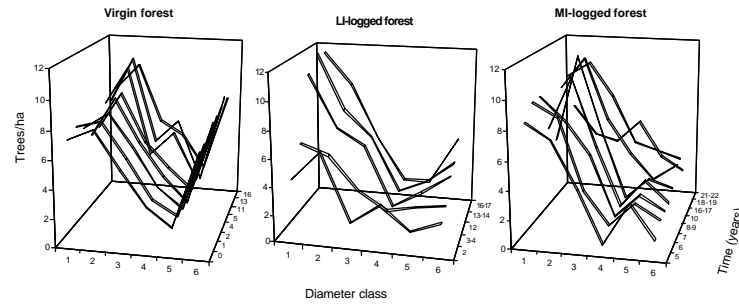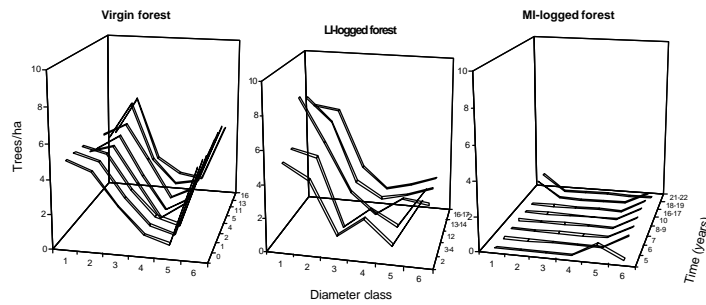
129

Figure 7.7   Changes in the population structure in time of trees that belong to the Dipterocarpaceae genera *Dipterocarpus, Shorea*, and *Dryobalanops* having a wood density between 0.5 and 0.79 g/cm3 (plant functional type M) in virgin forest plots, LI-logged, and MI-logged plots. Time refers to time since first measurement in virgin forest plots, and time since logging in logged forest plots.

Figure 7.8   Changes in the population structure in time of trees that belong to the Dipterocarpaceae genera *Dipterocarpus, Shorea*, and *Dryobalanops* having a wood density between 0.8 and 1.2 g/cm3 (plant functional type H) in virgin forest plots, LI-logged, and MI-logged plots. Time refers to time since first measurement in virgin forest plots, and time since logging in logged forest plots.

Discussion

Although commercial logging operations in East Kalimantan has increased since the late 1960s (Kartawinata *et al.* 1981), the effects on tree diversity are largely unknown (Cannon *et al.* 1998). Recently Cannon *et al.* (1998) found high tree species richness in logged-over forest in West Kalimantan. Their results, however, are debatable due to their small plot size and their time span chosen (up to 8 years after logging) (see Sheil *et al.* 1999). Logging intensity in Indonesia is high and the extraction of timber trees can reach up to 20 trees per hectare (Kartawinata *et al.* 1981). Logging intensity in the ITCI concession is moderate to low in comparison to these Figures. Therefore, the results on tree species diversity and shifts in species composition after logging should be treated with caution and cannot simply be extrapolated to the other areas in Kalimantan.

Alpha-diversity

Logging had no significant effect on tree alpha diversity (measured as Fishers' a) nor did alpha-diversity significantly change over time. In addition to that, logging intensity did not affect Fishers' a. With respect to this result the total damage between both types of logging was more or less equal, although the number of logged trees differed. In low-intensity logged plots the larger amount of additional tree damage and mortality was caused by the construction of more skidder roads (van Eijk-Bos 1996). Because pre-logging data were not available we could not test whether Fishers' a in logged plots changed immediately after logging. Two chronosequence studies carried out in East Kalimantan also found an unaffected Fishers' a with logging history (Slik *et al.* 2002, Verburg *et al.* 2001). In contrast, logging did increase species richness in the Budongo forest reserve in Uganda (Plumptre 1996), while Cannon *et al.* (1998) recorded an increased species-to- stem ratio due to logging in West Kalimantan. According to the Intermediate Disturbance Hypothesis (IDH) and Gap-phase Regeneration Hypothesis (GRH) species diversity was expected to increase after logging. However, adding disturbance (i.e., logging) to relatively 'high dynamic' forests that are found on the left-hand-side of the 'hump' of the IDH curve would further reduce species richness in such forests. Diversity indices, such as Fisher's alpha or Shannon Weaver, may not be sensitive enough to detect small changes in the contribution of species and stems in high-diverse tropical rain forest (ter Steege *et al.* 2001). When for example the contribution of a number of species is reduced (due to logging) while simultaneously a (small) set of species (i.e., pioneers) is introduced, Fisher's a hardly changes. Fishers' a can only be affected considerably when the number of new recruited species is substantially large and their abundance low compared to the number of species found in a forest plot. Therefore, the indices commonly used to measure the effects of disturbance on diversity in hyper diverse tropical rain forests may not be very applicable. In addition to this, recently the GRH has been under criticism as a mechanism to maintain species diversity due to new empirical evidence that show only a marginal increase in species diversity caused by tree-fall gaps (e.g., Hubbell *et al.* 1999).

Species composition

Logging did not result, contrary to what was expected, in more similar tree communities in different plots. Because the pre-logging state of the selectively logged plots was unknown, the direction of recovery could only be studied from the first measurement after logging onwards. Up to 50 cm DBH transitions in PCA space were significantly larger in both types of logged forest plots compared to virgin plots. However, patterns in compositional shifts are very difficult to detect. Indeed we found large transitions in the direction of the second principal component for a number of logged plots in the smallest diameter class. This component was associated with two pioneer species, *Anthocephalus chinensis* (Rubiaceae) and *Macaranga pearsonii* (Euphorbiaceae). Also in the next, 20-30 cm, diameter class some logged plots had small, but detectable transitions in the direction of the second principal component. All selectively logged plots that showed this pattern had in common a large abundance of the pioneer *A. chinensis*, while this species was completely absent in the logged plots that did not show these transitions. At larger

diameter classes the patterns were fuzzy and no clear trends could be detected. Large transitions in species composition did occur after logging in larger diameter classes, but the direction of the transitions is not predictable.

Multivariate techniques have been used to study patterns in species composition in tropical rain forests (e.g., Austin & Greig-Smith 1968, Austin 1977, Newbery *et al.* 1996, Sheil 1999b) but the effects of logging have never been analysed in such way. Sheil (1999b) found a clear intrinsic convergent trend during succession of a tropical rain forest in Uganda. However, the end stage of this succession was a relatively species poor, monodominant stand. Moreover, mainly primary succession was the focal point in this unreplicated study design (Sheil 1999b). In our study we used replicate plots. The different PCA showed that the initial states with respect to species composition varied largely among the plots. That will make studies involving chronosequences troublesome to interpret, because forest plots with a different logging history do not necessarily have equal initial states, as shown by our study.

Plant functional types
As expected, an increased fraction of softwood stems was found in the smallest diameter classes after logging. While two softwood species had only in the two smallest diameter classes a high contribution in the PCA, the increased fraction of softwood stems in logged forest plots was detectable up to 50 cm DBH in the PFT approach. Up to the 40-50 cm diameter class a delayed increase of the softwood fractions L1 and L2 was seen 18 years after logging. The increase of softwoods L1 and L2 in logged forests was clearly at the expense of medium-hardwood stems. The hardwood fraction was hardly affected in the logged plots. Although these trends were clearly observable, no significant trends in time among PFT fractions in logged forest plots could be detected. This is partly the result of the large differences in the fractions of PFT among logged plots. Brown & Lugo (1990) who reviewed secondary succession in terms of replacement of trees of different wood density classes found similar results during the first years of succession. After more than 20 years the fraction of softwood stems decreased while the fraction of hardwood stems slowly but steadily increased (Brown & Lugo 1990).

Virgin forest plots contained a large fraction of softwood emergent stems (L3 type) in the size class of 40 cm DBH and onwards. Those included *Shorea parvifolia* in almost all plots and *Agathis borneensis* in large quantities in two virgin forest plots. This PFT was almost absent in the logged forest plots. Twelve years after logging only a small fraction of *S. parvifolia* trees was found in the 30-40 cm diameter class in the LI-logged plots, while softwood emergents were not found in the MI-logged plots. *S. parvifolia* is one of the major timber trees in Kalimantan and may have been logged, but information on tree species removal is not available. It is alarming that softwood emergents are not found in the smallest diameter class after logging. Future regeneration of this PFT depends on the available stock of small stems. Hence the regeneration of logged forest may be seriously hampered with respect to this PFT.

Model studies have been carried out to simulate shifts in PFTs during primary and secondary succession in tropical rain forests (e.g., Köhler & Huth 1998, Chave 1999). Both models distribute species unevenly over the different PFTs. As in our study the pioneer-like PFT only comprises a fraction of all species, while most species are allocated in a single, but very large PFT. The response of softwood species to disturbance, such as logging, is well documented. In contrast, the response of a single large group such as the medium-hardwoods is much less understood. Therefore such a large group should be subdivided in smaller portions using additional criteria. Potential tree height as used in our study to subdivide the softwood group and seed mass, as shown by ter Steege & Hammond (2002) may be potential criteria.

Concluding remarks and implications for management

At first sight, small-scale logging did not seem to affect species diversity and composition too much. However, logging intensity in the ITCI concession is low compared to other areas in Kalimantan. Logged forest plots did not have a significantly lower alpha diversity than virgin forest plots. The gaps created by logging facilitated large ingrowth of softwood tree species. LI-logged plots had twice as many softwood stems (type L1 and L2) than MI-logged plots. However, it could not be tested if this was the result of logging intensity or that other factors such as spatial position of the plots affected this pattern. In both LI- and MI-logged forest plots regeneration of medium-hardwood and hardwood Dipterocarpaceae tree species occurred in the smallest diameter class, but no regeneration of the softwood, L3 type Dipterocarp *Shorea parvifolia* was observed. Hence it is recommended to put a number of large softwood *Shorea* spp. stems aside during logging to ensure this species group can recover from logging.

As Sheil *et al.* (1998) pointed out, the study of the recovery of logged forests needs a long monitoring period because secondary succession spans many decades. The 20 years of study is simply too short to make final conclusions about the recovery pathways. However, this study is one of the very few that does analyse the recovery over such a long time period and is therefore very important for the understanding of secondary succession after logging. Therefore, the permanent sample plots in the ITCI concession need to be monitored in the future, although the recent El Niño drought and fires of 1997/98 seriously damaged some of the plots. In the near future much emphasis should be put in permanent sample plot studies since the recovery pathways after logging are still relatively unknown. However, such a study clearly needs a firm experimental set-up and statistical design. The study presented here would have benefited from a higher number of replicate plots in both logged and virgin forest, as well as identifying species composition in the pre-logging phase of the selectively logged forest plots.

8   LONG-TERM EFFECT OF TIMBER HARVESTING IN THE BARTICA TRIANGLE - CENTRAL GUYANA[1]

Hans ter Steege, Ivan Welch, Roderick Zagt

Abstract

In one of the longest time series available, we present a comparison between forest inventories of 1924, 1964 and 1999 of an 800-km^2 forest harvesting area in central Guyana. Harvesting mainly targeted one species *Chlorocardium rodiei* (Greenheart), of which the population declined by 63% over the 75 years of harvesting. The decline of the population was not only detectable in the harvested size classes (> 30 cm) but also among the smaller size classes. In 1999, however, Greenheart still ranked third in abundance. There was little change in the overall species composition, proportion of disperser groups or proportion of functional groups in the tree community. There were also no detectable changes in tree diversity. The conservation value of these unique forests can still be considered high. Thus, while the long-term sustainability of Greenheart harvesting is low, other ecological criteria of sustainability are met. Short-term recovery of Greenheart is not to be expected due to low population growth and small numbers of seed trees. Strategic choices will have to be made with regard to harvesting the remaining Greenheart stands – three scenarios are discussed.

Introduction

Large tracts of the Guianas are still covered with forest. Even though the deforestation rate of the Guianas has been among the lowest worldwide (Lanly 1982, Luning 1987, Burgess 1993), timber harvesting has been an important component of the use of the vast hinterland forest resources. Of the c. 17 million ha of forest in Guyana c. 13 million are designated state forest land (Figure 8.1). In 1997 roughly three quarters of this area had been given out as forest concessions (van der Hout 1999). At present it is estimated that some 2.2 million ha have been logged (van der Hout 1999). Traditionally, harvesting was carried out by local concessionaires but more recently foreign loggers have been attracted to the large unused timber resources of the country, causing some international concern (Colchester 1994, 1997, Sizer 1996). Greenheart (*Chlorocardium rodiei*) has been the pillar on which the forest industry in Guyana has rested for most of its logging history. The traditional logging method could be referred to as selective harvesting, but was carried out without much concern for the remaining stand (van der Hout 1999). Average harvesting volumes are estimated to be as low as 5 m^3 ha^{-1} (van der Hout 1999). Although the damage to the forest at large may be relatively small, local damage to the forest may be substantial (ter Steege *et al*. 1996, Zagt 1997, van der Hout 1999), due to the patchy distribution of commercial species.

Only recently Greenheart has been surpassed by Baromalli (*Catostemma* spp.) as the major timber species of Guyana, due to the establishment of a large, foreign owned plywood mill. Log production of Greenheart remained at the same level, however. For a more detailed history of logging in Guyana see Vieira (1980) and van der Hout (1999).

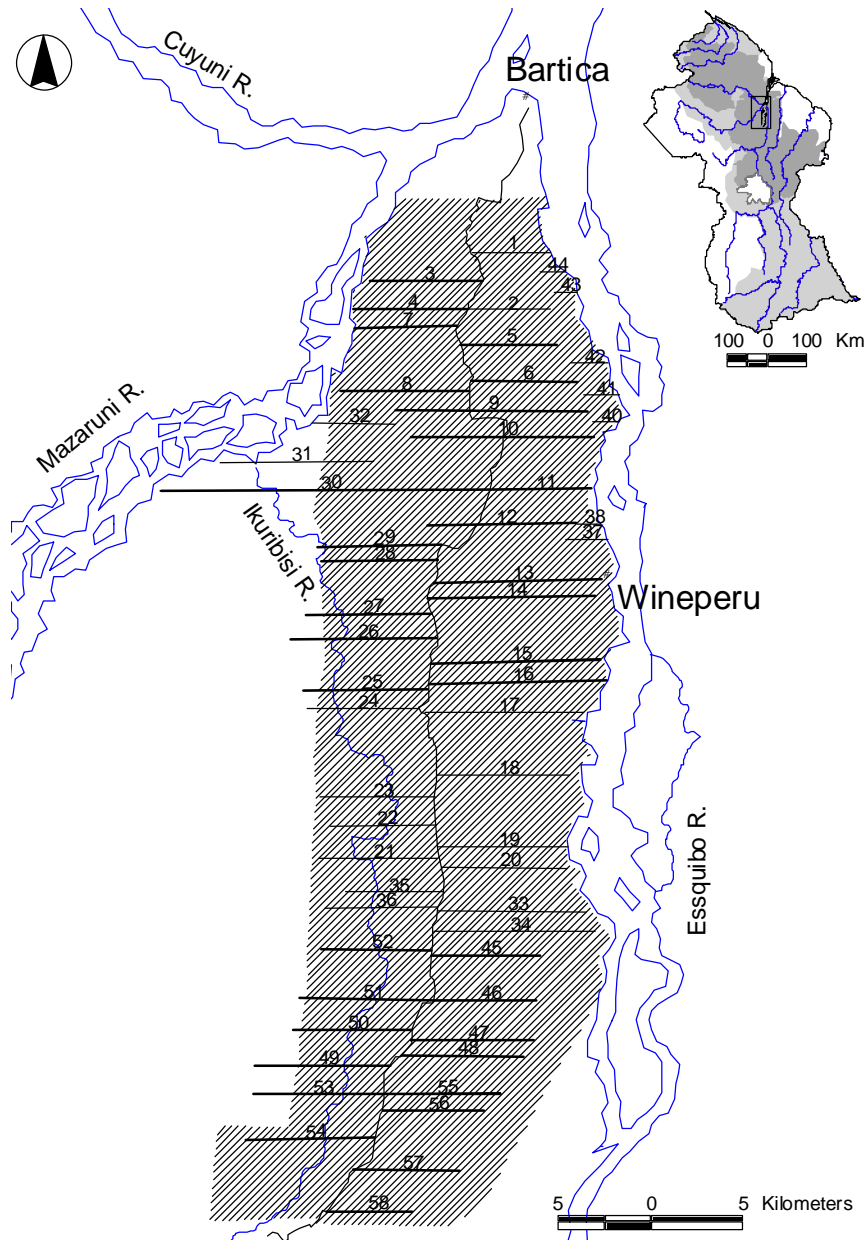[1] Also appeared in *Forest Ecology and Management* 170: 127-144, 2002.

Figure 8.1 Location of inventories in the Bartica Triangle. The hatched area is the area inventoried in 1924. Thick lines are part of the 1964 and 1999 inventory; thin lines were only inventoried in 1964. Inset shows the location of the Bartica Triangle in Guyana. Light grey: Permanent Forest Estate; dark grey: allocated forests in 2002 (source: Guyana Forestry Commission). The white shape within the PFE is the Iwokrama Forest (see Kerr 1997).
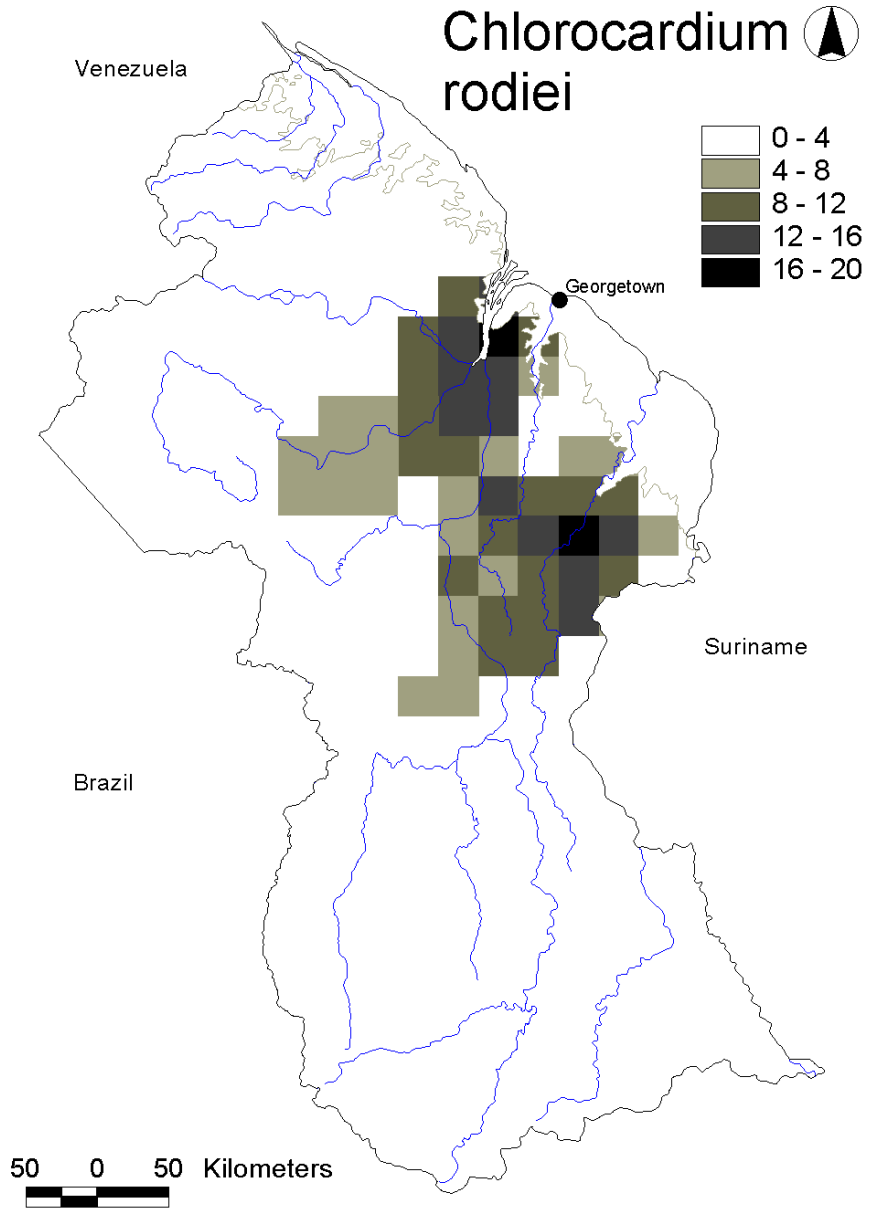
136

Figure 8.2   Community dominance (% of trees in the forest stand > 30 cm) of *Chlorocardium rodiei* in Guyana, with exception of the coastal belt, where the species is practically absent (data courtesy Guyana Forestry Commission, see ter Steege (1998)). *Chlorocardium* is practically endemic to Guyana (ter Steege 1990, 2000) and its main concentrations are in central to east Guyana on the sandy soils of the 'Berbice Formation'.

