

Secondary forest succession
Processes affecting the regeneration
of Bolivian tree species

Marielos Peña-Claros



PROMAB Scientific Series 3

The Programa de Manejo de Bosques de la Amazonía Boliviana (PROMAB) is an international research, training and extension program advancing the sustainable exploitation and management of timber and non-timber forest resources in northern Bolivia. PROMAB is a joint effort of the Instituto para el Hombre, Agricultura y Ecología, the Universidad Técnica del Beni, Bolivia, and Utrecht University, the Netherlands.

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Secondary forest succession: Processes affecting the regeneration of Bolivian tree species

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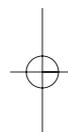
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Secondary forest succession
Processes affecting the regeneration of Bolivian tree species

Successie van secundair bos
Processen die de regeneratie van Boliviaanse boomsoorten
beïnvloeden
(met een samenvatting in het Nederlands)

Sucesión de bosques secundarios
Procesos que afectan la regeneración de especies arbóreas
bolivianas
(con un resumen en español)



Proefschrift

ter verkrijging van de graad
van doctor aan de Universiteit Utrecht
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in het openbaar te verdedigen
op maandag 2 april 2001
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Marielos Peña-Claros

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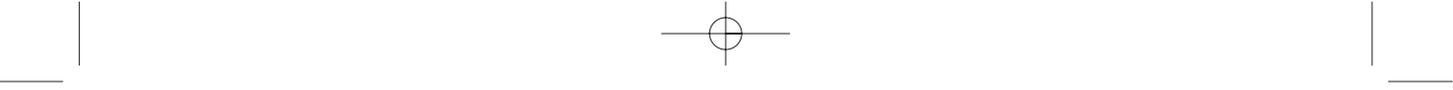


Promotor: Prof. Dr. M.J.A. Werger
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Verbonden aan de Faculteit Biologie
van de Universiteit Utrecht



Universiteit Utrecht

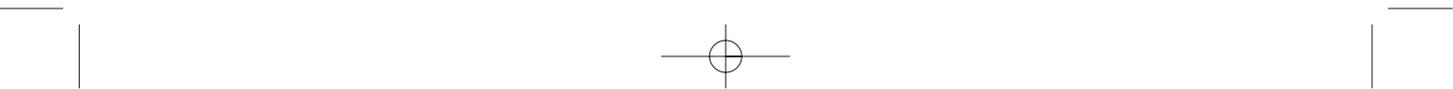
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To Lourens



*Caminante,
no hay camino,
se hace el camino al andar.
(Antonio Machado)*



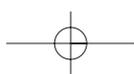
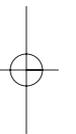
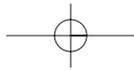
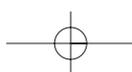
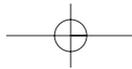


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Chapter 1

Introduction

Secondary Forests

Tropical rain forests experience different types of natural disturbances, ranging from highly localized disturbances that have a small impact to those that occur at large scale and have a great impact. The first type of disturbance includes small gaps created in the forest canopy by the fall of a tree branch, while the second type refers to large forested areas affected by hurricanes, floods, or fires. On an area based, disturbances are nowadays mainly caused by human activities. Human activities can result in an increase in light levels in the understory through the harvesting of palms leaves, in the creation of gaps through selective logging, or in the total destruction of the vegetation due to clear cutting of the forest for the creation of agricultural fields or pastures. In the latter cases, areas created are used until productivity decreases (Theile 1993 cited in Smith et al. in press), and then they are abandoned. At the same time they are recolonized by plants, so that a forest gradually develops. These forests are referred to as secondary forests (Brown & Lugo 1990), and are the focus of this study. Residual forests or logged forests are not included in this definition because they maintain the structure and floristic composition of mature forests.

In Latin America the area occupied by secondary forests has increased over the last decades. It has been estimated that in 1990 165 million ha were covered by secondary forests, while 871 million ha were covered by natural tropical forests (FAO 1996). A precise estimation of the total area is however still lacking. This uncertainty is due to the fact that different definitions of secondary forests are used, and that the current remote sensing technique is still not able to distinguish between mature and secondary forests (Sips et al. 1997).

Importance of secondary forests

In the past secondary forests were seen as “waste land”. This view has changed over the last decades, and secondary forests are now believed to play an important role in both ecological and economic terms (Brown & Lugo 1990, Smith et al. 1997). Secondary forests help to restore the productivity of the area and to reduce the weed populations after the agricultural use of the site. They are also the source of a variety of products, which vary from edible fruits to timber, and from medicinal plants to plants used for handicrafts. Additionally, they may serve as hunting ground because they support a higher animal production than mature forests (Brown & Lugo 1990, Smith et al. 1997). Secondary forests are usually located close to human settlements and are, therefore, particularly suitable for the extraction of forest products. As a consequence, it is believed that the appropriate management of secondary forests would reduce the pressure on primary forests (Brown & Lugo 1990, Sips et al. 1997, Sips 1997).

Several characteristics of secondary forests are likely to make their management more feasible than the management of primary forests. Secondary forests are characterized by high biomass production rates, high densities of economically important tree species, which have high growth rates and are more or less of similar age (Finegan 1992). In secondary forests of Costa Rica it was found that 50 % of the species present in the stands had commercial value, and that the majority of them belonged to the long-lived pioneer group of species (Müller & Solís 1997). Increase in the growth rates of the species can be achieved by applying silvicultural treatments, such as liberation thinning (Guariguata 1999), and opening of the canopy (Finegan 1992, Mesquita 2000). In the case that the species of interest are present at low densities or are absent, seeding during the crop phase or enrichment planting during the fallow period can be undertaken (Smith et al. in press).

The interest in managing secondary forests varies substantially from country to country and from region to region (Smith et al. in press). In countries like Costa Rica, where large areas have been deforested, secondary forests are likely to play a more important role as a source of forest products than in countries with lower deforestation rates (Finegan 1992). Additionally, several socioeconomic factors will influence the decision of farmers to manage their secondary forests. Among them is the existence of a market for lesser-known timber species or for non-timber forest products, accessibility to the

market and to land, land tenure, stage of the agricultural frontier, and governmental policies (Smith et al. in press). In agricultural frontiers of Nicaragua, Brazil and Peru it was found that the management of secondary forests for the harvesting of non-timber forest products was more likely to occur than for timber production. This was due to the fact that the former can be produced in shorter periods of time, which fits better with the agricultural cycle (Smith et al. in press).

Succession

Secondary forests are formed due to succession of the vegetation. Succession has been defined as “a progressive alteration in the structure and species composition of the vegetation” (Grime 1979). It is classified into primary and secondary succession. Primary succession refers to the establishment and development of plant communities in areas that have never been occupied by plants before, such as new sand dunes, sand deposited by meandering rivers, lava flows. Secondary succession takes place in areas where the natural vegetation (partially) was removed by a major disturbance (Ricklefs 1993) but that have maintained a well-developed soil and a seed bank. These factors enhance regrowth of the vegetation.

Succession has fascinated researchers for a long time, and several theories have been proposed to explain this phenomenon. These theories have varied from an approach in which the vegetation was seen as an entity, moving in a predictable way towards a climax (Clements 1916), to a more individualistic approach, in which species enter into the system by chance and are found together with other species in time simply because their environmental requirements overlap (Gleason 1926). The initial floristic composition hypothesis proposed by Egler (1954) is part of the latter group of theories, and it is central to the latest secondary forest succession model (Gómez-Pompa & Vásquez-Yanes 1981, Finegan 1984). It proposes that most of the species occurring in an area undergoing succession become established early in succession (in the first five years), and that the species dominate the site at different periods in time, depending on their life histories, growth rates and sizes at maturity. Species that dominate early in succession have been called early successional species, while species dominating in consecutive successional stages have been referred to as mid- or late successional species (Bazzaz 1979) (Fig. 1)

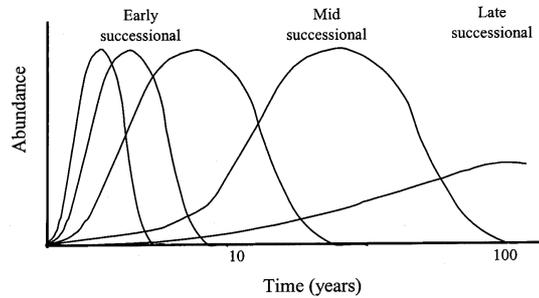


Fig. 1. Simplified representation of the initial floristic composition model of succession. Species are categorized according to when they dominate the canopy of secondary forests during a successional series.