137

Bartica has traditionally been a focal entry point for forestry and mining in the interior of Guyana. Its central position at the confluence of the Essequibo, Cuyuni and Mazaruni Rivers (Figure 8.1) and the high abundance of Greenheart in the surrounding forests (Figure 8.2) both probably contributed to this. The Bartica Triangle, the area enclosed by the Essequibo and Mazaruni Rivers south of Bartica, was opened for commercial logging in 1924. At that time the area was virtually untouched by man, in terms of timber harvesting (Wood 1926). In that same year a large-scale forest inventory was carried out (Wood 1926). Since 1924, four major concessions, Charleston Sawmills (now Guyana Sawmills Ltd.), Willems Timbers and Trading Co. and British Guiana Timbers (now Caribbean Resources Ltd.) and later Toolsiepersaud Ltd., have worked in the Bartica Triangle. A second large-scale inventory was carried out in 1964. The 1964 inventory, known as "Valuation Survey No. 40-64" was carried out to "*determine what volume of merchantable timber, including Greenheart, there is, in worked over areas of Crown Forest Leases*". Due to lack of computational capacity a comparison with the inventory from 1924 was not made in 1964 or thereafter.

In 1999, after 75 years of more or less continuous harvesting in the area, several of the concessionaires (pers. comm.) claimed that it was no longer possible, in economic terms, to extract Greenheart from the area. Thus, with results of the 1924 inventory and a near-complete dataset of the 1964 inventory available, there was an unique opportunity in 1999 to re-inventory this area to study the effect of 75 years of conventional timber harvesting in Guyana on a large scale.

The main objectives of the 'Bartica Inventory 7 – 47 Miles 1999' were:

1. To determine the changes in tree species composition and -diversity
2. To determine the (change in) population size of Greenheart
3. To determine the regeneration potential of Greenheart

This is the longest reported time study of conventional harvesting at this scale in South America and perhaps worldwide. It provides an opportunity to examine three important research questions/concerns voiced in relation to the impact of logging on tropical rain forest worldwide.

Due to the strong focus of logging on Greenheart, a significant decrease in its population was expected. This expectation was strengthened by the fact that individuals under the minimum allowable cutting size (30.5 cm, or 12") are naturally scarce (e.g. Davis & Richards 1934, ter Steege *et al*. 1996). This 'infamous' dip in the population structure and the slow growth rate of the species (Prince 1971, 1973, ter Steege 1990, ter Steege *et al*. 1996, Zagt 1997) do not allow fast recovery of the harvested population.

Assuming, thus, that Greenheart would be unlikely to replace itself, we asked: what species established in the gaps created by the logging?" General theory of the relationship between disturbance and diversity (see Huston 1994 for a review) predicts that the selective removal of individuals of a dominant species should lead

to higher diversity. We suggested before (ter Steege & Hammond 2001) that the low levels and small scale of forest dynamics in central Guyana has led to monodominance, and that higher dynamics and higher diversity are indeed associated in Guyana. Much of the expected increase in tree diversity after logging in Bartica is to be expected from fast growing species with relatively low wood density and relatively small seeds, characteristics that are also associated with 'high-diversity' forests in Guyana. As the many endemics that are found in the Bartica Triangle (ter Steege 1998, ter Steege *et al*. 2000a), are generally species with dense wood and large seeds (ter Steege & Hammond 2001), we expect that they are slow growing species (Greenheart among them) and that they will not have benefited much from the logging gaps in this forest.

This study also provides an opportunity to evaluate the impact on population size of a species that has recently been declared "*facing a high risk of extinction in the wild in the medium-term future, due to a population reduction (observed, estimated, inferred or suspected reduction) of at least 80% over the last 10 years or three generations (based on direct observation and the actual or potential levels of exploitation)*" (WCMC 1998), a view that has met local criticism (e.g. D.S. Hammond, unpublished letter).

Harvesting still continues in a similar fashion in Guyana but several initiatives have been taken in the late 90s to introduce better forest management practices and national standards of forest management. This study will provide an important framework for these initiatives as it provides the first large-scale assessment of long-term trends of a major timber resource and of the impacts of its harvesting on tree biodiversity in Guyana. Thus, the results of this study are expected to be of great relevance to policy and management.

Methods

Area description

The Bartica Triangle is situated south of Bartica in central Guyana (Figure 8.1). The climate is typical of central Guyana with an annual rainfall of 2764 mm at Bartica Station (Hydromet data 1958-1975) and with two dry and wet seasons. Soils and forests in the area are strongly associated (Wood 1926, Davis & Richards 1933, 1934, Fanshawe 1952). Just over half of the area is covered by mixed forest on brown sands and loams (ferralic Arenosol and haplic Ferralsol) with a high abundance of commercial timber species. The most common trees are *Eschweilera sagotiana/subglandulosa, Chlorocardium rodiei, Mora gonggrijpii, Licania alba/majuscula, Swartzia leiocalycina, Mora excelsa, Pentaclethra macroloba, Eperua falcata, Pouteria guianensis* and *Inga* spp. Just over 1/3 of the area is covered by dry evergreen forest, locally called Wallaba forest, which is found almost exclusively on excessively drained, bleached white sands (albic Arenosol). The most common trees in this forest are *Eperua falcata, Eperua grandiflora, Catostemma fragrans, Talisia squarrosa, Aspidosperma excelsum, Licania densiflora, Ormosia coutinhoi, Swartzia* spp., *Lecythis corrugata* and *Alexa*

139

imperatricis. The remainder of the area is covered by swamp forest, often on peaty soils (terric and fibric Histosols), and riverine forest on alluvial soils (distric Fluvisol). Here, the most common trees are *Mora excelsa, Chlorocardium rodiei, Pterocarpus* spp., *Pentaclethra macroloba, Eperua grandiflora/rubiginosa, Tabebuia insignis, Eperua falcata, Symphonia globulifera, Catostemma* spp., and *Couratari* spp.

"Valuation of the forests of the Bartica-Kaburi Area" (Wood 1926)
The first large-scale forest inventory of the Bartica Triangle was carried out in 1924. For this inventory a strip valuation survey of 2% intensity was used. The main baseline was formed by the Bartica-Kaburi Road up to a point 60 km south of Bartica, then following Roth's trace down to the Kaburi River. Cross lines were made every 914 m (1000 yards) at right angles with the main baseline and were divided in sections of 1.61 km (1 mile). Trees were enumerated in a strip of 30.5 m (100 ft) wide at one side of each cross line. For all trees the diameter was measured with callipers above the buttresses(!). Trees were recorded in classes of 10.1 cm (4 ins) from 20.3 (8 ins) up in the case of *Eperua* spp. and 40.6 (16 ins) for all other species. Trees were identified with the aid of local tree spotters. Booking was carried out by an experienced forester and each 1-mile section was booked separately. The sub-area from the Ikuribisi R. to the Essequibo R., consisting of two blocks, generally known as 'Valuation Area No. 9 – Ikuribisi valley and left bank Essequibo' (53,600 ha, Fanshawe 1949a), covers most of the inventory area of 1964 and 1999 and will be used as our baseline data for undisturbed forest in the area. The Valuation Survey 8/8A (Mazaruni – Ikuribisi) covers the most westerly part of the 1964 and 1999 surveys but extends much further west and will not be used for detailed comparisons.

"The Bartica Triangle forest valuation survey – Survey No 40 – 64" (Welch 1964)
In 1964 a 1% inventory was designed in a 6.5 – 13 km wide strip along the Bartica-Potaro Rd., from Mile 7 to Mile 47. The inventory area was divided into 29 blocks of c. 4 km (200 chains) wide but differing in length and, consequently, in area. In each block two strip lines of 20.1 m (1 chain) wide were cut. The location of each strip line was randomly chosen within the block. The total survey area was c. 72,700 ha. The total strip line area was 754 ha (c. 1%), on which all trees with DBH ? 30.5 cm (12 ins) were measured. Trees were recorded, sound and hollow trees separately, in size classes of 10.1 cm (4 ins) by forest type per strip line. Hence the recording and analysis units are strip lines, unequal in size. All stumps on the strip lines were identified to the species and their DBH measured and recorded per strip line. As stumps decay very slowly in the forest of central Guyana (Figure 8.3) they are an indication of harvesting intensity. For some of the strip lines the original data sheets were missing but fortunately for all lines there were summary sheets listing the total number of trees per DBH class for the whole line. Sub-plots were made to sample smaller trees but this data was incomplete and not used here. Trees were identified with the help of some of the most experienced tree spotters in Guyana and are considered to be relatively consistent and accurate.

Bartica Triangle Inventory 7 – 47 Miles – 1999

The inventory in 1999 was set up in such a way as to find the best compromise between being fully comparable with the inventory of 1964 and time availability. Using the old maps and partly the same crew, new strip lines were cut at locations as exactly as possible on the locations of the lines in 1964. Due to time constraints not all lines, nor complete lines could be measured. A set of lines closest to Bartica (expected heavy exploitation) and furthest from Bartica (expected lower exploitation) were chosen. Plots of 50 x 20m (0.1 ha) were laid out at 100 m distance between the plots. All trees with DBH ? 30 cm were recorded. For Greenheart, all individuals with DBH ? 5cm were recorded. In addition to that, the number of individuals with DBH < 5cm was counted on a sub-plot of 5 x 20m. Plot data recorded included forest type, soil type and presence of stumps. All plots were numbered individually and used as input for the final database but the unit for analysis is the strip line, as in 1964. Trees were identified with the assistance of trained tree spotters, some of whom had also conducted the 1964 inventory. This provided us with high consistency in tree identification between 1964 and 1999.

Figure 8.3   Stump of large *Mora gonggrijppi* felled with an axe. The tree was felled before 1967, when the chainsaw was introduced in Guyana. The photograph was taken in 1999.

Data analysis

"Valuation of the forests of the Bartica-Kaburi Area" (Wood 1926)
None of the original data of the 1924 inventory were still available. However, the report of Wood (1926) gives a complete species list with number of trees per unit area (trees per 1000 acres). In addition to that, it reports on volumes for a number of commercial species per inventory section of the Essequibo block. In this block 106 of such sections (c. 1.61 km) were enumerated. This information was used to calculate average volume per area and its standard error. Because we have no other detailed data available, we assume that the number of trees per ha will have shown a similar error, as volume was derived from the number and DBH of all trees. This procedure was only used for Greenheart, the species for which the most accurate information was present.

"The Bartica Triangle forest valuation survey – Survey No 40 – 64" (Welch 1964)
The block set-up of the 1964 inventory calls for an analysis with blocks and two lines per block with unequal sample size. In 1964 a weight was calculated for each block, based on the areas of the two strip samples. The method is detailed in Vink (1957). However, the number of trees per unit area on line pairs within a block did not show a positive correlation, due to the high variability in stem density of the forest, and we concluded that there was essentially no block effect on stem number. In addition to that, assuming that all strip lines with their area and trees give an estimate of the same population mean and its standard deviation, we can rephrase assumption of an identifiable mean density of trees per unit area into one of a linear relationship between area and the number of trees. A regression analysis of the number of trees against sample area then accounts for un-equality in sample areas. A comparison with Welch (1964), who analysed the data using area corrections, showed that the results were practically identical with the procedure used there and differences were in part due to rounding procedures made in 1964. Therefore we used regression analysis to calculate tree densities. Densities were calculated for all forest types combined (for comparison with 1924) and for mixed forest alone.

"Bartica Triangle Inventory 7 – 47 Miles – 1999"
For the 1999 inventory the analysis per strip line was identical to 1964. All trees were summed, as was the area. This was done for each line and each forest type on each line separately. Again this resulted in areas, unequal in size and regression techniques were used to calculate the number of trees per unit area. Tree densities were calculated for all forest types combined (for comparison with 1924) and for mixed forest alone.

Comparisons between the inventories
Comparison between 1964 and 1999 was made with regression analysis (Zar 1984). We basically tested for homogeneity of slopes, which is equal to testing for a difference in the number of trees per unit area. Because virtually no raw data was available for the 1924 inventory, except for Greenheart volume, the comparisons with 1924 cannot be supported by statistical analysis, except for the density of Greenheart.

Because Greenheart is the main extracted species, analyses focussed on that species. We also tested whether other species had increased abundance against a zero hypothesis that new recruits were a random sample of the available species pool (i.e., no change in relative abundance).

'Plant Functional Types'
Pioneers are thought to take most advantage of newly created openings and have traditionally been subdivided into short-lived pioneers (SLP) , arriving early in the succession and long-lived pioneers (LLP), coming later and living for a prolonged period (see e.g. Finegan 1996). Classifications as these contain a certain amount of subjectivity. For this study we defined three groups of species based on life history characteristics that are thought to be important for the successional status of species (see Finegan 1996, Favrichon 1994, ter Steege & Hammond 1996, ter Steege & Hammond, 2001). Based on: 1) the fact that all pioneers cited in the above references had an air-dry wood density below 700 kg m^{-3} and 2) the fact that among the pioneers, the SLP tend to have the smallest seeds (Chapter 1), we classified species on the basis of their wood density and seed mass (logarithmic classes sensu Hammond & Brown 1995, data from ter Steege & Hammond 2001). The three 'plant functional types' thus derived can be summarised as:

1.   Small seeded softwoods (SSW)   : wood density < 0.7, seed mass < 0.1 g
2.   Large seeded soft woods (LSW)   : wood density < 0.7, seed mass = 0.1 g
3.   HWD (hardwoods)   : wood density = 0.7

Dispersal Types
To disperse their seeds plants have developed a variety of mechanisms such as, for example; berries dispersed by birds or primates, winged seeds dispersed by wind, or large undispersed seeds. It appears obvious that bird- or wind-dispersed seeds are better dispersed (Howe & Smalwood 1982, Howe *et al.* 1985, Nathan & Muller-Landau 2000) than undispersed seeds but supporting data are generally not available. Hammond *et al.* (1996) suggested that logging in the Guianas disproportionally selects for trees with a specific dispersal type (in Guyana for unassisted dispersal). To test if this had a long-term effect we also tested if trees with unassisted dispersal (the sum of all individuals of species with unassisted dispersal) had decreased in density, compared to other dispersal types. Dispersal type data was taken from Hammond & Brown (1995) and ter Steege & Hammond (2001).

Endemics
The Bartica Triangle is an area with high abundance (ter Steege 1998) and richness (ter Steege *et al.* 2000a) of endemic species, species that are adapted to the poor soils in the region. As endemic species have a high conservation value for Guyana, we also tested if the density of endemic species had decreased in 1964 and 1999, as compared to the baseline data of 1924. The list of potential endemics includes *Aldina* spp., *Chlorocardium rodiei*, *Dicymbe* spp., *Eschweilera potaroensis*, *Licania buxifolia* (Marishiballi), *Licania cuprea* (Konoko), *Maburea trinervis*, *Swartzia leiocalycina*, *Swartzia* spp. (Itikiboroballi) and *Vouacapoua macropetala* (see ter

143

Steege 1998 for more information). Identification of some of these endemic species, notably *Licania* spp. and *Swartzia* spp. was a problem in 1924.

Species composition and diversity
Comparison of species composition could only be done in a qualitative manner due to statistical limitations of comparing differently structured data sets. Because the species identification was much less complete in 1924 this inventory was not used in comparisons of species diversity between years.

The difference between species diversity in 1964 and 1999 was compared with Fisher's ? , a measure that is relatively insensitive to sample size (Fisher *et al*. 1943, Taylor *et al*. 1976, Leigh 1996, Rosenzweig 1995), and the Shannon-Weaver Index (Zar 1984).

Results

Due to the large area involved a 1% inventory still results in huge sample sizes. In 1924 c. 98,000 trees with DBH = 40 cm were enumerated. At that time, Greenheart was the most abundant species in the area and made up 20.5% of all trees recorded. In 1964 close to 55,000 trees with DBH = 30 cm were measured. At this time Greenheart ranked 3rd in abundance among trees = 40 cm DBH, behind *Eperua falcata* and *Eperua grandiflora*, with close to 7% of all individuals. In 1999 a total of 12,476 trees with DBH = 30 cm were enumerated. At this time Greenheart still ranked 3rd among trees = 40 cm DBH, behind *Eperua falcata* and *E. grandiflora*.

In 1964 a total of 2474 stumps were counted, 2004 (81%) of which were Greenheart stumps. Wallaba (*Eperua*) accounted for 14.5% of the stumps, and *Mora excelsa* for 1%. Thirty-three other species made up the remaining 3.5% of the stumps. Most, if not all, logging occurred in the mixed forest (Welch 1964) and, assuming that was indeed the case, stump density in mixed forest ranged from 0 to 18.6 stumps ha^{-1}, with an average of 7.9 stumps ha^{-1}.

Total tree density of stem = 40 cm in 1924 was 48.9 trees ha^{-1}. In 1964 total tree density was 36.7 stems ha^{-1}, compared to 47.1 stems ha^{-1} in 1999. These differences are not significant, however.

Greenheart volume and density
Based on the 106 sections in the Ikuribisi-Essequibo block of the 1924 inventory, where Greenheart volume was measured, the average volume of Greenheart (all forests types combined) in 1924 was 24.6 m^3 ha^{-1} with a 95% confidence interval of 21.9 - 27.2. The density of Greenheart trees of DBH = 40 cm in the total inventory area was 10.0 trees ha^{-1} (Table 8.1). This is consistent with the average volume estimate – viz. c. 2.5 m^3 per tree. Assuming that the sampling error of tree density was similar to volume (see methods), the 95% confidence interval for the density of Greenheart in the Essequibo block would be roughly 9 – 11 trees ha^{-1}. The standing volume of Greenheart in the Mazaruni-Ikuribisi-block was higher – 36 m^3 ha^{-1}

Table 8.1   Density per hectare of Greenheart (*Chlorocardium rodiei*) in all forests and in mixed forest separately in the Bartica Triangle in 1924, 1964 and 1999. The 95% confidence interval for 1924 is an estimate based on the volume of 106 inventory sections (see text).

	Trees ha-1 > 40 cm	95% CI[*]	Trees ha-1 > 30 cm	95% CI
All forests				
1924	10.01	9.0-11.00		
1964	4.54	2.59-6.50	6.31	4.00-8.61
1999	1.96	0.37-3.55	3.41	0.55-6.27
Mixed forests				
1964			8.99	6.58-11.39
1999			7.10	4.91-9.27

[*] The 95% confidence interval for 1924 is an estimate based on the volume of 106 inventory sections (see text)

(Wood 1926). In 1964, in all forest types combined, the average density of Greenheart trees with DBH = 30 cm was 6.31 (95% CI = 4.00 – 8.61) trees ha^{-1} (Table 8.1). Trees with DBH = 40 cm (for comparison with 1924) had a density of 4.54 (95% CI = 2.59 – 6.50). Because the confidence intervals of 1964 and 1999 are very far apart, we consider this a significant difference. The density of Greenheart in 1999, in all forest types combined, was lower than in 1964 (Table 8.1) but not significantly so (regression - homogeneity of slopes: $t_{(2),89} = 0.635$, P = 0.527). The same is true for mixed forests alone ($t_{(2),89} = 0.420$, P = 0.675).

Size class distribution of Greenheart

Most Greenheart trees felled were between 30 and 60 cm of DBH (Figure 8.4). In 1964 the DBH limit for the inventory was 30.5 cm, so we cannot assess the effect of the harvesting on the smaller size classes in that period. As 30.5 is the legal
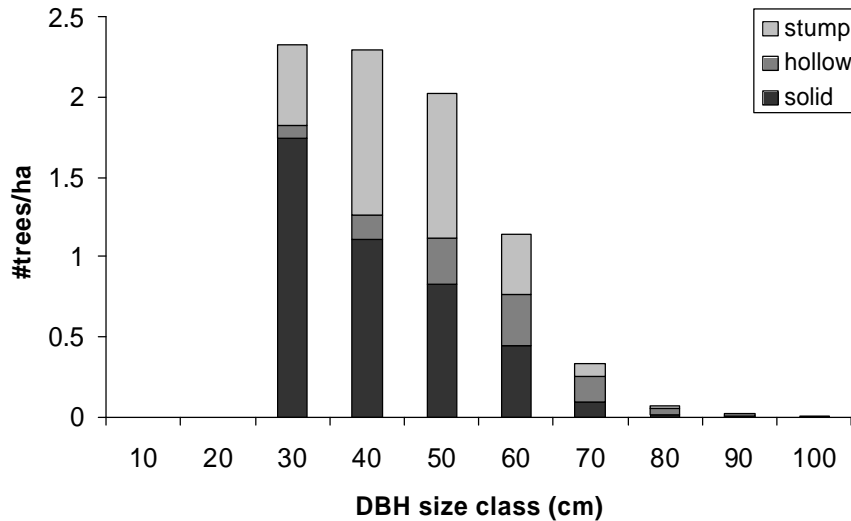

Figure 8.4   Size class diagram of Greenheart trees in the Bartica Triangle in 1964. Solid and hollow are actual trees inventoried. Stumps are also inventory based.

145

minimum diameter for logging in Guyana, most of the trees below this size should have remained except in the case of fatal damage. The number of Greenheart trees between 10-30 cm in 1999 were indeed lower than in a range of natural forests in Central Guyana (Figure 8.5). Greenheart trees over 30 cm DBH were less abundant in 1964 than in 1924 in each of the size classes. A further decline seems apparent from 1964 to 1999 (but see Table 8.1). It is also clear from Figure 8.5 that future recovery of the Greenheart population will take a very long time as the density of the smaller size classes are still below those of the larger size classes.

General composition and tree diversity of the forest
In 1924 the total number of species enumerated in this block was (only!) 85. The ten most abundant species were Greenheart (20.5 % of all trees), *Eperua* spp. (Wallaba, 21.0%), *Mora gonggrijpii* (Morabukea, 6.5%), *Mora excelsa* (Mora, 6.3%), *Eschweilera sagotiana/subglandulosa* (Black Kakaralli, 8.1%), *Catostemma* spp. (Baromalli, 3.9%), *Licania* spp. (Kautaballi, 3.9%), *Swartzia* spp. (Parakusan, 0.8%), *Swartzia* spp. (Wamara, 2. 3%) and *Aspidosperma excelsum* (Yaruru, 2.1%).

Many rare trees were apparently misclassified in 1924 into the more common congenerics or potentially unrelated species (most of the detailed names come from Fanshawe 1949b, see Mennega *et al*. 1988). As the most common commercial species (Greenheart, Wallaba, Morabukea, Mora, Wamara) are also the best known, they were undoubtedly well classified. The names Black Kakaralli, Kautaballi, Baromalli, and Parakusan are almost certainly composed of more than one species but also almost certainly of species within one genus.
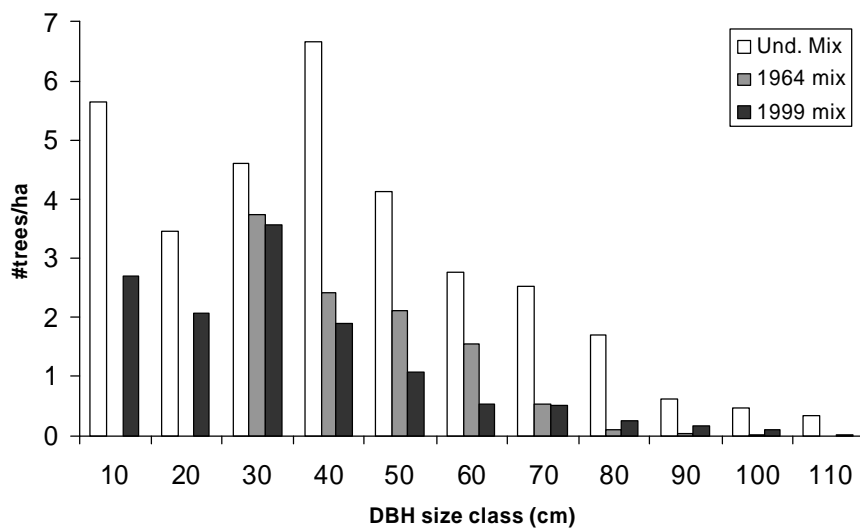

Figure 8.5   Size class distribution of Greenheart (*Chlorocardium rodiei*) in logged mixed forest in 1964 and 1999 compared to an average of comparable natural forests (Waraputa, ter Steege *et al*. 1993, Forest Reserve Mabura Hill, ter Steege *et al*. 2000b, 24 Mile Reserve, Guyana Forestry Commission, unpublished data).

Table 8.2   Density (Number of trees ? 40 cm /ha) of the 25 most abundant genera in the Bartica Triangle in 1924, 1964 and 1999. The most obvious change is the decrease in abundance of Greenheart (*Chlorocardium*) and increase in Wallaba (*Eperua*).

Genus	Local name	1924	1964	1999
Eperua	Wallaba	10.27	10.55	16.50
Chlorocardium	Greenheart	10.01	3.36	2.46
Mora	Mora/Morabukea	6.28	5.32	3.52
Eschweilera	Kakaralli	3.96	2.24	2.23
Licania	Kauta/Kautaballi	3.33	1.57	1.77
Catostemma	Baromalli	1.91	0.81	1.04
Swartzia	Wamara/Itikiboroballi	1.56	1.51	1.78
Pouteria	Asepoko/Asepokoballi	1.32	1.00	2.62
Aspidosperma	Yaruru	1.26	0.84	1.96
Talisia	Sand mora	0.82	0.66	0.01
Pentaclethra	Trysil	0.73	0.38	0.77
Ormosia	'Lucky seeds'	0.68	0.62	1.30
Ocotea	Silverballi's	0.58	0.43	0.54
Alexa	Haiariballi	0.48	0.47	0.65
Inga	'Whities'	0.34	0.41	0.70
Terminalia	Fukadi	0.30	0.36	0.73
Goupia	Kabukalli	0.27	0.22	0.17
Peltogyne	Purpleheart	0.23	0.14	0.19
Parinari	Burada	0.23	0.06	0.01
Pterocarpus	Corkwood	0.22	0.18	0.17
Moronobea	Manniballi	0.22	0.09	0.11
Chrysophyllum	Limonaballi	0.21	0.13	0.15
Lecythis	Kakaralli	0.20	0.42	0.46
Pithecellobium	Manariballi	0.20	0.21	0.33
Chaetocarpus	Ruri	0.20	0.09	0.15
Protium	Kurokai/Haiawa	0.19	0.18	0.31
Schefflera	Karohoro	0.19	0.11	0.20
Licaria	Brown silverballi	0.18	0.08	0.09
Pradosia	Kurokai	0.17	0.12	0.22
Diplotropis	Tatabu	0.17	0.03	0.07

The diversity of the forest in the Bartica triangle in 1924 cannot be estimated with the data at hand. We do have data for other areas in central Guyana, however, and the Forest Reserve Mabura Hill is probably well comparable with the un-logged situation in the Bartica Triangle in 1924 (ter Steege *et al.* 2000b). The diversity in 1964 and 1999 and undisturbed forest based on the number of individuals and species per strip line did not differ significantly (Fisher's? : 1964 = 23.65; 1999 = 22.21, FRMH = 25.17; $F_{[2.102]}$ = 0.97; P = 0.38). The same is true for the Shannon Weaver index ($F_{[2.102]}$ = 2.50; P = 0.08).

Table 8.3   Density of functional groups (DBH > 40 cm) in the Bartica Triangle in 1924, 1964 and 1999.

Year	SSW avg	95% CI	LSW avg	95% CI	HWD	95% CI
1924	0.68		5.43		42.78	
1964	0.77	0.32-1.23	5.25	3.58-6.92	36.79	26.48-47.12
1999	0.91	0.11-1.72	6.74	4.24-9.24	41.71	32.18-51.23

Plant Functional Types
Densities of SSW (Small seeded Soft Woods or pioneers), LSW (Large seeded Soft Woods or long lived pioneers) and HWD (HardWooDs or climax species) remained essentially the same from 1924 to 1964 and 1999 (Table 8.3), i.e. there were no significant changes in density between 1964 and 1999 when analysed with regression analysis (no further data shown). There were no differences in the size class distributions of SSW and LSW (data not shown), which might have been indicative for a wave of pioneers growing up.

There were small non-significant differences in the densities of the 'dispersal types'. Rodent dispersed individuals and individuals with unassisted dispersal were less abundant in 1964, when compared with 1924 (Table 8.4). This difference can almost fully be explained by the selective removal of Greenheart.

Endemic species
The total abundance of trees of endemic species in the area is high but this is mainly due to the occurrence of Greenheart. In 1924 24.5% of all individuals ? 40 cm DBH belonged to 3 at that time identifiable endemic taxa: *Chlorocardium rodiei*, (the most common endemic, in fact most common species), *Licania buxifolia* (Marishiballi), *Swartzia leiocalycina* (this name probably included the Itikiboroballi's (other *Swartzia* spp.) as well in 1924). *Aldina* spp., *Dicymbe* spp., *Eschweilera potaroensis* and *Vouacapoua macropetala* were not found in 1924 but these species are not very abundant. *Licania cuprea* (Konoko) was also not found, but this species is not rare, and was most likely misclassified as Kauta or Kautaballi. Another common endemic tree, *Maburea trinervis*, usually does not grow over 40 cm. The percentage endemics, excluding Greenheart, was 4.1%. In 1964 this was 4.3% (1.3 – 1.9 trees / ha) and in 1999 3.6% (0.95 – 1.5 trees / ha).

Table 8.4   Density of trees with different dispersal types (DBH > 40 cm) in the Bartica Triangle in 1924, 1964 and 1999.

Dispersal	1924	1964	1999
Rodent	32.5	22.1	28.3
Unassisted	28.8	21.0	25.8
Primate	17.9	13.0	16.8
Bat	5.4	3.5	4.0
Water	5.2	4.6	5.4
Bird	4.0	3.9	5.3
Wind	2.3	2.2	3.6

Discussion

Comparison with internationally accepted standards, such as FSC or Smartwood, suggests that the long-term sustainability of Greenheart harvesting in the Bartica triangle is low, while other criteria of sustainability appear to be met. Greenheart itself does not appear to be threatened with extinction yet.

More specifically, there are a number of important conclusions that can be drawn from the results:

1.   The extraction of Greenheart (*Chlorocardium rodiei*) in Central Guyana mainly has led to a population decline of the target species itself,
2.   Even after a decline of 63% Greenheart still ranks third in abundance,
3.   Species composition has essentially remained the same,
4.   There has been no change in relative contribution of dispersal types in the tree community,
5.   Endemics (except Greenheart) have not changed in abundance,
6.   There are no detectable changes in quantitative measures of species diversity.

These points need further discussion.

1.   The extraction of Greenheart (*Chlorocardium rodiei*) in Central Guyana mainly led to a population decline of the target species itself.

This was not unexpected as most of the trees felled (81%) were in fact Greenheart trees, and the species is known to regenerate slowly. Greenheart has been the mainstay of the Guyanese timber industry and we hypothesise that in other areas where the species has been harvested for a prolonged period a similar decline is to be expected. What is more surprising is that:

2.   Even after a decline of 63% Greenheart still ranks third in abundance.

Greenheart was in fact so common in the Bartica Triangle that one out of every five trees ? 40 cm DBH enumerated was a Greenheart individual. Although the decline has been serious, sufficient Greenheart individuals remain to suggest that the species is not threatened with local extinction. Obviously, the best stands (reefs) have been fully depleted of large healthy trees. Whether the heavy selection will lead to a genetic erosion of the species can only be guessed. The recovery, both commercial and biological of the species is also a point of concern and will be discussed below.

3.   Species composition has essentially remained the same.

This result was unexpected as the decennia-long logging altered the conditions for establishment and growth of small trees. Infrequent, continuous disturbance creating small natural gaps was replaced by pulse-wise disturbance, creating large logging gaps. We had expected that species that are capable of benefiting of the occurrence

of large frequent gaps and that have high maximum growth rates would have increased in abundance at the cost of slow-growing species that do not perform well in gaps (for Guyana, see Rose 2000). This would have shown in a relative increase in the numbers of SSW and LSW compared with HWD. We suggest that the extremely low natural density of pioneer like species (see also ter Steege & Hammond 2001), SSW and LSW, in Central Guyana, which is related to a low natural frequency of large gaps, prevent them from effectively colonising logging gaps. For some species (*Cecropia* spp., *Goupia glabra*) this could be related by a failure to maintain large enough seed banks, for these and other species by dispersal limitation (Hubbell *et al*. 1999) - viz. failure to colonise gaps as a result of long dispersal distances. It is to be expected though that with increased and continued harvesting such species will finally predominate. Another reason for a low pioneer occurrence in the logging areas is the fact that until the late sixties trees were felled by axe and extracted with oxen, tractor and other relatively small equipment. Hence the disturbance was relatively low, compared with present day skidding damage. Pioneers mainly thrive when bare soil is exposed and this occurred mainly along the roads and main haulage tracks, where indeed pioneers were observed (Welch 1964).

4.   There has been no change in relative contribution of dispersal types in the tree community.

With faster growing and pioneer species we would have expected an increase in wind, bird and bat dispersed species. The low increase in pioneer genera (see point 3) only resulted in a minor change.

5.   Endemics (except Greenheart) have not changed in abundance.

We had expected that individuals of endemic species would have declined in their proportion of the total forest community. Two reasons may have contributed to the lack of this effect. Firstly many of the endemics occur in the white sand patches (ter Steege *et al*. 2000a) that are not affected by the logging. Secondly, the changes in the hardwoods (HWD), to which most of the endemics belong, were too small to allow significant changes to be detected (Table 8.3) in the group as a whole. As the endemic species, with the exclusion of Greenheart, are only a small part of the HWD group, it is unlikely that a change in their densities would be significant. Finally, the endemic species were not all classified well in 1924, which makes a comparison difficult.

6.   There are no detectable changes in quantitative measures of species diversity.

Surprisingly, removal by harvesting of the dominant species did not result in a change in diversity. In an ecological sense, the intermediate disturbance hypothesis predicts that this should in time lead to an increase in diversity (see Huston 1994 for a review). Mathematically, the removal of the dominant species also leads to an increase in diversity, when expressed as an evenness measure (Magurran 1988). More on this below.

Is recovery of Greenheart to be expected?
The data showed that Greenheart has experienced a dramatic decline in its population size in the last 75 years. Can recovery be expected after such a decline and at what rate? Because Greenheart has shown to be capable of attaining a very dominant position in the forest community in Central Guyana and because it is still the third species in abundance, it would appear reasonable to assume that its position can be maintained and even expanded compared to its current levels but only if pressure on its population decreases significantly or ceases. The reason for this is the way Greenheart is thought to have attained its dominance.

This mechanism is most likely a combination of shade tolerance of young individuals in the understory and a high longevity (Zagt 1997). This strategy is likely to be only successful in areas with low disturbance (ter Steege & Hammond 2001). In the present situation Greenheart would need to benefit disproportionately from the openings in the canopy in order to regain its former abundance. Indeed, Greenheart is capable of enhanced growth in logged forest, both as a tree (Prince 1971, 1973) and as a sapling (Rose 2000), but there is no evidence that suggests that this growth increase is higher than that of other species (Zagt 1997, Rose 2000). Given the near random replacement of Greenheart by other long-lived species fast recovery is unlikely under the present circumstances.

Due to the large reduction of adult trees in the population, seed production will also be strongly reduced in the Bartica forest. Hence, survival of the existing seedlings and saplings in the forest understory becomes even more critical. In any logging system the care of seedlings and saplings is thus of paramount importance and the need for reduced impact logging is evident (van der Hout 1999), as most seedlings are found clumped around the parent.

The suitability of inventories and biodiversity indices as tools to measure trends in tree species diversity
This study suggests that biodiversity indices commonly used are not sensitive in detecting changes in an area with so many individuals and species. An example will illustrate this. In 1924 the total number of individuals enumerated in the Ikuribisi-Essequibo watershed was 20,226 in 85 species, resulting in a Fisher's ? of 11.35, and a Shannon-Weaver of 2.93. Removing 65% of all Greenheart individuals will increase Fisher's ? to 11.61 and the Shannon-Weaver index to 3.08, due to greater evenness in the sample. After a number of years the total stem numbers will have approached the 20,226 again and if Greenheart has not increased and the regional species pool has not increased (see below), Fisher's ? will be again 11.35. If the increase in species is more or less divided equally among all the other species then Shannon-Weaver will be 3.09. This change is far too small to be detected given the errors with which the latter index can be measured at this scale.

The regional species pool
As predicted by the intermediate disturbance hypothesis, a decline of a dominant species or, at smaller scales, forest dynamics, will result in an increase in diversity. However, as most of the species likely to profit most from the increased disturbance

are already present in the area (in small numbers) it is unlikely that the total number of species found in the area will increase. Hence the regional species pool or – richness, one of the components of biological diversity, will not increase. The increase in diversity is one of shifts in evenness, the second component of biological diversity (Magurran 1988). At smaller scales such an increase is likely, however (see Ek 1997).

The use of large-scale forest inventories
Another question that needs to be addressed is whether large-scale, low intensity forest inventories are the most appropriate tool for studying changes in species composition and diversity. For Central Guyana the answer is a yes and a no. The Bartica Triangle consists for one half of mixed forest and for the other half of swamp-, riverine- and wallaba forest. The inventory in 1924 did not report separately on densities of species for these forest types. While logging is only carried out in the mixed forest, it was not possible to focus on this forest type when comparing 1924 with 1964 and 1999. In addition to that most commercial species, including Greenheart, show a very clumped occurrence. Thus logging tends to concentrate in areas with high abundance of Greenheart, locally called 'reefs', where the destruction can be substantial (ter Steege *et al.* 1995, 1996, Zagt 1997, van der Hout 1999). In such areas pioneer abundance can be very high (pers. obs.). In a matrix of non-logged forest these changes in these relatively small patches are masked. Permanent sample plots (or at least marked populations) are needed for monitoring change more directly where it occurs. In addition to that, it is possible that local species names change and unlikely that tree spotter-skills remain the same or comparable over the long periods examined. The later was definitely a problem in comparing 1924 data with 1964 and 1999 data. PSP's with marked trees would also solve this problem (e.g. Silva *et al.* 1995, de Graaf *et al.* 1999). For the analyses with functional groups, commercial species and dispersal types, however, this will have had very little impact.