Classification of species

Species can also be classified depending on the basis of their requirements for germination and establishment into pioneer (with subgroups based on adult size and longevity) and climax species (*sensu* Swaine & Whitmore 1988), or into light demanding and shade tolerant species. Pioneer species need high light levels for their germination and establishment, so that their recruitment is restricted to very early successional stages or large gaps (Uhl 1987, Richards 1996, Kyereh et al. 1999). Shade tolerant species, on the other hand, are able to establish and grow under low light conditions (e.g., Popma & Bongers 1988). Consequently, they are thought to regenerate during the successional stages that are dominated by pioneer and long-lived pioneer species. In between these two extremes, there is a large group of species that have intermediate characteristics (Budowski 1965, Denslow 1980). In this study, this group is referred to as long-lived pioneer tree species. Long-lived pioneer tree species are thought to establish also in early successional stages but they have a considerably longer life-span than pioneer tree species (Budowski 1965, Finegan 1996). Although it is not clear what features characterize the species in this group (Poorter 1998), it is expected that they will have a broader range of regeneration requirements than pioneer tree species do (Finegan 1996). In this study I included species differing in shade tolerance, with emphasis on long-lived pioneers to generate basic information about this species group.

Stages of secondary succession

After abandonment, areas used for agriculture or pasture are rapidly occupied by plants through secondary succession. As succession progresses

there is an increase in vegetation height, leaf area index, and basal area (Brown & Lugo 1990, and references therein), so that with time the forest structure resembles more that of a mature forests. These changes during succession modify the environmental conditions of the area. For example, light aboveground decreases as succession progresses (Saldarriaga 1994), while leaf litter thickness and organic matter increase (Brown & Lugo 1990). Along with the changes in forest structure, the number of plant species increases. Secondary forests of 80 years or (much) younger have a similar number of species as mature forest (Saldarriaga et al. 1988, Brown & Lugo 1990). A similar number of species does not mean, however, that the species composition is similar to the one of mature forests (Brown & Lugo 1990, Finegan 1997). In old secondary forests, canopies are dominated by long-lived pioneer tree species (Finegan 1996), while the canopies of mature forests contain mainly shade tolerant species.

In the neotropics the first 100 years of secondary succession can be described in three phases (Finegan 1996). In areas that are not degraded and are close to seed sources, the first phase of succession is short (< 3 years), and is dominated by herbs, shrubs and climbers, which establish quickly after disturbance and disappear under the shade of the emerging pioneer tree species. These pioneer tree species rapidly form a canopy and dominate the second phase of succession for 10 - 20 years depending on their lifespan. As they die off, they are replaced by long-lived pioneer tree species. The long-lived pioneer species are the dominant ones during the third phase of succession, which may last for 75 - 100 years again depending on the lifespan of the species. The more shade tolerant species are thought to colonize the site continuously during the last two phases of succession (Budowski 1965, Gomez-Pompa & Vázquez-Yanes 1981, Finegan 1996).

It is fairly well known when in the course of succession species with a given light requirement will dominate the canopy of secondary forests. It is not clear, however, when long-lived pioneer and shade tolerant species actually enter the system (Finegan 1996). The question is whether they are present since the start of the succession (Gómez-Pompa & Vázquez-Yanes 1981, Finegan 1984), or only when the pioneer species have formed a closed canopy. In this thesis I have looked into this question in two ways. The first approach was to relate the abundance of tree species found in secondary forests to the age of the forest. In this way, it was determined the patterns in which different groups of species appear in the successional series. The other method was to compare the germination and survival of tree species differing in shade

tolerance in secondary forests of various ages. In this manner, it was evaluated whether species are restricted to a given successional stage because of their requirements for establishment.

Mechanisms and processes

Several mechanisms have been proposed to explain the phenomenon of succession of natural vegetation. Facilitation was considered by Clements (1916) as the driving force of succession, while the theories of Gleason (1926) and Egler (1954) rely more on inhibition and tolerance. Succession has been seen as the outcome of these three mechanisms (Connell & Slatyer 1977); they were used to describe the effect of the presence of one species on the probability of establishment of another species. Currently, succession is considered as the result of a combination of processes and factors. Competition, differences in life history among species and environmental conditions of the area undergoing succession are thought to play an important role in determining the course of succession (Finegan 1984, Glitzenstein et al. 1986, Pickett et al. 1987, Bazzaz 1991). A hierarchical framework in which all these processes are considered has been developed (Pickett et al. 1987). In this framework, there is an emphasis on differences in the life cycles and the life histories among species. Three conditions for succession to occur are distinguished: 1) availability of open sites, 2) differential availability of species to colonize a site, and 3) differential performance of species at the site. Open sites can be colonized by any species. Species differ in their dispersal rates, and in their ability to establish in a given area. Therefore, the species that will finally be present in the site will be those of which propagules were available, and of which individuals managed to establish and grow under the environmental conditions of the site and were able to out-compete their neighbors.