Conservation of Central Guianan forests
The Bartica triangle presents an interesting case for conservation in tropical rain forests. One of the values of the Central Guyanan forests is in the occurrence of dominance communities (Davis & Richards 1933, 1934, ter Steege 1998, ter Steege *et al.* 1993, 2000b) and the high prevalence of endemic habitat specialists (ter Steege *et al.* 2000a) which are often characterised by high wood density and large, poorly dispersed seeds (ter Steege & Hammond 2001). It is not a traditional "mega diversity" forest in terms of tree diversity (Conservation International 1990, ter Steege *et al.* 2000b, c) nor animal diversity (Voss and Emmons 1996, Kay *et al.* 1997), that ranks high on lists of conservation priorities. Indeed, the Guianan Forest is absent from WWF's and CI's hot spots of biodiversity (Davis *et al.* 1997, Myers *et al.* 2000). Further, while the main commercial species is significantly depleted the forest's biodiversity shows remarkable resilience to the impacts of prolonged selective logging. This raises questions about criteria for selecting conservation priorities. Is high diversity the main goal of conservation in central Guyana, or preservation of unique (in Neotropical sense), albeit low diversity, forests (ter Steege

et al. 2000c, ter Steege & Hammond 2001). Maybe more importantly can conservation and utilisation be combined?

Implications for forest utilisation

Seventy-five years of harvesting have lead to a significant decline of Greenheart and no significant recovery in stem numbers of Greenheart or in the appearance of a wave of juvenile trees (Figure 8.5). By conventional definitions of sustainability this suggests that commercial selective Greenheart logging is not sustainable at the time scale considered. This conclusion confirms the emerging consensus in Guyana that Greenheart, if managed sustainably, requires very long harvesting cycles (Zagt 1997, van der Hout 1999, J. Willems, pers. comm.). As a result of this the Guyana Forestry Commission-Management Plan guidelines have recently changed from a 20 yr rotation cycle to a recommended 60 yr cycle. In the light of the above analysis this may still be too short given the logging intensity employed. However, the species remains common (3rd in abundance) and today logging continues even in areas that had been harvested before.

When a broader concept of sustainability is applied as used by international criteria and indicators of sustainable forest management, a much more complex picture emerges. While in some areas commercial Greenheart stocks appear to have been depleted, logging continues in other areas. Harvested forest remains a source of Greenheart for local markets and subsistence use and Greenheart continues to be a dominant element in the area's forest. Structurally, the forest appears to return to a more or less intact state (pers. obs.). In old logging areas (e.g. around the stumps and transhipment points) the vegetation has regenerated into high forest, even though the species composition may have changed at small spatial scales and now includes tall canopy individuals of fast growing species such as *Goupia glabra, Inga alba, Laetia procera, Schefflera* spp., *Jacaranda copaia*, and *Pentaclethra macroloba*. Large patches of intact forest remain throughout the area and remain a potential resource for other currently not marketable timbers. Forest degradation appears localised to small areas around settlements and gold mines.

We showed that tree biodiversity has essentially remained the same and the structural intactness of much of the forest suggests that changes in diversity of other plant and animal species groups may be limited. Intrusion by miners, agriculturalists and miners in areas opened by forestry is local, while agricultural conversion mainly takes place in the area close to Bartica.

As the soils in the area are predominantly sandy, evidence from comparable areas (Jetten 1994, Brouwer 1996, ter Steege *et al.* 1996) suggests that logging impacts on hydrology and nutrient dynamics are generally limited. This is strengthened by absence of visible signs of large scale soil degradation (pers. obs.)

Few active measures to protect sensitive areas and/or biodiversity have traditionally been applied in logging the area. In addition to that, only one reserve (24 mile reserve of 1 square mile) exists in the area. Establishment of more of such reserves may prevent the eventual loss of larger scale pristine examples of primary forest

where Greenheart and other endemics continue to be present in high abundance. Such reserves, provided they are large enough, could also satisfy the need to protect examples of the typical low dynamical, low diverse central Guyanan forest. Similarly, harvesting methods employed are not designed to minimise impacts on the soil or remaining stand, even though the low logging intensity prevents the occurrence of large scale damage in most places.

Hence, an analysis of medium-term sustainability of forest management using (environmental) criteria commonly applied for timber certification in the Bartica Triangle would reveal a mixture of negative impacts on the commercial sustainability of Greenheart harvesting and an approximately neutral impact on other forest functions such as local timber resources, hydrological function and biodiversity function.

Would this trend hold over a longer term? The trend of unchanging low Greenheart availability in previously logged areas is cause for concern in the face of the dependence of Guyana's timber industry on this species. Several studies have shown that timber harvesting in Guyana can only be profitable if a major percentage of the harvested volume is Greenheart (Landell-Mills 1997, de Souza 1999). Another cause for concern is the essential incompatibility between this forests' origin in low dynamic conditions and the higher dynamism introduced in the forest by human activity (Steege & Hammond 2001), principally logging. Even though changes in species composition could not be demonstrated at the large scale over the time frame examined, local changes have taken place and are expected to spread over other areas in the forest once logging continues.

We are thus faced with a major question: what to do with the remaining Greenheart stands? There may be three options:

1. Liquidate the resource to support national development. This is the current pattern, although government revenues from logging have been very low (GFC, pers. comm., Sizer 1996),
2. Liquidate the resource as above but create representative Forests Reserves,
3. Implement forestry that does not deplete the species at this rate.

Option 1 implies that the logging industry will have to shift away from Greenheart once it will no be longer profitable to harvest it or will have to concentrate on local markets. International market trends, certification or even bans (e.g. a New York ban of Greenheart timber in 1998) and conservationist action (WCMC 1998) may prevent this choice altogether. Current national policy embraces principles of sustainable management with a view of continued availability of Greenheart, implying a choice for other options than this one. The current practice probably still reflects this option.

Option 2 is also not a sustainable option from the viewpoint of commercial Greenheart logging, but would preserve undisturbed examples of the Greenheart forest. If well-planned and well-marketed, this approach may assist in achieving timber certification (and therefore access to privileged markets) for the remaining Greenheart stands. Still, it is not expected that Greenheart forests will sustain more than a single logging cycle at short term. Alternatives for Greenheart logging will have to be developed. But as shown, if mainly Greenheart is harvested, the forest still retains much of its conservation values. A carefully constructed agenda to achieve this objective: including certification, and biodiversity reserves needs to be developed.

Option 3 is best in agreement with the principles of sustainable forest management but the route is fraught with difficulties. Ecological evidence (Zagt 1997) makes it hard to imagine a sustainable management system based on Greenheart that has a short enough rotation to be commercially attractive. A main problem here is the small size of the local industry trying to market many rare and technically different timbers on an international market.

All three options suggest that strategic choices must be made about the future of Greenheart logging in Guyana. A credible conservation strategy will assist attempts towards certification. The timber industry must examine ways to continue to operate in these forests by widening the choice of species and shifting away from the typical high volume-low value operation towards maximisation of value per unit volume.

9 A MATHEMATICAL FRAMEWORK FOR THE INTERMEDIATE DISTURBANCE– AND DYNAMIC EQUILIBRIUM HYPOTHESES

René Verburg, Feike Schieving

Abstract

In this paper we examine the mathematical background of the intermediate disturbance- and dynamic equilibrium hypotheses (IDH and DEH), and we used a minimum amount of assumptions at which the hypotheses could function for a non-spatial case. We found that a simple hierarchy of species-specific intrinsic population growth rates suffices for the IDH to operate with in addition a simple additive series of competitive interactions. We showed that disturbance intensity and frequency, which affect species diversity, interact in a non-linear way. Due to the non-linear dynamics of the differential equations we used in this study, the amount of species that can coexist after disturbance cannot be solved analytically. For this we used a simulation model of 50 species. We found that at any time step not all (potential) species can coexist at any disturbance regime. In addition to the observed hump-shaped number of species that can coexist with disturbance type described by the IDH, we found that the maximum amount of species that can (potentially) coexist with varying disturbance intensities or frequencies can also be described with a hump-shaped curve. Moreover, also the absolute values of the population growth rates of species, the relative differences between the species-specific growth rates, and the value of the competitive coefficient affect both the species diversity curve and the maximum amount of species after disturbance. The effects of these population parameters on species diversity and maximum number of species also follow a hump-shaped pattern.

Introduction

In the previous chapters the Intermediate Disturbance Hypothesis (IDH) is embraced as a conceptual model to explain an expected increase in species diversity and concomitant increase in the density of fast growing softwoods (i.e., pioneer species) after disturbance. The IDH proposed by Connell (1978) and further developed by Huston (1979, 1994) as the Dynamic Equilibrium Hypothesis (DEH) is in the past often applied with success to different ecosystems (e.g., During & Willems 1984, Dial & Roughgarden 1999, Chesson 2000, and see Sheil & Burslem 2003 for an up-to-date review). These two disturbance models appear to be a valid explanation for high species diversity at intermediate levels of disturbance. Although the IDH concept has appealing ecological mechanisms, and axioms have been postulated under which conditions the IDH must hold (e.g. Sheil & Burslem 2003) an underlying model is not well defined.

In this chapter we explore some of the mathematical backgrounds on which the IDH and the DEH are based, and in detail the effects of competitive exclusion and disturbance on species coexistence in a non-spatial environment. The IDH and DEH predict a replacement pattern of species if disturbances do not occur (Figure 9.1). Such a replacement series is explained by ecologists as caused by competitive exclusion of species. In other words, among all species a competitive hierarchy should exist that results in exclusion of the weaker species. However, the precise conditions for such a competitive hierarchy are usually not well defined. To obtain a better idea what the precise conditions are which lead to the patterns as found in the
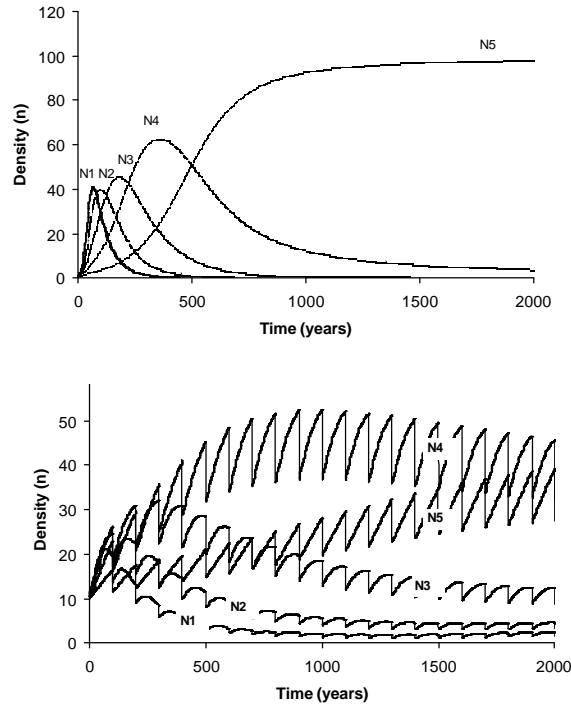
Figure 9.1   A species replacement series (upper graph), and a pattern of species coexistence after repeated disturbance (bottom graph) as predicted by the IDH and calculated with eq. 3 for a 5-species system. In both cases $N_1-N_5=1$, $K=100$, $?=1/(K*4)$, and in the bottom graph: $?=0.7$, and $?_T=100$ years. For explanation of the parameters, see text.

IDH, we take a closer look at a two and three species system. Therefore, we will study two simple cases, i.e., a two- and three-species system, in which the order and magnitude in the competition hierarchy will be derived analytically.

In the conceptual IDH model disturbance type is used in a rather loose way. The different types of disturbance (i.e., intensity, frequency, and size) are put on the same axis (see Figure 1.2, Chapter 1) suggesting these types operate in an orthogonal manner. If the IDH is to be used as an explanatory theory, an understanding how these disturbance types affect one another seems necessary. Therefore, we also explore the effects of disturbance intensity and frequency and their relation. In its original form the DEH predicts a shifting maximum species diversity with increasing disturbance type and population growth rate (Huston 1994, Figure 1.3, Chapter 1). Since species in various rain forest types may differ in growth rates we look more closely to what extent the relationship between population growth rates and disturbance type has on the maximum number of species that can coexist. By using numerical simulations in a multi-species system

158

(i.e., a 50 species system) the relation between disturbance type and number of species that can coexist are further explored (see also Chapter 10).

Competitive exclusion in a 2-species system

In a classical Lotka-Volterra system only 2 species can stably coexist on a single resource (see Chesson 2000, for an extensive review). Recently, Huisman & Weissing (1999) showed that fluctuations in the density of a single resource that is consumed by species could maintain coexistence in a multi-species system by means of oscillations and chaotic dynamics. In the IDH model competition for resources is not explicitly defined, although competition for light may cause the succession or replacement pattern of species in tropical rain forest after disturbance. Huston (1979) used a Lotka-Volterra equation to describe maintenance of species diversity in an ecosystem that contained 6 species. However, Huston (1979) and Huston and Smith (1987) did not show the differential equations and the way disturbance was introduced. Here we introduce the simplest case of a two-species system. We can denote a two-species system using the following differential equations:

$$dN_1/dt = r_1 N_1 (1 - N_1/K_1 - \alpha_{12} N_2) \qquad (1a)$$
$$dN_2/dt = r_2 N_2 (1 - N_2/K_2 - \alpha_{21} N_1) \qquad (1b)$$

In which: N_1, N_2 = the density of the 1st and 2nd species; r_1, r_2 = intrinsic (population) growth rates of the two species; α_{12}, α_{21} = the negative effect of species 2 on the growth rate of species 1 and the negative effect of species 1 on the growth rate of species 2 respectively (the competition coefficients); K_1, K_2 = the carrying capacities of the 1st and 2nd species.

In eq. 1 we assume that the carrying capacities of both species are equal, since there is no *a priori* reason why competitive superior or inferior species should have a larger carrying capacity. Therefore, we take $K_1 = K_2 = K$. Moreover, we state that competition between both species has negative effects on the realised growth rates, but we do not define explicitly on what resource species are competing for. Since we state that the competitive inferior species must be replaced by the competitive superior species, we take the value of the competitive interaction $1/\alpha_{12} = K$, while for the coefficient α_{21} we assume $1/\alpha_{21} > K$ (as is visualised in Figure 9.2).

In figure 9.2 the directions of the growth vector field are visualised together with the zero-growth isoclines for the two species. Furthermore, the solution curve starting with the initial values (at t_0) of N_1 and $N_2 = 1$ is shown. As visualised in this figure, the point ($N_1=0$, $N_2=K$) is a stable equilibrium point (which can be verified by evaluating the Jacobian matrix for this point). Also for the point $N_1=K$, $N_2=0$ one can show in the same way this is an instable equilibrium point. In a way figure 9.2 shows the minimal conditions to make species 2 the superior competitor of the pair. I.e., in a system with $K_1=K_2=1/\alpha_{12}=K$, species 2 will outcompete species 1 if $1/\alpha_{12}=1/\alpha > K$.
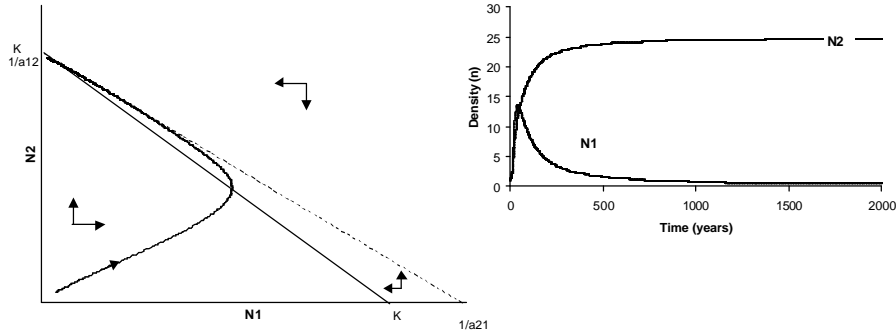
Figure 9.2   The phase-plane and trajectory of species N_1 and N_2 with zero-isoclines. Solid line $d_tN_1=0$, dashed line $d_tN_2=0$ (large graph), and the density of species N_1 and N_2 over time (inset right graph).

Now as is visualised in figure 9.3a, we can come to an even simpler system of differential equations if we set $?_{21}$ to zero. That is, we assume that species 2 only experiences intra-specific competition effects, while for species 1 we assume that the experienced intra- and inter-specific competition effects are the same (i.e., $K=1/?$). Figure 9.3b visualises for such a situation the solution curve starting in the same initial point as in Figure 9.2.

Implementation of the competition hierarchy in a 3-species system

Once we understand the patterns as found for a two-species system, the results can easily be extended to say a 3-species, 5-species, or say a 50-species system. We have stated previously in the two-species system that species 1 experiences competition from itself and from species 2, while species 2 only experiences competition from
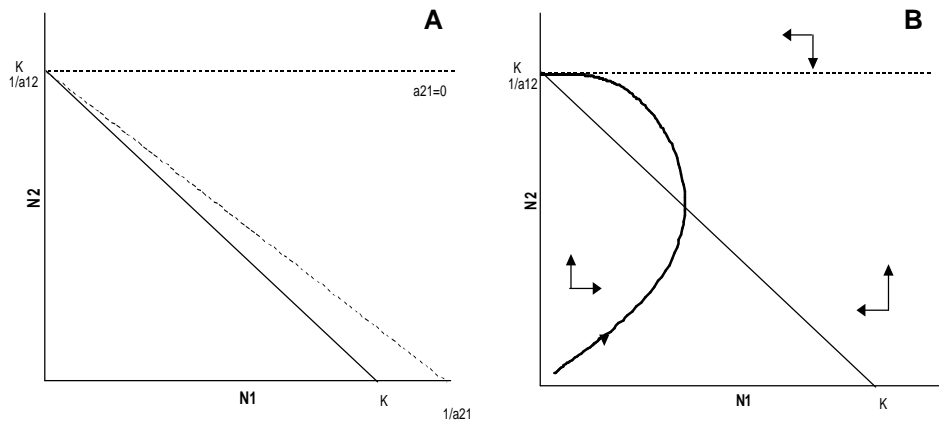

Figure 9.3   The phase-plane of species N_1 and N_2, where $?_{21}$ is set to zero (A), and the corresponding solution curve (B). Solid line $d_tN_1=0$, dashed line $d_tN_2=0$
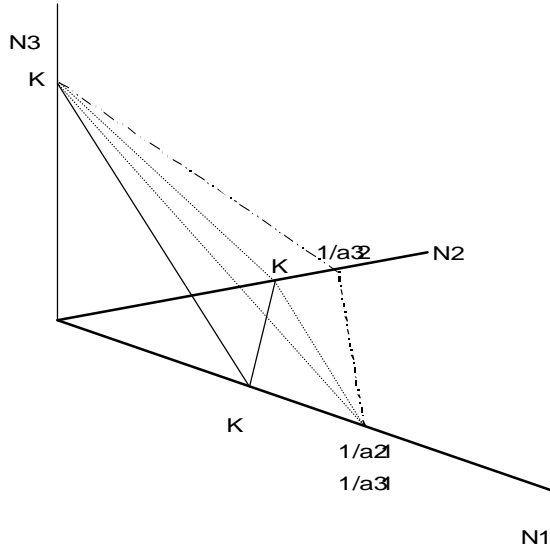
160

Figure 9.4: The phase-plane of a 3-species system, with the zero-growth isoclines $dN_1=0$ (plane with solid lines), $dN_2=0$, (plane with dashed lines), and $dN_3=0$ (plane with point-dashed lines). The imposed hierarchy among species 1-3 is $s_3>s_2>s_1$ and the competition coefficients $1/?_{21}=1/?_{31}=1/?_{32}>K$.

itself and that the (negative growth) effect of intra-specific competition is equal to inter-specific competition ($?_{12}=1/K$). In a 3-species system we can state a similar condition: species 1 experiences competition from species 2 and 3, species 2 only from species 3, all species experience intra-specific competition and the effect of intra-specific competition is equal to inter-specific competition. Hence $?_{21}=?_{31}=?_{32}=?$. As visualised in figure 9.4, for a 3-species system, we can obtain a competition hierarchy $s_3>s_2>s_1$ if we take the system of differential equations:

$$dN_1/dt= r_1N_1(1 - N_1/K - N_2/K - N_3/K) \qquad (2a)$$
$$dN_2/dt= r_2N_2(1 - ? N_1 - N_2/K - N_3/K) \qquad (2b)$$
$$dN_3/dt= r_3N_3(1 - ? N_1 - ? N_2 - N_3/K) \qquad (2c)$$

with $? < 1/K$. Thus the competition interaction matrix of the system can be written as:

	N_1	N_2	N_3
N_1:	? 1/K	1/K	1/K ?
N_2:	?	1/K	1/K
N_3:	? ?	?	1/K ?

with $? < 1/K$

161

For a n-species system we can just write:

	N_1	N_2	N_3	…	N_n
N_1:	? 1/K	1/K	1/K	…	1/K ?
N_2:	?	1/K	1/K	…	1/K
N_3:	?	?	1/K	…	1/K
.					
.					
N_n:	? ?	?	?	…	1/K ?

(with ? < 1/K).

Definition of disturbance in terms of disturbance interval and intensity and the effects on species coexistence

The graphical representation of the IDH (Figure 1.2, Chapter 1) places disturbance intensity, frequency (interval) and size (but the latter type will be ignored in this chapter) on the same horizontal axis. It is not difficult to imagine that disturbance intensity and frequency may share the same side of a coin. However, a possible interaction between these types of disturbance cannot be deduced from the conceptual representation of the IDH. For example does this interaction has an additive effect or should the effects be multiplied, and can the interaction be described in a linear or in a non-linear way? In this section we analyse disturbance intensity and frequency in more detail.

To formalise disturbance we use again the 2-species system. We adapt eq. 1 to write disturbance as follows:

$dN_1/dt = r_1N_1(1-N_1/K-N_2/K) + ?(t-I?_T) . (? -1) . N_1$ (3a)
$dN_2/dt = r_2N_2(1-N_2/K_2-? N_1) + ?(t-I?_T) . (? -1) . N_2$ (3b)

Here I=0,1,2,…, $?_T$ is the time interval between two disturbances, while ? is the fraction of the individuals remaining after the disturbance. Also $?(t-I?_T)$ is the Dirac-delta function, i.e., the function t ? $?(t-I?_T)$ pulses with infinite high intensity at t=0, $?_T$, 2.$?_T$, … .

Figure 9.5 visualises the (N_1, N_2) trajectory under a disturbance interval $?_T$= 30 (years) and for a removal fraction of (? -1)= 0.45 (45%). As we can see from figures 9.5 and 9.6, the qualitative pattern is in essence the same for 1/? set slightly larger than K, and for 1/? set to an infinity high value.

Simulations of the 2-species model show that coexistence between species 1 and 2 will only occur if the intrinsic population growth rate of species 1 (the inferior species) is larger than the intrinsic growth rate of species 2. Thus setting the growth rates equal, or making r_1 smaller than r_2, will lead to exclusion of species 1 after disturbance. To see why we can obtain coexistence between species 1 and 2, we
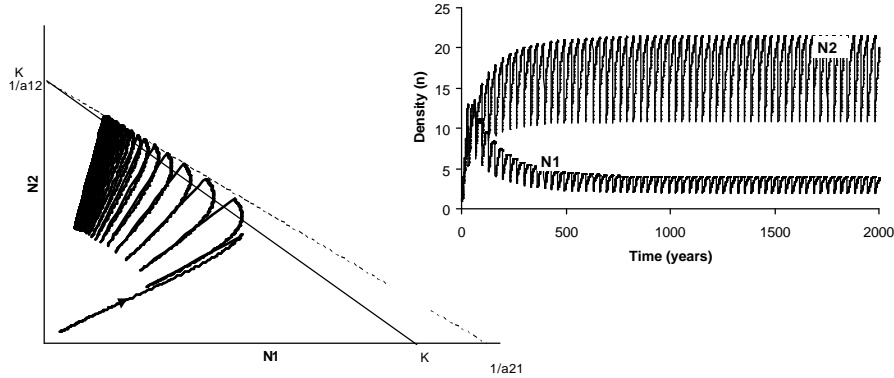
Figure 9.5: The phase-plane and trajectory of species N_1 and N_2 with zero-growth isoclines; solid line $d_tN_1=0$, dashed line $d_tN_2=0$ (large graph), and the density of species N_1 and N_2 over time (inset right graph) when disturbance is added. The competition coefficient $?_{21} > 1/K$

must take a closer look at the growth vector field for sufficiently small values of N_1 and N_2. In that case the ratio between the population growth rates d_tN_1 and d_tN_2 can be written as:

$$\frac{d_tN_1}{d_tN_2} ? \frac{r_1N_1}{r_2N_2}$$

If we plot the solution curve of N_1, N_2, and assuming that $r_1>r_2$, we obtain figure 9.7a. For $r_1>r_2$ the solution curve is concave upwards with respect to the N_2-axis for N_1 and N_2 sufficiently small (box 1 in Figure 9.7a). However, the solution curve is concave downward with respect to the N_2-axis for sufficiently large values of N_1 and N_2 (box 2 in Figure 9.7a). Thus for $r_1>r_2$ the solution curve is in essence shaped in the form of a S-curve, and it is this form which explains the phenomenon of coexistence under disturbance.
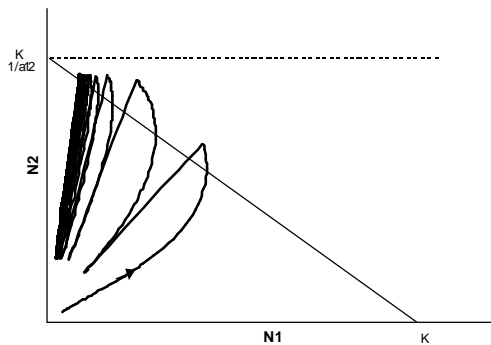

Figure 9.6   The phase-plane and trajectory of species N_1 and N_2 zero-growth isoclines; solid line $d_tN_1=0$, dashed line $d_tN_2=0$, when the competition coefficient $?_{21} = 0$.
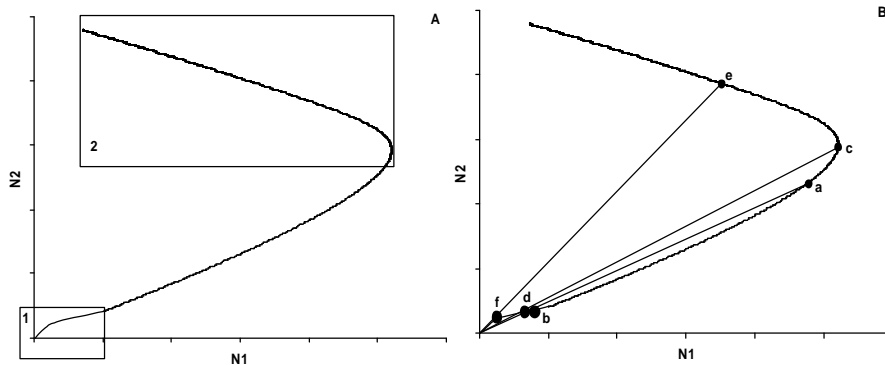
163

Figure 9.7   The solution curve in the N_1-N2 phase-plane. **A**: The visualisation of the S-shaped form of the curve, in box 1 at small values of N_1 and N_2, and box 2 at large values of N_1 and N_2. **B**: The effect of disturbance interval length on the position of the 2-species system on the solution curve. Points a, c, e represents disturbance events with an increasing order of magnitude of disturbance interval lengths, while points b, d, f represents the resulting points on which the system is reset due to the disturbance.

If a certain disturbance interval $?_T$, together with a certain disturbance intensity (1-?) leads to coexistence between the two species, this can only be the case if immediately after the disturbance the system is reset on the same solution curve. This can only be the case if the solution curve is S-shaped. In figure 9.7b the effect of disturbance interval $?_T$ is visualised. At a short interval length the solution curve reaches point a, with a certain density of species 1 and 2. The system is reset by the disturbance to point b and will grow again to point a until the next disturbance event takes place. Thus the variation in interval length $?_T$ can be visualised by points a, c, and e with an increasing order of interval lengths, while the points b, d, and f visualise the resulting densities of species 1 and 2 on the solution curve after the disturbance. Thus at increasing interval lengths the system has more time to grow along the solution curve and hence the system will grow towards high densities of species 2 and low densities of species 1. The variation in the magnitude of the disturbance intensity (1-?) works out in a different way. When at a certain point on the solution curve (point a in Figure 9.8) a disturbance occurs with a small intensity, the system is reset to point b (Figure 9.8). At larger intensities the system is reset on respectively points c and d with increasing order of intensities. From figure 9.8 we can see that at small disturbance intensities the system is reset on a new solution curve that is placed on the left of the original curve (point b). At large intensities the system is reset on a new solution curve placed on the right of the original curve (point d)

The interaction between disturbance interval and intensity on species coexistence

To get a better understanding of the interaction between disturbance interval $?_T$ and intensity (1-?) we take a closer look at figure 9.7b.We have already seen that an
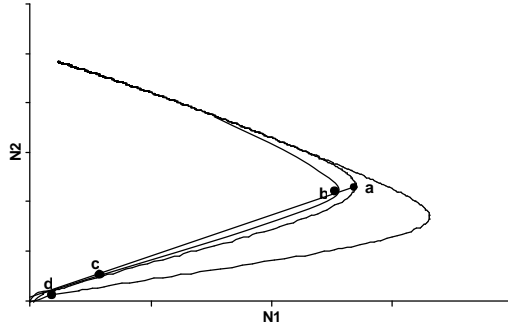
Figure 9.8: The effect of disturbance intensity on the position of the 2-species system on the solution curves. At point a the system is reset to points b, c, or d depending on the level of intensity. At low disturbance intensity the system is set on point b on a new solution curve left to the original curve, at an increasing intensity to point c at the same solution curve and to point d at high intensity on a new solution curve right of the original curve.

increase in disturbance interval length $?_T$ leads to more time the system can grow along the solution curve. And hence the system grows towards large densities of species 2 and low densities of species 1. Now, if we remove for large time intervals $?_T$ a small number of individuals, i.e., the remaining fraction $?$ is large, this will mean that the system will be reset on the same solution curve (point b in Figure 9.9), and hence we will observe a shift towards a larger dominance of species 2 relative to species 1. To obtain a situation of coexistence, the remaining fraction $?$ must be decreased (thus the disturbance intensity must increase). An increased removal would mean that the system will be reset on a solution curve lying to the right of the one we started with (point c in Figure 9.9) and we will observe a shift towards a larger dominance of species 1 relative to species 2. If the time interval $?_T$ is small we see the opposite pattern: for small values of $?$, a relative increase in the dominance of the fast growing species 1 can be found. Thus to get for short time intervals $?_T$ a situation of coexistence, the disturbance intensity should be relatively small. This is what we also intuitively expect.
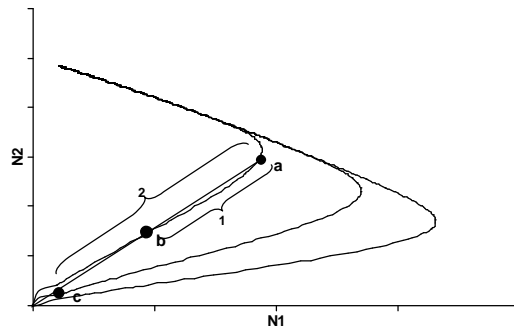

Figure 9.9. The solution curves in the N_1-$N2$ phase-plane. Disturbance at point a on the solution curve reset the system to point b on the same solution curve at a small disturbance intensity (1), or to point c on a new solution curve at the right of the original curve at a larger disturbance intensity (2).

165

So to generalise, to obtain a situation of coexistence, at an increase in disturbance time interval $?_T$ a concomitant increase in the disturbance intensity (1-?) should occur, and in the same way: a decrease in interval length should concur with a decrease in the disturbance intensity to get coexistence. An important element of this analysis is that we cannot analytically solve the densities of species 1 and 2 at a certain disturbance interval length and intensity. This is because of the non-linearity of the system of differential equations. Thus it certainly does not mean that a doubling of $?_T$, i.e. a halving of the frequency, suggests that to obtain the same limit disturbance cycle, the intensity (1-?) should be doubled. Since we cannot analytically solve the density of both species in the 2-species system at a certain disturbance regime, we can also not analytically solve the amount of species that can coexist in a multi-species system. To gain further insight in the effects of disturbance interval length and intensity on species coexistence in a multi-species system, we rely on numerical simulations.

Numerical simulations of disturbance frequency and intensity on species coexistence in a 50-species system

As we have seen previously in our two-species system, disturbance creates a limit cycle, enabling species to coexist. We can analyse the boundaries that are set on the amount of species that can coexist under a range of disturbance intensities and frequencies by carrying out numerical simulations of a 50 species system. The model that includes 50 species is an extrapolation of eq. 3. In the model all species differ in population growth rates in such way that $r_1 > r_2 > \ldots > r_{50}$. Moreover, all species have an equal carrying capacity (K=100) and a competition coefficient $? = 1/(K*2)$. The initial densities of all species are equal and set to a value of 1.

We ran the model at different but fixed disturbance intensities with increasing values of disturbance interval lengths. The simulation runs are depicted in figure 9.10 and show the typical hump-shaped curves predicted by the IDH.

In figure 9.10 we can also observe two important aspects that are not captured by the axioms defined for the IDH. Firstly, we see that the maximum number of species that potentially could coexist (i.e. the 50 species we started the simulations with) cannot be reached for any combination of disturbance interval lengths and disturbance intensities. Secondly, the maximum number of species that can coexist differs between chosen interval lengths and intensities. In the case of the simulation runs depicted in figure 9.10, the maximum number of species is found at a disturbance intensity of 50% stem removal and an interval length $?_T$ of 7 years. All other combinations gave a lower amount of species. The maintenance of species diversity in the 50-species system by disturbance should be analysed graphically with the solution curves, comparable to the 2-species system. However in the case of a 50-species system, we have a 50 dimensional space to analyse rather than only two dimensions in a 2-species system, which makes it impossible to analyse species coexistence graphically. But it is not difficult to imagine that the positions of species
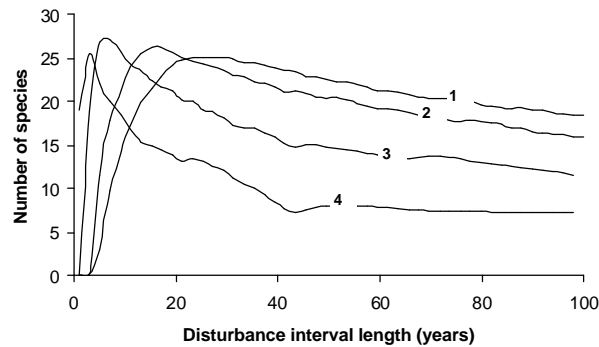
166

Figure 9.10 The relationship between the amount of species that coexist in the 50 species system calculated over 2000 simulated years, with increasing disturbance interval lengths at different but fixed rates of stem removal (disturbance intensity). Curve 1: 90% stem removal, curve 2: 80% stem removal, curve 3: 50% stem removal, and curve 4: 20% stem removal.

on the different solution curves and resetting the positions after disturbance works in a similar way as visualised in a 2-species system. The rate of movement along the solution curves and the various shapes of the solution curves can magnify the effects of disturbance intensity and frequency. The rate of movement is determined by the intrinsic population growth rates of species. The population growth rates of species can differ in two ways. Firstly, the growth rate of all species can be large or small, for example in rain forests with a set of only fast or slow growing species. By multiplying the species-specific population growth rate r_n with a scaling term r' we can introduce variation in the overall growth rates. This will have an effect on the rate of movement on the solution curve. Secondly, the array of species may vary in their relative differences in population growth rates. For example rain forests having species with a narrow bandwidth in growth rates in contrast to forests with a broad range in growth rates. Variation in species specific growth can be denoted as ?r. Growth rate differences affect the shape of the solution curve (a more horizontal line at increasing densities of species N_1 relative to species N_2 in the case of a 2-species system when ?r is large). Variation in the competition coefficient ? can range between 0 and < 1/K and we have seen previously that ? affect the solution curve of the superior species (see Figure 9.3). Different simulation runs with fixed disturbance intensities (i.e., 50% stem removal and interval lengths ?$_T$ of 7 years) show a pattern depicted in Figure 9.11. It turns out that population growth rate r', the differences in population growth rate ?r, and competition coefficient ? all have a 'hump-shaped' effect on the maximum number of species that can coexist. At intermediate levels of all these three population parameters and at intermediate levels of disturbance intensity and interval length the maximum number of species can be maintained, albeit not all 50 species could be maintained at every time step.
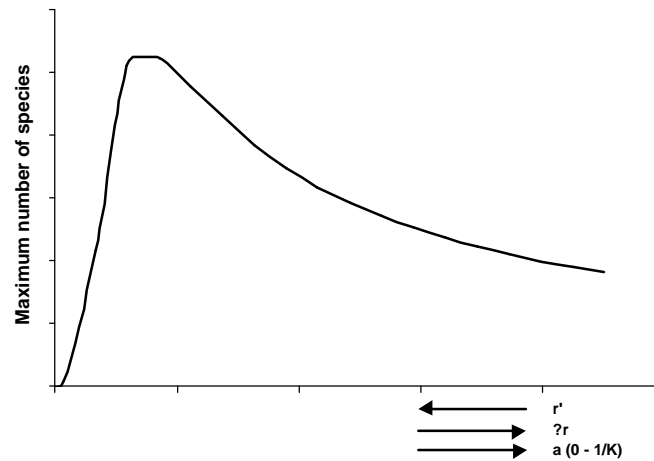
167

Figure 9.11 The graphical representation of the effects of population growth rate r', differences in population growth rate ?r, and competition coefficient ? on the maximum number of species that can coexist.

Discussion

From simple models to complex ecosystems

Simple rules make a model. To find a balance between the minimum amount of assumptions in simple models and the complex interactions in real ecosystems is perhaps the greatest challenge in ecology. The conceptual Intermediate Disturbance Hypothesis (IDH) comprises an array of ecological mechanisms which makes this hypothesis difficult to operate, and the IDH may therefore run the risk of 'explaining everything' without any understanding of ecosystems. In this chapter we explored a set of minimum assumptions under which a non-spatial IDH may function. Such a 'parsimonious' model is no proof that indeed ecosystems function in this way, but it should be a starting point for ecological research. In an extensive review, Chesson (2000) described many alternative mechanisms to maintain species diversity in ecosystems.

Although it is not our purpose to go in depth how these model types behave, and we therefore refer to the review paper of Chesson (2000), one important aspect should be noted here. In a classical Lotka-Volterra system not more than 2 species can stably coexist on a single resource. This behaviour has brought many researchers to the idea of niche partitioning (see Chesson 2000). Tilman (1982) introduced the resource competition theory, in which species are jointly limited by a single resource but species could only persist at a certain resource level. In other words, it is the variation in the resource levels that induces niche differentiation among species. Recently, Huisman & Weissing (1999) showed that many species could coexist on a single resource when that resource is consumed so that fluctuations of available resource provided 'ephemeral niches' for species. The system they simulated

showed chaotic dynamics and thus the suite of species that could be maintained remained unpredictable.

In the simple 2- and 3-species system we did not explicitly incorporate resource competition nor did we include niche partitioning. We assumed that the carrying capacities of species were equal, that differences among species were imposed by differences in growth rates, and that the negative growth effects of the superior species 2 placed on the inferior species 1 (i.e., the inter-specific competition) was equal to the negative effects species 1 experienced from itself (i.e., the intra-specific competition). In other words, we assumed the effects of intra-and inter-specific competition were equal, thus $?_{12} = 1/K$. One can argue from an ecological point of view that this assumption is unrealistic, and that the effects of inter-specific competition should be larger than the effects of intra-specific competition. If we assume the latter case, i.e., $?_{12} < 1/K$, the stable equilibrium point $K=1/?_{12}$ determined by the zero-growth isocline of species 2 will move upwards. Thus both zero-growth isoclines become two parallel lines. Also in this case, the solution curve will keep its characteristic S-shape and the outcome of disturbance on species coexistence does not show any difference. We have also shown the opposite effect that the negative growth effect of the inferior species 1 has on species 2. If this effect is zero, than the zero-growth isocline of the superior species 2 becomes a horizontal line, which does not affect the shape of the solution curve much and thus the outcome of disturbance.