Several processes and factors affect the different stages of the life cycle of a tree, as well as the transitions between life cycle stages (Fig. 2). In this study, I have studied the processes of seed removal, germination, survival and growth, and I have related them to environmental conditions, that change during succession (such as canopy openness, leaf litter thickness, liana density). By comparing the performance of tree species in secondary forests of various ages, I was able to evaluate whether the success of a species was limited by the same process in different successional stages.

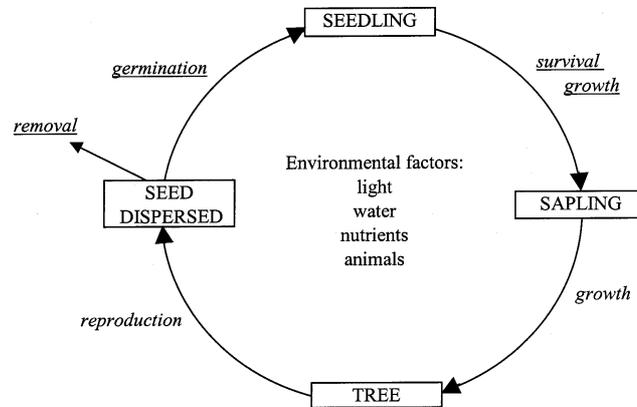


Fig. 2. Life cycle of a tree in an area undergoing succession. Seeds are dispersed to the area by wind or animals vectors, or are present in the seed bank. Different life stages are shown in boxes. Processes that affect the transitions between stages are in italic. Underlined processes are covered in this study. The environmental conditions of the area affect the different life cycle stages and the different processes; therefore, they are located in this diagram at the center of the life cycle.

Objectives of this study

The aims of the present study are:

1. to study which processes determine the presence and abundance of tree species in secondary forests, and how they vary with successional stage,
2. to provide information on the survival and growth requirements of long-lived pioneer tree species,
3. to evaluate a management option for secondary forests.

Outline of the thesis

The line of this thesis moves gradually from more descriptive (Chapter 2) to more experimental studies (Chapters 3 - 5), and from more basic (Chapter 2 - 5) to more applied questions (Chapter 6). First, secondary forests are described in terms of changes in forest structure and species composition through time. Then, various processes that influence the regeneration of tree species in secondary forests are addressed. The processes presented in this thesis are related to the earlier stages of the life cycle of a tree: seed removal, seed germination, and seedling survival and growth. All these studies were done in secondary forests of various ages, and included 6 - 9 tree species differing in shade tolerance. The growth rates and architectural differences among larger

individuals (≥ 1 cm DBH) have also been studied; the results of this study will be presented elsewhere. Finally, one management option for secondary forests is discussed in depth. The different Chapters are briefly introduced below:

Chapter 2 describes the changes through time that occur in the forest structure and species composition in the successional series developing on agricultural fields undergoing secondary succession. Secondary forests ranging in age from 2 to 40 years are compared among each other and with mature forests. Changes in the diversity, dominance and composition between the understory, subcanopy and canopy layers are discussed.

Chapter 3 deals with the importance of seed removal for the regeneration of tree species in areas undergoing succession. Seeds of nine tree species were artificially dispersed in secondary forests of 2, 10 and 20 years and in mature forests. The seed removal was monitored over a seven-week period, and the seed removal rate was related to several stand characteristics.

Chapter 4 moves a step further in the life cycle of a tree. It studies the germination, and early seedling survival and growth of six light demanding species to determine whether the regeneration of light demanding species is restricted to young successional stages or not. Seeds were put to germinate in agricultural fields, in secondary forests of 2, 10, and 20 years and in mature forests. Germination, survival and growth were monitored periodically for 13 - 19 months, and were related to canopy openness and thickness of the litter layer.