In our example of the 3-species system we showed that the competitive hierarchy among species could be defined as a simple additive series. The most inferior species experiences negative growth effects from all other (superior) species while the most superior species experiences only small negative (growth) effects by the other species when $? < 1/K$ or no effect when $? = 0$. Also in this case, one can argue that the competition effects differ between specific species-to-species interactions. For example, the negative effect species 3 places on species 2 may be smaller than the effects placed on species 1 (i.e., when the species hierarchy is $s_1<s_2<s_3$). Also in this case, varying the values of each species-to-species competition interaction, does not affect the shape of the solution curves and hence the effects of disturbance on coexistence. Based on these observations we can formulate the boundaries and conditions that must hold for the simple, non-spatial, IDH-model to operate:

1. The intrinsic population growth rates of species *must* differ, in such way that the most inferior species has the largest growth rate. Thus $r_1 > r_2 > r_3 >…> r_n$.
2. The relative values of the competitive interactions among species do not really matter, as long as there are negative growth effects experienced by inferior species.

Given the above simple rules the next obvious question is if the IDH can be made operational in (ecological) field studies. The above conditions clearly show that differences in intrinsic population growth rates among species determine species coexistence, and thus these growth differences are the 'driving force' on which the

simple IDH-model operates while competitive differences among species are much less important. However, in permanent sample plots where recruitment and mortality rates are usually measured, those rates provide information on the *realised* population growth rates, rather than the *intrinsic* (per capita) rates. The latter growth rate type may therefore be very hard to measure under field conditions and thus the application of the IDH to a series of species difficult to make.

The interaction between disturbance frequency and intensity: predicting the effects of disturbance on species coexistence

We have shown in our 2-species system that disturbance interval length $?_T$ (frequency) and removal fraction $1-?$ interact in a non-linear way. Thus for example, doubling the amount of stems that are removed and doubling the interval length $?_T$ will not lead to the same amount of species that can coexist. For each fixed fraction of stems that are removed with increasing interval length (or vice versa) the characteristic 'hump-shaped' curve is found. However, we cannot analytically solve the amount of species that can coexist at any particular disturbance intensity and frequency, nor can we predict the densities of species at any disturbance regime in a simple two-species system. The reason for this inability lies in the dynamics of the differential equations, which are non-linear. The 'behaviour' of the Lotka-Volterra equation, which is the basis for this IDH-model, is its tendency to move to a single equilibrium point, whether this is in a 2-species system or in an n-species system. This behaviour is deliberately chosen, since we have stated, and is also required (see Sheil & Burslem 2003), that without disturbance a species-system should move towards a state of mono-dominance by one species. Disturbance (both intensity and frequency) reset the species-system away from this equilibrium, enabling more species to coexist. After the disturbance the system gradually grows back towards the equilibrium until a next disturbance event takes place. So what is the amount of species that can coexist? Is that the amount just after resetting the system, or just before the disturbance event? Thus, the IDH is a clear example of a non-equilibrium model by which it's intrinsic dynamics are affected by disturbance that leads to a recurrent replacement or succession pattern of species.

In the dynamic equilibrium hypothesis (DEH), Huston placed population growth rate as one determining variable that explain increased species diversity as caused by disturbance (1994). Although we cannot analytically solve the number of species that can be maintained by disturbance in an n-species system, by carrying out numerical simulations we calculated this number. For this we used a simulation model with 50 species. In this model we applied the growth rate hierarchy (i.e., $r_1 > r_2 > ... > r_{50}$) and a competition coefficient $? < 1/K$. Simulations with the 50-species model showed that three 'population' parameters affect species diversity. Firstly, the absolute value of the intrinsic population growth rates, which we denoted as r' affected diversity (*sensu* Huston 1994). Secondly, the relative differences in growth rates, denoted as $?r$, affected diversity, and thirdly, the value of the competition coefficient $?$ affected diversity (see Figure 9.11). However, we can add to Huston's DEH model that 1) the shape of the 'hump-back' IDH curve is affected by the population growth rate r' and 2) that the maximum diversity that can be maintained

is also a function of the above three population parameters (Figure 9.11). The first point suggests that with increasing population growth rates r', the IDH curve has a much more skewed or 'peaked' maximum than when the growth rate r' is low. In the latter case the curve has a much more 'flattened' top. Thus, in highly productive rain forests where the intrinsic population growth rates of all species is high, a small variation in disturbance regime can lead to much larger differences in species diversity than in low productive rain forests with species having low intrinsic population growth rates. The second point suggests that the maximum species diversity is a function of the three population parameters. Thus maximum diversity increases with decreasing r' (species systems with slow growing species can hold less species), increases with increasing ? r (species systems with relatively large differences in growth rate can hold more species), and increases with an increasing value of the competitive interaction.

In all previous examples disturbance intensity and frequency occurred in a pure deterministic manner. This of course does not hold for real ecosystems in which disturbances do not occur in regular time intervals with predetermined intensities. We can add more realism to the simple 50-species model by introducing stochastic elements, but the interpretable patterns may get lost. Figure 9.12 depicts the average number of species over 100 runs, in which disturbance intensity was fixed (30% stem removal for all species) while the disturbance frequency varied randomly between 1 and 100 years (Figure 9.12A). In the second case, the opposite is shown in which the disturbance intensity varied randomly between 10% and 90% stem removal while the interval length was fixed at 50 years (Figure 9.12B). The patterns in Figure 9.12 show that randomly varying disturbance interval lengths (with fixed removal intensities) lead to more unpredictable patterns than randomly varying removal intensities with fixed interval lengths. Although the latter case shows large variation in the amount of species, the patterns are, to a certain point, highly predictable and mostly caused by the chosen disturbance interval length. In contrast, the former case does not hold any predictability in the amount of species that can coexist.

The spatial component in the IDH
Species live in a spatially heterogeneous environment. Therefore the spatial component has been thoroughly investigated in the ecological theory of species coexistence and it is shown, for example by Levin (1974), Tilman (1994), Lehman & Tilman (1997), and Hubbell (2001) that dispersal limitation of species can lead to (stable) coexistence. In other words, adding the spatial element leads to coexistence of many species on a single resource (i.e., 'space' can be treated as a 'resource'), which is in sharp contrast to the results of the classical, and non-spatial, Lotka-Volterra models. There are two important aspects, among many, in these spatial models that need a closer look in light of the implementation of space into the IDH. First, since these spatial models predict coexistence of many species, the assumption of mono-dominance in the absence of disturbance in the IDH (e.g., Sheil & Burslem 2003) seems to be contradictory. Secondly, the models of Levin (1974), Tilman (1994) and Lehman & Tilman (1997) all assume an apparent trade-off between competition and dispersal limitation. Thus the best competitors are much stronger
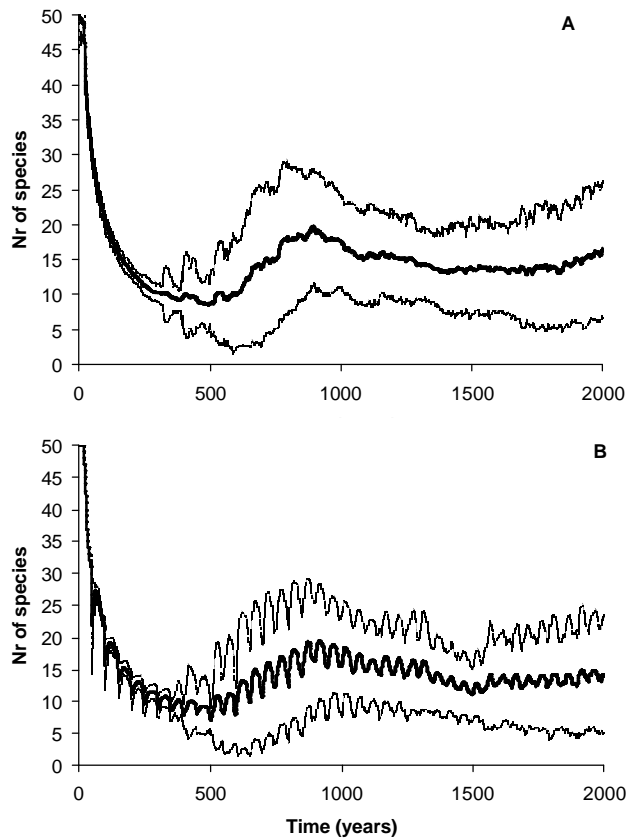
Figure 9.12 The effects of random varying disturbance frequency or intensity on the number of species. **A**: fixed removal fraction ? = 30% removal with a random interval length ?$_T$ (between 1-100 years). **B**: fixed disturbance interval length ?$_T$= 50 years with a random ? (between 10% - 90% stem removal). In both cases the average over 100 runs (bold lines) (± SD, thin lines) is depicted.

limited in their dispersal than weak competitors. If dispersal limitation could be coupled to the intrinsic population growth rates of species in our non-spatial model, than slow growing species should exhibit strong dispersal limitation to obtain coexistence of both fast and slow growing species in the IDH. Indeed, it is shown that fast growing tropical tree species (i.e. pioneer species) are often small-seeded, while slow growing (climax) species almost always have large seeds (see Chapter 1). However, the relation between seed size and dispersal distance may not be that straightforward. On the other hand, the unified neutral theory (UNT) developed by Hubbell (2001) assumes there are no differences among species for any plant trait, including dispersal limitation and population growth rate. The UNT predicts coexistence of many species, but due to random walk this amount will be reduced to a single-species state in small communities. In small communities this 'fixation' will be prevented by recurrent species immigration and in large ones by speciation. Thus, an apparent trade-off between competition/growth rate and dispersal limitation may

not seem necessary. However, due to its complete neutrality, species composition in the UNT is highly unpredictable. Although tropical rain forests can be extremely species rich, the 'dominant species' of the community in a climax stage can largely be predicted from a relatively small suite of species, all of them having low population growth rates (ter Steege & Hammond 2001, Chapter 10). If space is to be included in the IDH and species have strong dispersal limitation, open sites caused by disturbance may enable a similar replacement series of species as shown by the non-spatial IDH model (e.g., Chesson 2000).

From complex ecosystems to simple models

Hubbell *et al*. (1999) studied species composition and diversity in gaps and surrounding vegetation on Barro Colorado Island and argued against the IDH as an underlying mechanism (but see Sheil & Burslem 2003 for a critique). One of the points they made was the relatively low amount of pioneer species invading new gaps. In our IDH model, species were defined on the basis of only two characteristics: their intrinsic population growth rate and their position in the competitive hierarchy. Thus in other words, there are no predefined 'pioneer' or 'climax' species in our model. Disturbance increased the amount of fast growing and weak competitors in the species system. Therefore, the non-spatial IDH, as we defined, does not depend on the pioneer-climax species concept and can therefore be applied to any stage of forest succession, as long as there are species-specific differences in population growth rates. Nevertheless, we acknowledge the long-standing observations that fast growing (i.e., pioneer) species require relatively high levels of light availability to recruit. However, we did not incorporate light dependent recruitment in our IDH model presented here, although a density-dependent regulatory mechanism was introduced by the competitive interactions. In a survey of model evaluations we did include such a recruitment limitation (which operated on the intrinsic population growth rate r_n), but this limitation did not qualitatively affect the outcome of the model runs. To make the IDH model as simple as possible, we excluded such a regulatory mechanism. This observation therefore suggests that a small set of pioneer species does not necessarily have to invade gaps after disturbance as a proof for the IDH to operate. Based on the model we have presented here, we only expect an increase in relatively faster growing species after disturbance than the species already present in the forest. These new species do not necessarily have to be typical pioneer species.

10 LONG-TERM CHANGES IN TROPICAL TREE DIVERSITY: SYNTHESIS AND IMPLICATIONS FOR MANAGEMENT

René Verburg, Hans ter Steege, Roderick Zagt

Introduction

The main theme of this book is how disturbance, whether natural or man-caused, influences forest composition and diversity of tropical rain forests. From this book we learn that the impacts can be profound but also difficult to discern. Studies on the development of species composition after disturbance show that after c. 50-65 years of succession secondary forests can be as species-rich as mature forest (Saldarriaga *et al.* 1988, Brown & Lugo 1990, Finegan 1996). Even if they are similar in diversity, secondary forests usually differ substantially in composition compared to virgin forest, suggesting that diversity and composition may vary independently (Brown & Lugo 1990, Finegan 1996). The long-term observations of vegetation re-growth after disturbance in Chapters 3 - 8 in tropical rain forests across different continents all comprised measurements of both diversity and composition that perhaps allow a generalisation of the successional patterns to be made.

In the introduction we asked a number of questions:

1.   Are the predictions by the Intermediate Disturbance Hypothesis (IDH) confirmed by field observations?

Because the IDH makes use of the term diversity we are in need of a measure that captures it effectively and allows us to detect changes. Thus we need to answer the following questions first:

2.   Are the measures of diversity currently in use sensitive enough to detect changes in a meaningful and significant way?
3.   Can changes be effectively measured and monitored and are permanent sample plots a good way to monitor changes?

In most cases of tropical rain forest we are challenged by the very high species numbers and a simplification may be necessary:

4.   Is it possible to predict responses of tree communities to disturbance on the basis of selected life history characteristics?

Then, finally we can tackle the first and following two questions:

5.   How is tree diversity affected by disturbance?
6.   How is tree composition affected?

Because question four is important to understand and predict changes in forests as a result of planned disturbance (e.g. logging), and will be used in testing the IDH, we will start with a review of the evidence put forward in the contributing Chapters on these issues. Then we will try to answer questions two and three, one and finally five and six.

Life history characteristics: do they predict the responses of species to disturbance?

Seed mass is a life-history characteristic with information on the regeneration potential of species
In Chapter 2 Rose & Poorter showed, on the basis of a review of 14 studies, that seed mass is an important life-history characteristic for the establishment of seedlings. In summary, species with larger seed mass:

1.   have higher survival in the shade (but not in high light conditions),
2.   have larger initial seedling size, conferring a competitive advantage over other, smaller, seedlings,
3.   have lower inherent relative growth rates RGR,
4.   are less capable of adjusting RGR,
5.   and, thus, can be out-competed by seedlings of smaller seeded, more plastic, species that grow faster in the presence of sufficient light.

The universal tendency of seedlings of larger seeded species to invest in (large) structural size is well shown by their low Leaf Area [by mass] Ratio (LAR (cm^2 g^{-1}), Figure 10.1), the 'leafiness of a plant' (Chapter 2) and one of the components of Relative Growth Rate (RGR, see Chapter 2). Based on their substantial review Rose & Poorter concluded that the role of seed size in establishment of seedlings has been supported.

However, as studies, described in Chapters 5, 6, 7, have shown, recruiting species are not necessarily characterised by a higher or lower seed mass than species already present. There may be two reasons for this: 1) the time between measurements may have been too short to allow new seedlings to recruit into the size classes used in the permanent sample plots, 2) the effect of seed mass is not as important in the natural forest as has been suggested by the experiments but recruitment is influenced more by other ecological factors. In one set of experiments this was explicitly tested (Rose 2000). Here it was shown that, whereas the effect of seed mass on growth was very strong in controlled experiments, its significance decreased consistently when the experiments were carried out under increasingly realistic natural conditions. In a large-scale logging experiment, comparable to the situation in Chapters 5, 6 and 7, the effect of seed mass on recruitment was negligible (Rose 2000). Thus, although the effect of seed mass is real (and statistically significant if tested) its ecological significance may yet be limited under realistic natural conditions (Rose 2000).
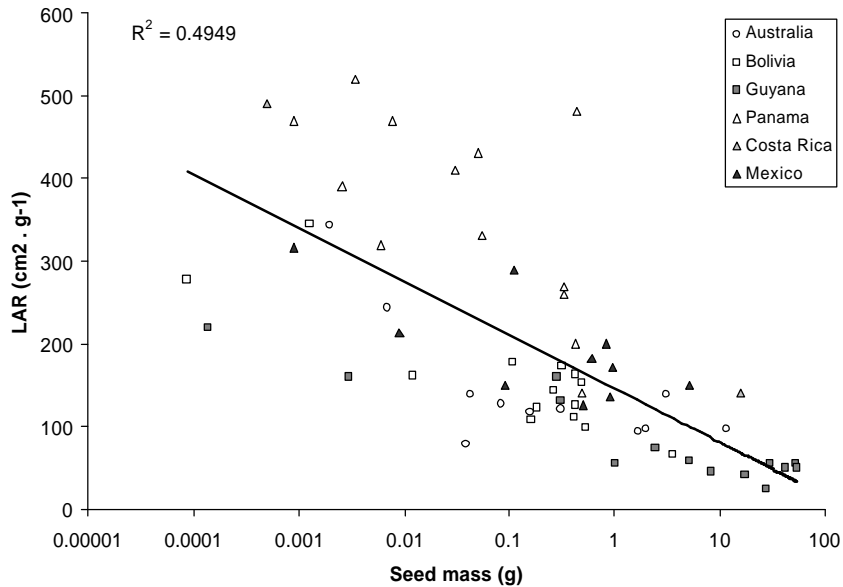
Figure 10.1 Seedlings from seeds with large seed mass tend to produce seedlings with high structural investment and thus low Leaf Area Ratio (LAR, cm^2 g^{-1}) (Chapter 2). This, and a low Net Assimilation Rate (NAR), results in low relative growth rates, especially noticeable under high light conditions. Data sources (shade plants): Australia – Osunkoya *et al.* (1994); Bolivia – Poorter (1998); Guyana – Boot (1993), ter Steege (1994, unpubl. data); Panama – Kitajima (1994); Costa Rica – Fetcher *et al.* (1983); Mexico - Popma & Bongers (1988).

Wood density is a good 'universal proxy' of potential annual diameter growth rate

Wood density has a profound relation with the maximum potential diameter growth rate of species irrespective of geographic location (Figure 10.2). While wood density may not be a good estimator of average annual growth rate, it appears to be a good estimator of maximum annual growth rate (the upper boundary of the distribution of points in Figure 10.2). As many more factors will also have an effect on diameter growth, these will obscure the relationship. If such factors interact rather than act in an additive manner, standard regression methods are not capable of detecting the proper relationships.