Chapter 5 studies the survival, growth and biomass allocation of established seedlings of nine tree species differing in shade tolerance. The questions were whether survival of seedlings was restricted to a given successional stage, and whether seedling growth varied with successional stage. The seedlings were planted in secondary forests of 1, 10, and 20 years, and their survival and growth were followed during two years, after which biomass growth was measured.

Chapter 6 deals with enrichment planting as a management tool for increasing the density of desired tree species in secondary forests. Seedlings of *Bertholletia excelsa* (the Brazil nut tree), one of the most important economic species of the region, were planted in lines of different widths cut in a secondary forest. The survival and height growth of the seedlings were evaluated during four years, and were related to light availability.

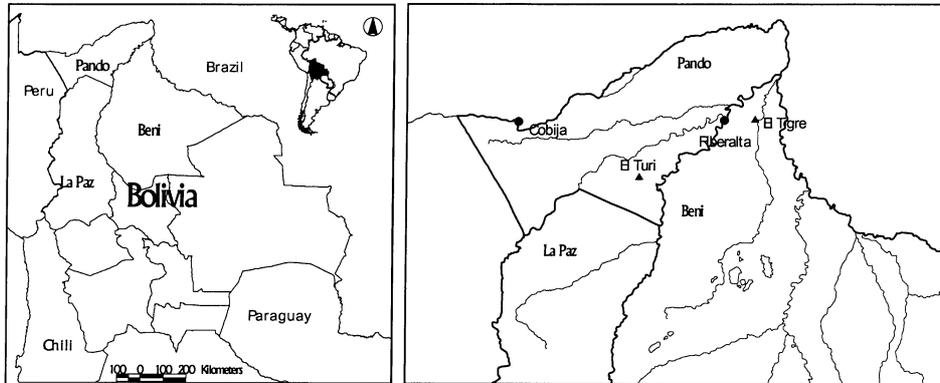


Fig. 3 Map of Bolivia, indicating department boundaries (left map), and of the Bolivian Amazon (right map). Main towns are indicated with dots, and areas where this study was carried out with triangles.

Chapter 7 summarizes and connects the different studies carried out, and provides some management guidelines for secondary forests.

Regional context

This study was carried out in the Bolivian Amazon, which comprises the Pando department, the Vaca Díez province (Beni department) and the northern part of the Iturrealde province (La Paz department) (Fig. 3). The Bolivian Amazon occupies an area of 104.560 km² (INE 1992). The region is characterized by a mean annual temperature of 26° C, and a mean rainfall of 1830 mm in Cobija (Pando) and 1780 mm in Riberalta. There is a marked dry season from May to September, in which less than 100 mm precipitation per month falls (Beekma et al. 1996).

The landscape is undulating with altitudes that vary from 80 to 280 m.a.s.l. The area is crossed by meandering white water rivers such as Madre de Dios and Beni, and by several black water rivers such as Manuripi and Yata (Beekma et al. 1996). The upland soils are mainly xanthic ferrasols in the west, and haplic ferrasols in the east (DHV 1993). The region is covered by forest, although some very small areas of savannas can be found. The forests can be divided into upland forests (terra-firme forests) and (periodically) flooded forests. The upland forests have a canopy of about 25 – 35 m height, with some emergent trees reaching a height of 45 m. They have been classified as evergreen tropical rain forest (Hueck & Seibert 1972), semi-evergreen tropical forests (DHV 1993), and mainly evergreen ombrophyllous closed

lowland forest (Mapa Forestal de Bolivia 1995). In this thesis the more general term lowland moist tropical forests will be used.

About 94 % of the area is still covered by largely intact forests (data from 1990), 3 % is under forest fallow and another 3 % has been cleared for agricultural land and pasture (Beekma et al. 1996). The deforestation rate of the region is low (about 0.15 % year⁻¹ in the period 1986 - 1992, DHV 1993), although local variation exists (Stoian 2000a). For example, the province of Nicolás Suárez (Pando) experienced a deforestation rate of 1.52 % year⁻¹ had in the period of 1986 - 1993 mainly due to the expansion of cattle ranching (Keijzer 1993). In 1992 there were in the Pando department about 15000 ha being used for agriculture (INE 1992).