Recently, a more advanced regression method has become available for ecology (Cade *et al.* 1999) that has been pioneered in the field of econometrics (Koenker & Basset 1978). With this technique, known as quantile regression, interacting factors may be studied even if not all these factors have been measured[1]. Both the 90th and

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[1] Limiting factor theory assumes that factors influencing the dependent variable act heterogeneously (read: independently) over the landscape. Near the upper bound of the distribution, the factor under consideration is considered to be actively limiting the dependent variable. Variation below these maxima is caused by the interacting influence of other (often unmeasured) factors. We used quantile regression (Koenker & Basset, 1978; Cade *et al.*, 1999) to examine whether maximum growth was correlated with wood density. We used the programme Blossom (Cade & Richards 2001) to calculate the regression statistics and permutation significance tests.
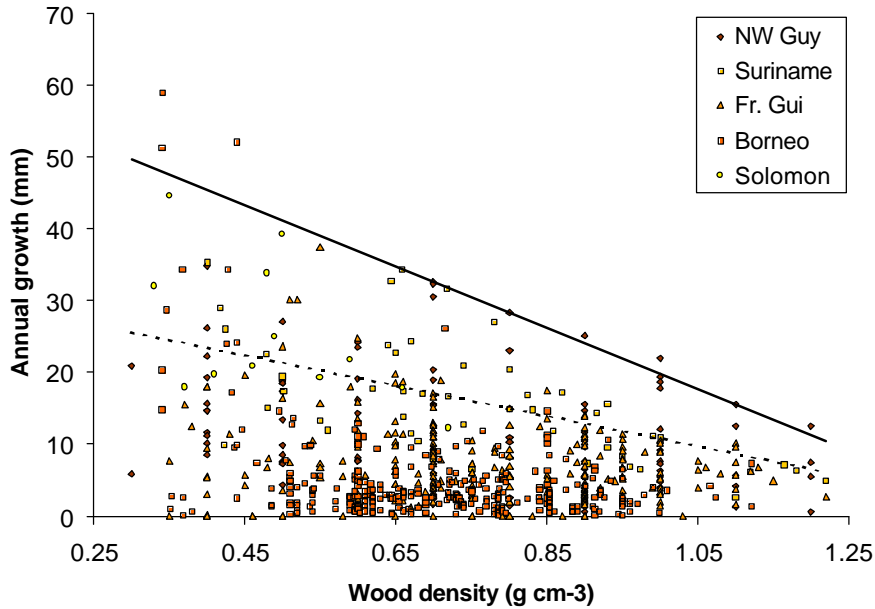
177

Figure 10.2 The relationship between maximum annual diameter growth and species specific wood density. The dashed line represents the 90% percentile regression. The solid line represents the 99% percentile regression and therefore represents the best estimate for potential maximum growth rate. Regression based on stem growth measures in Kolombongara (Chapter 4), North west Guyana (Chapter 6), Suriname (Chapter 5), French Guiana (Favrichon 1994, 1995), and Borneo (Chapter 7).

99th quantile regression lines were statistically significant ($P << 0.001$; rank score test, 10,000 permutations). Because of its significance and closeness to the edge of the upper boundary of the point cloud, we conclude that the general relationship between maximum growth rate and wood density is best described by the 99th quantile regression (Figure 10.2) but it may differ a bit by location. With this result Figure 10.2 can be interpreted as follows: with increasing wood density the maximum annual growth rate decreases significantly. High growth rates will never be found in species with high wood density. This is very obvious from the graph. A low wood density, however, will not always result in high annual growth but it could. The most important cause for reduced maximum growth rate is likely that several species, especially those with fewer censused individuals, are found under sub-optimal conditions such as e.g. shade or poor soil. Secondly, not all species will invest in or allocate their carbohydrates maximally in stem diameter growth. In other words, the interspecific differences in growth rate may reflect differences in carbon allocation.

It is important to note that in each of the tropical areas under study, wood density has an effect on annual diameter growth and that to some extent wood density can be taken as a proxy for maximum potential growth rate. If wood density helps to explain growth rates, community composition in terms of wood density may be indicative of 'community growth rates'. Figure 10.3 shows the stem distributions
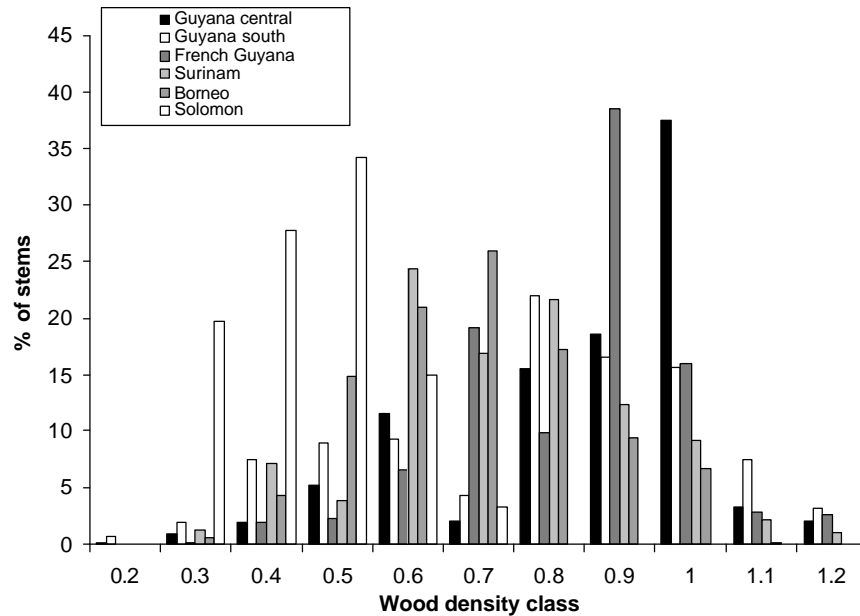
Figure 10.3 Frequency distribution of stems in different wood density classes of rain forests in central Guyana and south Guyana (ter Steege unpubl. data), French Guyana (Favrichon 1994, 1995), Surinam (Chapter 5), Borneo (Chapter 7), and Solomon Islands (Chapter 4).

over different wood density classes of stems of species found in different rain forests. This figure shows that the array of forest types includes two extremes. On one side, the rain forest of the Solomon Islands (Chapter 2) is mostly characterised by softwood stems with high potential annual diameter growth rates. On the other extreme, the rain forests of central-, south-, and French Guyana (Chapter 8, Favrichon 1994, 1995, ter Steege unpubl. data) consist mainly of hardwood stems, consequently having small annual diameter growth rates (Figure 10.2).

While several studies indeed show an increase of species with low wood density after disturbance (Chapters 3, 4, 6, 7) other studies show a failure of higher recruitment of such species (Chapters 5, 8).

Logging and disturbance - what can we learn from the IDH?

From tree growth rate to population growth rate
We suggest that the large differences in stem distributions among rain forests can be explained by the Intermediate Disturbance Hypothesis (IDH) (as will be shown below). Moving from the species-specific investment in wood structures to the population growth rates of species requires a further step that has been not taken in the previous Chapters, however. For Kolombongara, Burslem & Whitmore (Chapter

179

4) showed that species that invest in softwood exhibit large annual recruitment and mortality rates, while species that invest in hardwood have low annual recruitment and mortality rates. But this was not the case in Suriname (Chapter 5). In addition to that, in Chapter 9 we have seen that by themselves, recruitment and mortality rates do not provide information on the intrinsic population growth rates of species. Nevertheless, we might assume that species that invest in softwood, and thus grow fast, reach maturity at younger ages than species that invest in hardwood and consequently grow slow. In other words, we take the step that species with large annual diameter growth rates also exhibit large intrinsic potential population growth rates. Of course, this assumption should be treated with caution since this relation is not proven yet, and has to be tested in future research. For now, if we take this assumption, then can we predict the distributions depicted in Figure 10.3 by the IDH?

Forest with different disturbance regimes differ in functional composition
To test this hypothesis, we use the 50-species model that was introduced in Chapter 9. In this model the stem distributions were simulated for rain forests that differ in 'natural' disturbance regime. We started the simulations with 50 species, each with an initial abundance of 1 stem. The growth rates of species were drawn from a random distribution. We ran the model for 2000 years to be sure that the stem density of the simulated forests stabilised. The results are shown in Figure 10.4. A
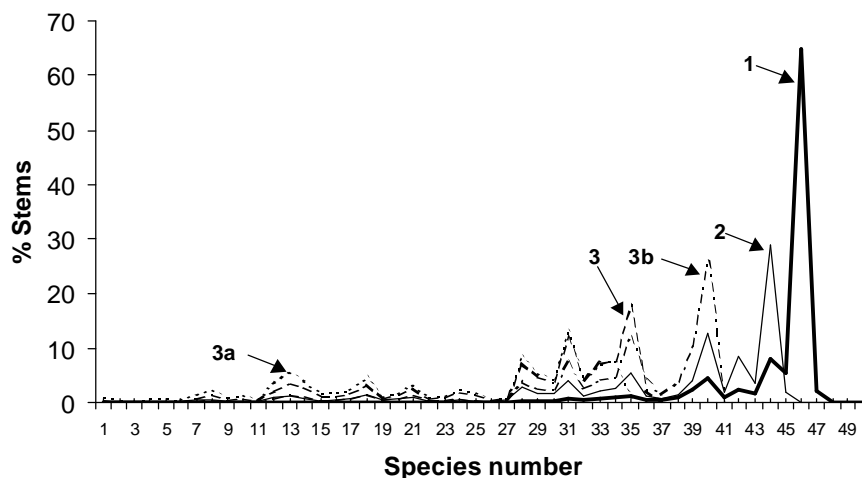

Figure 10.4 Frequency distribution of stems in simulated rain forests after 2000 simulated years. For the simulation, the 50 species model is used with an initial density n=1 for all species (1 –50), and values of intrinsic population growth rates drawn from a random distribution. Low dynamic forest: annual disturbance intensity of 1% (denoted by "1"), highly dynamic forests: annual disturbance intensity of 3% (denoted by "2"), hurricane-prone forest disturbance intensity of 80% stem removal (? =0.2) with a disturbance frequency of 20 years (denoted by "3"), with a disturbance intensity of 60% stem removal (? =0.4) with a disturbance frequency of 10 years (denoted by "3a"), and with a with a disturbance intensity of 90% stem removal (? =0.1) with a disturbance frequency of 40 years (denoted by "3b"). Species are ordered according to their growth rates (i.e., species #1 has the highest population growth rate and species #50 has the lowest population growth rate).

180

low dynamic forest is shown as distribution 1, which is typified by the rain forests in central-, and south Guyana, or French Guyana. In this forest an annual mortality rate of 1% is imposed, thus every year 1% of all stems is removed. Figure 10.4 shows a species poor (i.e., 7 species) rain forest that is typified by a stem spectrum of only slow growing species. Highly dynamic forests are typified by annual mortality rates of ca. 3%. The rain forest at the ITCI site on Borneo showed long-term mortality rates between 2-4% (Verburg, unpubl. data) and can be interpreted as highly dynamic rain forest. In Figure 10.4 the stem distribution of a highly dynamic rain forest (with an annual mortality rate of 3%) is shown as distribution 2. This forest type is typified by faster growing species than the low dynamic rain forest, while the highly dynamic rain forest is also more species rich (i.e. 19 vs. 7 species). Finally, rain forests that are subjected to large scale disturbances, such as the hurricane-prone rain forest of Kolombongara, have a stem distribution with only relatively fast growing species (distribution 3) and are even more species rich than the highly dynamic rain forest (i.e., 24 species) (Figure 10.4). The imposed disturbance regime on the hurricane-prone forest is a disturbance intensity of 80% (?=0.2, see Chapter 9) and a disturbance frequency of 20 years. Although the simulated disturbance regime imposed on the hurricane-prone forest in Figure 10.4 is already very large, the stem distribution of the rain forest on the Solomon Islands depicted in Figure 10.3 had many more fast-growing species than the simulated distribution nr. 3 of Figure 10.3. It is important to understand if a further simulated increase in disturbance intensity or in disturbance frequency would result in a stem distribution that is more comparable to the rain forest of the Solomon Islands. For this we left the disturbance regime as it is, but increased disturbance intensity with a concomitant decrease in disturbance frequency and vice versa, an increase in disturbance frequency and concomitant decrease in disturbance intensity. We observe in Figure 10.4 that an increase in disturbance frequency (distribution 3a) leads to a larger fraction of fast growing species than an increase in disturbance intensity (distribution 3b). However, the distribution 3a contains fewer species (i.e., 23 species) than distribution 3b (i.e., 26 species). Based on this simulation we suggest that the large fraction of fast growing species in the hurricane-prone rain forest of the Solomon Islands is rather the result of high disturbance frequency than high disturbance intensity.

Predicting future effects of logging on species composition and diversity in low and highly dynamic rain forests: simulations using the IDH model
As we have seen in the previous section, the 'natural disturbance regime' imposed on a rain forest strongly determines the functional- and species diversity of trees. Highly dynamic rain forests are predicted to have a larger number of species with relatively high growth rates, while low dynamic rain forest are predicted to be species poor with only slow growing species. Because these forest types strongly differ in diversity and (functional) composition, the effect of additional disturbances imposed by humans, such as logging, will be different both on species diversity and (functional) composition. Predicting these effects can assist policy-makers in developing appropriate guidelines to conserve and manage biodiversity in disturbed tropical rain forests. To give insight in the varying effects of logging on species richness and functional diversity, we simulated the effects of logging in a low and

highly dynamic rain forest. To start the simulation, we used two different stem distributions. The first distribution is from a typical low dynamic rain forest and for this we used distribution 1, obtained from the previous simulation (Figure 10.4). The second distribution is a typical highly dynamic rain forest for which we used distribution 2, also obtained from the previous simulation (Figure 10.4). In both low and highly dynamic rain forest we maintained the 'natural disturbance' (i.e., 1% and 3% annual mortality respectively), while in addition we imposed two different logging scenarios. In the first case a low-intensity logging operation is simulated in which 10% of all stems are killed. In the second case a high intensity-logging scenario is simulated in which 60% of all stems are killed. In both cases a logging cycle of 30 years is imposed, that is at the start of the simulation a logging operation is carried out and sequentially every 30 years thereafter. In Figure 10.5 the effect of both logging scenarios on the number of species is shown.

In low dynamic rain forests, a low-intensity logging operation (i.e., 10% logging) increases species richness (from c. 7 to c. 14 species, Figure 10.5A). High-intensity logging (60% stem removal) strongly increases the number of species, up to c. 32 species. The highest number of species is reached during the third cutting cycle. After the third cycle, the number of species decreases again. In highly dynamic rain forest, low-intensity logging does not affect the number of species much (Figure 10.5B). On the other hand, 60% stem removal (i.e., high intensity logging) strongly increases the number of species, comparable to the low dynamic rain forest with the same logging intensity. In the highly dynamic rain forest the largest number of species is found during the second logging cycle, after which the number of species decreases during successive logging cycles to the numbers found in unlogged forest.

Thus changes in species richness are close to what was expected from the predictions of the IDH. It is also observed, and predicted (Chapter 1) that the 'functional' composition changes (Figure 10.6). Both in low- and highly-dynamic forests that are subjected to large intense disturbance, the species composition shifts from species with low population growth rates to species with higher growth rates (and their associated lower wood densities).

Conclusions on the IDH so far
Based on the above we can conclude that (the mathematical model of) the IDH predicts a number of observations quite well:

1.   An increase in annual mortality rates (low vs. highly dynamics) causes an increase in species diversity and a change in species composition towards faster growing species. This is observed quite easy if we compare the cyclone-forest of Kolombongara (Chapter 4) with the forests of little disturbed Guyana (Chapter 8, see Figures 10.3, 10.4)

182

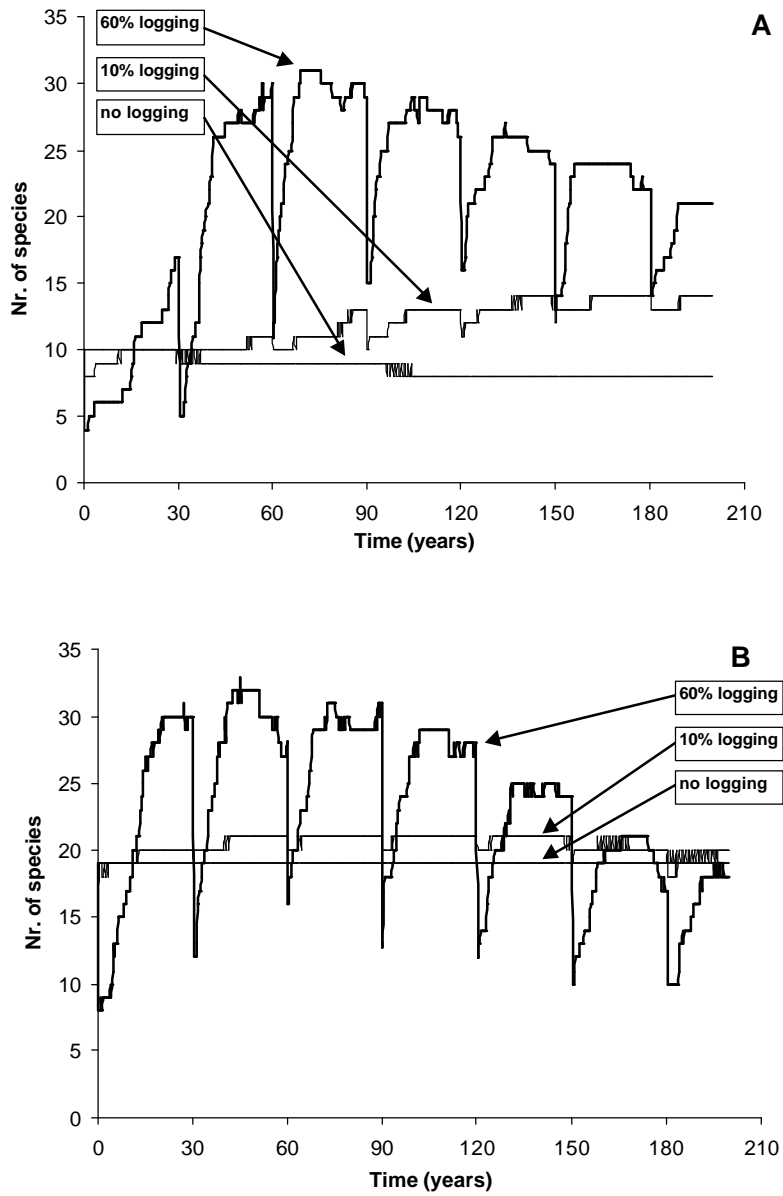Figure 10.5 The simulated effects of logging in low dynamic (**A**) and highly dynamic (**B**) rain forest on the number of species. Simulated are the effects of 60% stem removal (?=0.4) and 10% stem removal (?=0.9) with a logging cycle of 30 years. In low dynamic forest annual mortality is 1% calculated over all stems and species, in highly dynamic forest annual mortality is 3% over all stems and species.
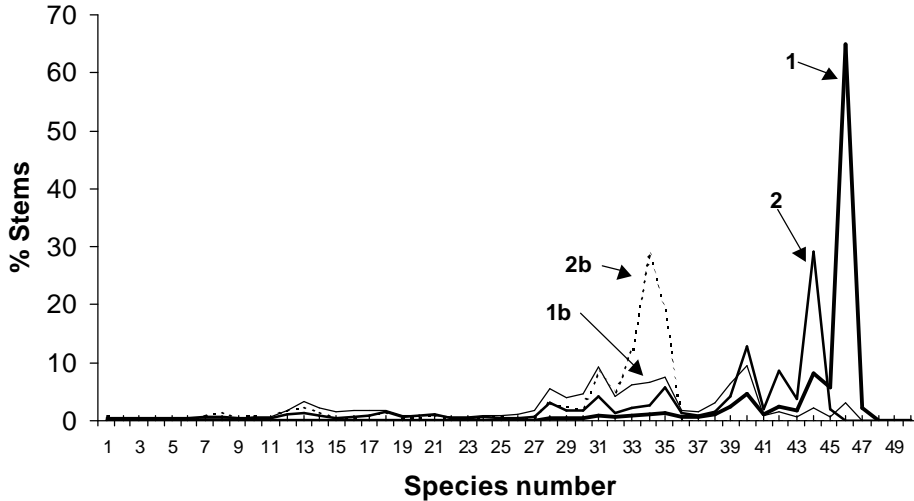
183

Figure 10.6 Frequency distribution of stems in simulated low dynamic forest (distribution 1), highly dynamic forest (distribution 2), low dynamic forest with additional 60% stem mortality caused by logging (distribution 1b), and highly dynamic forest with additional 60% stem mortality caused by logging (distribution 2b) (see also figure 10.5). The stem distributions of both logged forests are depicted after 160 simulated years (= after the 6th cutting cycle). Species are ordered according to their growth rates (i.e., species #1 has the highest population growth rate and species #50 has the lowest population growth rate).