Socioeconomic aspects

There are approximately 131.000 people living in the region, the majority of them (62%) in the three major towns (Riberalta, Cobija and Guayaramerin) (INE 1992). The main economic activities have been traditionally related to the extraction of forest products. In the 19th and 20th centuries the region has seen several boom and bust cycles of different forest products, such as Peruvian bark (quinine), rubber, and lately palm heart (Stoian 2000b). At this moment the economy of the region largely depends on the collection of Brazil nuts (from trees of *Bertholletia excelsa*) and timber extraction (such as *Swietenia macrophylla*, *Cedrela odorata*, *Amburana caerensis*) (Zuidema 2000). In 1998 these products generated, respectively, 29.3 million US\$ year⁻¹ and 16 million US\$ year⁻¹ (A. Bojanic, personal communication).

Rural communities have different strategies for obtaining their cash income, depending among other factors on the distance to major towns, amount of land available, and access to the market (Stoian in prep.). Moreover, within the community there is also some specialization, so that there are households that depend mainly on agriculture, extractive activities (Brazil nut collection, palm heart harvesting, hunting), or wage labor (Kaam 1999, Stoian in prep.). Subsistence agriculture, however, is almost always practiced, regardless of the source of cash income of the household (Stoian & Henkemans 2000).

The agricultural cycle

The most common type of agriculture performed in the Bolivian Amazon is slash-and-burn agriculture. For this type of land use, mature or secondary forests are cut to create a new agricultural field. The decision regarding what type of forest to cut depends on several socioeconomic factors, such as accessibility to land, distance to town and to household, family health, and

labor available in the household for the work (Stoian in prep., Henkemans in prep.). In communities close to the main towns, secondary forests are cut to create agricultural fields, while in communities further away mature forest is cut in about 70 % of the cases (Stoian in prep.). The crop to be planted also influences the decision regarding what forest type to cut: rice has higher yields in mature forest, while maize does better in secondary forest (Stoian in prep., Henkemans in prep.). The average size of the agricultural fields is 1.6 ha (range 1 - 2). Four crops are commonly cultivated: rice, manioc, plantain/ banana, and maize. After 1 - 2 or rarely 3 years the areas are allowed to fallow, and new areas for agriculture are selected. The fallow length varies but is generally short (it rarely exceeds five to six years, and it can be as short as 2 - 3 years) (Stoian in prep.).

Secondary forests

Farmers consider secondary forests as important because they are part of the shifting cultivation cycle (Arredondo 1998). These forests are also used to obtain several products. From the 56 species from secondary forests used by farmers of two communities in the region, half of them had more than one use. Species provided medicines (55 %), timber (38 %), materials for construction (27 %) and food items (18 %) (Arredondo 1998). Farmers of another community reported to use about 160 different species of trees, shrubs, herb and lianas (Henkemans in prep.). These species occurred in mature forests, secondary forests, agricultural fields and homegardens. Only 10 % of the species used were found exclusively in secondary forests. Apparently farmers prefer to extract forest products from primary forests rather than from secondary forests because in primary forests harvested plants have reached maturity (Henkemans in prep.).

In the Bolivian Amazon, secondary forests are not intensively used, probably because mature forests are not a scarce resource. There are farmers, however, that manage their fallows to increase the densities of economically interesting species, such as *Inga edulis*, *Bertholletia excelsa*, *Cedrela* spp. Several organizations are currently carrying out enrichment planting activities in young secondary forests. These activities are means to increase the cash income of local people, and to assure that people will have access to forest products close to their communities (IPHAE 1998). Nevertheless, there is a lack of information regarding different techniques that can be used for the management of secondary forests, as well as basic information regarding the processes that affect the regeneration of economically interesting tree species in secondary forests.

The Reserve El Tigre

The majority of the field work for this study was carried out in and nearby the forest reserve El Tigre (Fig. 3). El Tigre is the research and training area of the Programa de Manejo de Bosques de la Amazonía Boliviana (PROMAB), and is located 45 km to the east of the town of Riberalta, and 5 km to the north of the Riberalta - Guayaramerin road (10° 59'S, 65° 43'W). It has an area of 830 ha, and its vegetation consists of a mosaic of mature forest, a stunted, liana-rich forest ("chaparral"), some patches of secondary forests (3-20 years old) and an *Imperata* sp. dominated grassland (Poorter et al. 2000).