2.   Low intensity logging strongly affects species diversity and functional diversity (more fast growing species) in low dynamic forest, but hardly affects these parameters in highly dynamic rain forest

3.   The increase in species diversity caused by high intensity logging is temporary both in low and highly dynamic rain forest. After a number of cutting-cycles species diversity drops again, but species composition in both forest types strongly changes, from relatively slow growing species to (only) fast growing species. Thus the species composition changes to non-commercial species after a number of cutting-cycles. This will permanently affect the commercial potential of these forests.

Based on the above, we suggest that average community wood density is indicative for the natural disturbance regime (cf. ter Steege & Hammond 2001) and may help to forecast the changes that will be caused by logging. For our model to do this accurately more testing will be necessary. In the long term, the model suggests that forests that have high average community wood density will change more than forests that have low average community wood density. Although initially diversity increases in the model, a prediction already made by the conceptual IDH, the model shows that finally under heavy harvesting the diversity will return to similarly low levels but with different species.

Species diversity after disturbance: usefulness and sensitivity of indices – or 'can we measure change in diversity accurately?'

Many diversity indices are used to describe the number of species in a sample. Condit *et al.* (1998) and Chazdon *et al.* (1998) tested the stability of several and found that most indices were very sensitive to sample sizes. Among those, Fisher's ? and Shannon were the least sensitive, hence these indices are often used to assess and compare species diversity patterns in different tropical rain forest studies. Despite their common use, the underlying assumptions of both indices are not always recognised. For instance, Fisher's ? assumes a log-series distribution of stems over species (e.g. Hubbell 2001). This assumption may be met in virgin forest but perhaps not in disturbed forest.

Initially, the IDH was derived from Budongo rain forest in Uganda (see Chapter 3). The original data from Eggeling (1947a, see Chapter 3, Table 3.2) clearly showed low diversity in early and late successional stages and highest diversity in the intermediate stages. However, as the IDH was formulated based on these data, they cannot be used as a test of that same model. Species diversity (Fisher's ?) of logged forests in Guyana (Chapters 6, 8), Suriname (Chapter 5), and Borneo (Chapter 7) did not differ significantly from mature forest. In contrast, Burslem & Whitmore (Chapter 3) found a significant positive relation between Fisher's ? and disturbance intensity caused by hurricanes in rain forests of Kolombongara. However, in their study only one location of forest had a significantly larger Fisher's ? than the other studied locations (Chapter 4).

The results obtained from Guyana, Suriname and Borneo may thus suggest that diversity is unaffected by logging. When studying diversity patterns, however, it is important to evaluate diversity patterns in mature forest and to study whether the diversity measure can really capture changes caused by disturbance. The variation among plots in virgin forest was generally high. Average diversity values of plots in Guyana (Chapter 6, 8), Suriname (Chapter 5) and Borneo (Chapter 7) showed a large standard deviation in Fisher's ? . Albeit not significantly, in both Suriname and Borneo Fisher's ? tended to be (but not always) lower in logged than in virgin forest. Thus, the large variation of tree diversity in mature forest makes it difficult to detect significant differences between mature and disturbed forests.

Another problem with Fisher's a is its assumption of a log-series distribution of individuals over species, while in fact it is only calculated from the number of individuals and the number of species. As such, it is completely insensitive to changes in evenness, the way individuals are distributed over the species. The study in Guyana illustrated this (Chapter 8). When just a few species are extracted and no new species invade the area, the number of individuals and species will be similar before logging and after recovery. Even though there may have been significant shifts of individuals over the species, Fisher's a will be exactly similar. In addition to that, the changes are too small to be detected by the Shannon index that is sensitive to changes in evenness.

Are we measuring the right trees?

In addition to the potential insensitivity to logging of the biodiversity indices used, we can ask if we have been measuring the right trees. For practical reasons large-scale forest inventories have a lower diameter of 30cm and PSPs from 10cm DBH or 20cm and a sub-sample of 5-20cm (Alder & Synnot 1992). The data of Guyana (Chapter 6) illustrate the need to measure small stems (Figure 10.7). While there is a clear increase in Fisher's a among the saplings (2-5 cm DBH) after logging, this effect is neither seen for the poles (5-20 cm DBH) nor for the larger trees (= 20 cm DBH). Apparently, the species that account for the increased diversity in the smaller individuals may simply not have reached the larger size classes yet. However, in Borneo (Chapter 7), even after 20 years there was no measurable change in diversity. One reason may be that the increase in diversity in the smaller size classes is caused by pioneer species, the majority of which simply never grow to large sizes.

Again, the data of Budongo (Chapter 3) show near perfect progression of composition over the plots – species and individuals in the smaller size classes belong to a later successional stage, and within the plots – similar classes of successive measurements are also of a more advanced successional stage. In other words the trees of late successional stages in the smaller size classes are actually recruiting into the larger size classes.
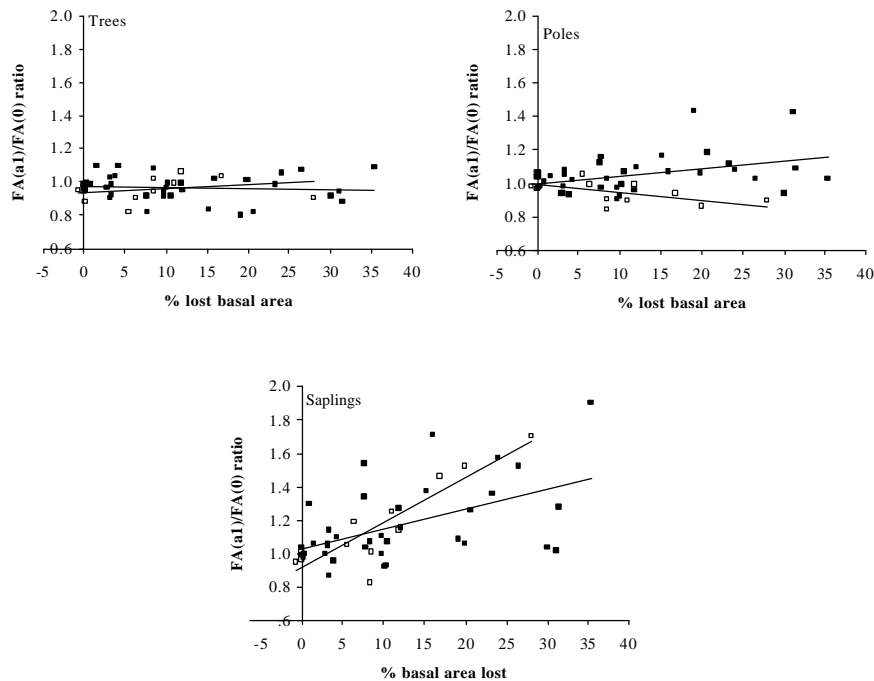

Figure 10.7   Ratio between Fisher's a 6 years after harvesting (FA(a1)) and initial Fisher's a (FA(0)) in a logging experiment in central Guyana (Chapter 5). Open symbols Pibiri, central Guyana, closed symbols Barama, northwest Guyana.

Logging and disturbance, what can we learn from the data?

Recovery after disturbance: species replacement or stem renewal?

While the tropical rain forests in Guyana, Suriname, and Borneo responded similarly to logging with respect to diversity, the (stem) replacement patterns after logging differed. Ter Steege *et al.* (Chapter 8) showed that the tree community (except the logged species Greenheart (*Chlorocardium rodiei*)) in central Guyana was not affected by tree extraction while in addition short-lived like pioneers (small seeded softwoods) failed to achieve a significant abundance in the community of large trees, perhaps simply because of their limited maximum adult size (see above). In contrast, the studies in Suriname (Chapter 5), Kolombongara (Chapter 4), and Borneo (Chapter 7) showed an increased abundance of fast growing (pioneer-like) species after disturbance, confirming common understanding. Why did fast growing pioneer species fail to recruit in Guyana while this was not the case in the other rain forests? Regeneration patterns after disturbance depend on a number of aspects: the available stock of seeds, seedlings, saplings and the resprouting of damaged trees. In a study on seedling recruitment in differently-sized and artificially made gaps in the tropical rain forest of Guyana, Rose (2000) found that between 60-70% of the recruited seedlings (stems) were shade-tolerant species, 15-25% intermediate species, and only between 2-10% were pioneer species (Figure 10.8). Surprisingly in this study, highest recruitment of pioneer species was not in the largest gaps, but in the intermediate-sized gaps (Figure 10.8). This study thus showed that fast-growing softwood species are able to recruit in logging gaps in Guyana. Seedling recruitment depends on neighbouring adult trees that provide seeds. About 30% of the recruited species were present as adult trees within a 20m radius (Figure 10.9). Thus,
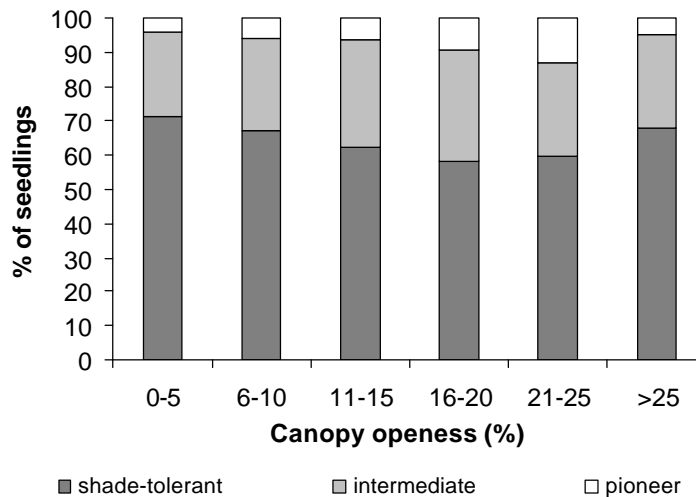

Figure 10.8 The relative abundance of seedlings in six different canopy openness classes, four years after the creation of canopy gaps. Seedlings were classified in three functional types; shade-tolerant, intermediate, or pioneer species. Data derived from Rose (2000).
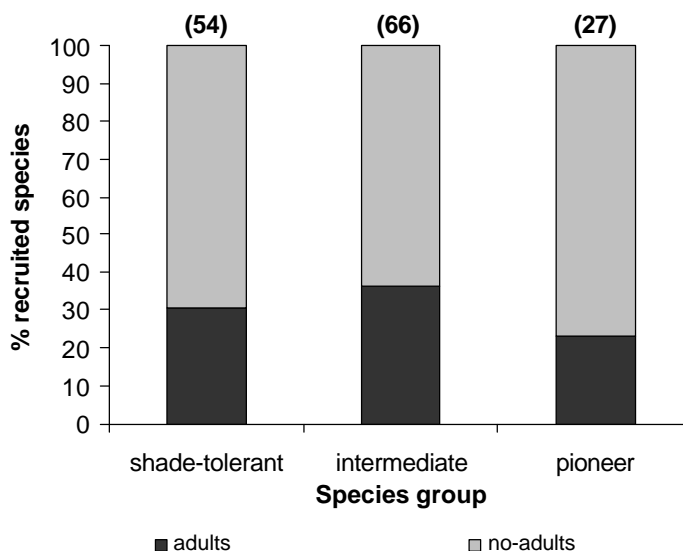
Figure 10.9   The percentage of recruited species (seedlings) in canopy gaps of which adult trees were present in a 20meter radius ('adults') or which adult trees were absent in a 20m radius ('no-adults'). Seedlings of species were classified in three functional types; Shade-tolerant, intermediate, or pioneer species. Between brackets the total number of species in each group. Data derived from Rose (2000).

recruitment after logging strongly depends on the abundances of species in the local species pool and their seed banks, as proposed by ter Steege *et al.* (Chapter 8). In central Guyana the undisturbed rain forest is characterised by a relatively poor tree community in which a few tree species make up the canopy and in which very few softwood species are found (ter Steege *et al.* Chapter 8). Seedlings from softwood species may not have recruited simply because there were no adult trees nearby to generate the seed rain during gap creation or to provide seeds for a long-term seed bank, arguably a simple case of dispersal limitation (Hubbell *et al*. 1999, Hubbell 2001). Therefore, the species assemblage of the tree community after logging could be fully predicted from the community before logging. In contrast, the species pools of the rain forests studied in Suriname, Borneo, and also Kolombongara contained softwood species, and disturbance enhanced recruitment of this functional type. Nevertheless, in both Suriname and Borneo the tree community before logging explained between 79% and 88% of the tree community after logging (Chapter 7), while in undisturbed forest ca. 95% of the tree community explained the community over the same time interval of ca. 20 years. This is also the case in Suriname (Figure 10.10).

These results **may** suggest that selective logging does not affect biodiversity much but this is **not** the case. Many tropical rain forest studies are statistically inadequate, simply because the systems are too species rich. About 90% of the species in a Bornean rain forest, for example, have fewer than 5 stems per hectare and amongst those the majority only have just one stem per hectare (cf. data from Suriname,

188

Figure 10.10). An elimination of ca. 10% of the rare species will not affect the statistical outcome much (but see Chapter 5). Additional logging damage, that can be considered random, brings about 10% stem damage (Borneo, Chapter 7). Due to the rarity of many species, it is highly likely that logging removed some species at the plot level, thus negatively affecting species richness, as was the case in Suriname (Chapter 5). This may not always observed in statistical tests, as may have been the case in Borneo, or fails to show up in larger-scale studies (such as Chapter 8), because rare species removal is random at plot level (Chapter 5) and few species will be removed from the regional species pool. Secondly, the design of the studies presented in Chapters 5-7 are in some way not representative of what happens in most logged forests. 'Normally' logged areas, especially in Borneo, are prone to additional disturbances after selective logging, such as illegal logging and forest fires (van Nieuwstadt 2002, van Nieuwstadt *et al.* 2001) that did not occur in the studies presented here. Such additional disturbances clearly have negative effects on species diversity and composition, but as such have hardly been investigated.

Usefulness of plant functional types in tropical rain forest studies
Many tropical rain forest studies have focussed on the pioneer-climax species dichotomy (e.g. Swaine & Whitmore 1988), and in many studies semantics to these definitions are used (see Chapter 1). This dichotomy is well understood and shows clear relation to perturbations in rain forests, i.e. recruitment of pioneers in logging gaps. In Chapters 5 to 8 seed mass, wood density, and potential tree height (Chapter 7 only) are used as *a priori* traits to group species. While seed mass determines shade tolerance (Chapter 2) and dispersal distance (ter Steege & Hammond 2001) and as such is considered to significantly affect the juvenile stage, wood density and potential tree height reflect traits that are involved with adult trees. Seed mass and wood density (the latter variable as proxy to adult growth rate) are positively correlated, although this relation is weak (ter Steege & Hammond 2001). Based on this, ter Steege *et al.* (2001, Chapter 8) derived from this relation three functional types; small seeded softwoods, which are interpreted as 'typical' short-lived pioneers with large growth rates and long seed dispersal distances, large seeded softwoods, which are interpreted as long-lived pioneers or 'emergent pioneers (Chapter 7) with high growth rates but short dispersal distances, and (large seeded) hardwoods, the typical climax species group. Apparently very few small seeded hardwoods exist. In Chapters 5-8 the relationship between wood density/growth rate and pioneer vs. climax species status is thoroughly explored and they need no further classification.

Assessment of long-term changes
Basically, two techniques are available to assess the long-term effects of logging on for example species composition in tropical rain forest. On one hand, long-term assessments can be obtained from Permanent Sample Plots (PSP), as in Chapters 3-7. This study design has the great advantage that population dynamics of stems and species, such as growth rates, and recruitment and mortality rates, can be evaluated on an individual basis. Moreover, when plots are laid out prior to logging or other disturbance, the effects upon the forest stand can be relatively easy be obtained. However, PSPs suffer from one major disadvantage. Due to their very nature, they

189

are very expensive to maintain and it will take many years before relevant results become available (see Sheil 1995b). Therefore, scientists often rely on space-for-time substitutions. In these cases, plots are laid out in forest patches that have had a (similar) disturbance event that differed in time. By putting the plots in a sequential order, changes in forest structures are studied. These so-called chronosequences have often been used in the study of forest re-growth after slash-and-burn agriculture (Uhl *et al.* 1981, Saldarriaga *et al.* 1988, Saldarriaga & Uhl 1991, Lugo 1992, Peña-Claros 2001, Kennard 2002). Chronosequence studies suffer from two major drawbacks. Firstly, in the chronosequence design it *must* be assumed that the forest stands within the different plots were equal before a disturbance event took place. This, however, is seldom the case. In rain forest with high ß-diversity and rareness of many tree species major differences are observed between replicate plots of mature forest. Indeed, Verburg & Slik (in prep.) showed that the species distributions differed significantly among replicate plots in virgin forest in a chronosequence. Secondly, in most chronosequence studies where plots were laid out in forest patches with a different disturbance history, the forest patch was replicated but *not* the temporal measurement. In other words, these studies suffered from pseudo-replication (see Lugo 1992). Although the latter shortcoming can be avoided, with some effort, by a proper statistical design, the former disadvantage cannot simply be prevented. Assigning species to different functional types prior to the analyses, as conducted in the previous Chapters, can partly reduce the effects of the 'initial site conditions' and may give better interpretable results (Verburg & Slik in prep.).

Conclusions

1.   Based on the various studies in this book we conclude that the IDH is a model that can be used to adequately describe the effects of disturbance on tree diversity and 'functional' composition (in terms of growth rates or wood density) of tropical forests. In most cases, the studies reported show that tree diversity changed in a manner that is expected by the theory and model constructed in Chapter 9 (Table 10.1).

2.   The diversity measures currently used to describe diversity associated with logging do not always capture all changes. This is partly caused by the high variation in tree diversity in natural 'undisturbed' forest, but also by the insensitivity of these measures to logging related changes in highly diverse systems. The tree composition could change considerably after logging, while information statistics, such as Fisher's alpha and Shannon index, detect no change. Fisher's alpha assumes a 'log-series' and does not take evenness into account. As a result Fisher's alpha should **not** be used to evaluate diversity changes in logged forests. Shannon's index does take evenness into account but is relatively insensitive to changes in abundance of the common species and strongly insensitive to change in the abundance of species in the tail of the distribution. Therefore, we advise to use these statistics cautiously when diversity in disturbed

Table 10.1   The effect of disturbance on the three parameters tested. Tree diversity, tree composition, functional group changes (Fseed if the effect is mainly caused by seed mass differences; Fwood is the effect mainly differential on the basis of wood density). + = a measured effect, - = no effect measured.

Chapter	Area	Tree diversity	Composition	Fseed	Fwood
2	Global			+	
3	Budongo, Uganda	+	+	+	+
4	Kolombongara, Solomon Isl.	+	+		+
5	Mapane, Suriname	+	-	-	-
6	Barama, Pibiri, Guyana	+	-	+	+
7	ITCI, Borneo	-	+/-		+
8	Bartica, Guyana	-	-	-	-

species-rich rain forests is evaluated. Currently there are **no** information statistics available that could describe adequately changes in diversity in species-rich rain forests caused by disturbances.

3.   Composition changes predictably from hardwood species to softer wooded species with disturbance. The intensity and frequency of disturbance determine how large these changes will be. Although changes are predictable they are generally small and forest composition before harvesting is often the best predictor of forest composition during recovery. This may suggest that the impact of logging on tree species diversity may be limited. There are two caveats to be made, though. One, logging in the experimental plots was carried out in a way that may not always describe the type of logging being practised outside the plots. Hence, we suggest that in most controlled studies the effects of actual logging practice are underestimated. Two, most experiments described in this book are based on single harvesting events. After multiple events, the forests are likely to change more towards highly disturbed communities, particularly if seed sources for the various pioneer species increase.

4.   Dispersal limitation may delay the effects of disturbance on forest composition as predicted by the Intermediate Disturbance Hypothesis. This is suggested to be of particular importance in previously undisturbed forest landscapes that are characterised by slow-growing heavy hardwoods.

5.   Functional groups are a good way to simplify both diversity and species composition in the complex forest system. Where changes in species composition are often difficult to detect due to scarceness of species and low predictability of species occurrence, grouping often leads to better more predictable patterns.

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