The forest canopy has a height of 25 - 35 m, with some emergent trees reaching a height of 45 m. The average canopy openness at the forest floor is 3.6 % (Arets 1998). The density of trees > 10 cm diameter at breast height (1.30 m) is 544 ha⁻¹, with an average basal area of 29.7 m² ha⁻¹. The number of tree and palm species is at least 81 ha⁻¹. The most common species are *Euterpe precatoria*, *Tetragastris altissima*, *Pseudolmedia laevis*, *Sclerobium* sp. 1 and *Brosimum lactescens*. Common emergent tree species are *Bertholletia excelsa*, *Couratari guianensis*, *Cedrelinga cataeniformis* and *Cariniana micrantha*. Palms are a conspicuous element of the forest (Poorter et al. 2000). Many canopy species are deciduous during the dry season, and thickness of the leaf litter varies accordingly (2.1 and 4.5 leaves per sample point in the wet and dry season, respectively) (Chapter 4).

Institutional context

This dissertation forms part of the Programa Manejo de Bosques de la Amazonía Boliviana (PROMAB), a research, extension and education programme of the Instituto para el Hombre, Agricultura y Ecología (IPHAE, Riberalta, Bolivia), the Carrera de Ingeniería Forestal of the Universidad Técnica del Beni (CIF/UTB, Riberalta, Bolivia) and Utrecht University (The Netherlands). Starting in 1995, PROMAB activities have included forest-ecological and socio-economic research, extension, technical assistance and training of the region's forest users with emphasis on farmers and rural communities, training of forestry students and the dissemination of knowledge and information to forest users and governmental bodies responsible for the implementation of the forestry law. The programme's main goal is to improve the living conditions of forest dependent people in Northern Bolivia through the sustainable use and conservation of their forests and forest resources.

This dissertation is the third publication in the PROMAB Scientific Series. The contents of existing and expected publications in this series are briefly outlined below:

1. Seedling growth of Bolivian rain forest tree species in relation to light and water availability (Poorter 1998). The influence of light and water availability on seedling growth is evaluated for a number of economically important rain forest tree species. Knowledge of the environmental requirements of tree species provides the ecological basis for the selection of species for, and design of, silvicultural treatments, forest enrichment activities, tree plantations and agroforestry systems.
2. Demography of exploited tree species in the Bolivian Amazon (Zuidema 2000). Three tree species yielding non-timber products are investigated: the “castaña” tree (*Bertholletia excelsa*) of which Brazil nuts are collected; the “asai” palm (*Euterpe precatoria*) of which palm heart is harvested; and the “jatata” palm (*Geonoma deversa*) of which leaves are used for thatching. The demography and the impact of exploitation of these species are analyzed. Models for population dynamics - matrix models - are used to evaluate the sustainability of different exploitation regimes.
3. Secondary forests succession: Processes affecting the regeneration of Bolivian tree species (this publication).
4. A forest based economic development?: The economic-environmental interactions in the Bolivian Amazon (Alan Bojanic, expected early 2001). This study evaluates and explores the tension between economic development and environmental impacts of commercial forest use in the northern Bolivian Amazon region. To obtain larger economic growth rates there is a need to intensify the extraction of forest products and hence to increase the degradation of natural resources. The dissertation studies and explains the economic and social implications of such interactions.
5. Livelihood strategies and perceptions of forest dwelling people in the northern Bolivian Amazon (Ariëne Henkemans, expected mid 2001). This study explores the potentials for sustainable forest livelihoods, based on the interest of former rubber tapping families and other forest residents living in two different forest settlement types. This study aims to improve our understanding of the overall importance of the forest within their past and present livelihoods, and within their household strategies for future development.

Additionally, the publication of the following study carried out by the University of Freiburg and CIFOR, in collaboration with PROMAB, is available:

Variations and dynamics of extractive economies: the rural-urban nexus of non-timber forest use in the Bolivian Amazon (Stoian 2000). The importance of marketable NTFP is determined at the levels of rural and peri-urban households as well as the regional economy. The study of the marketing chain of Brazil nuts and palm hearts elucidates the distribution of benefits accruing from their processing and sale. A better understanding of the temporal and spatial dynamics underlying the regional NTFP production systems can help develop more appropriate interventions aiming to promote the NTFP sector.

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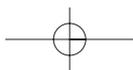
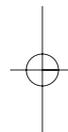
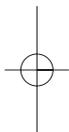
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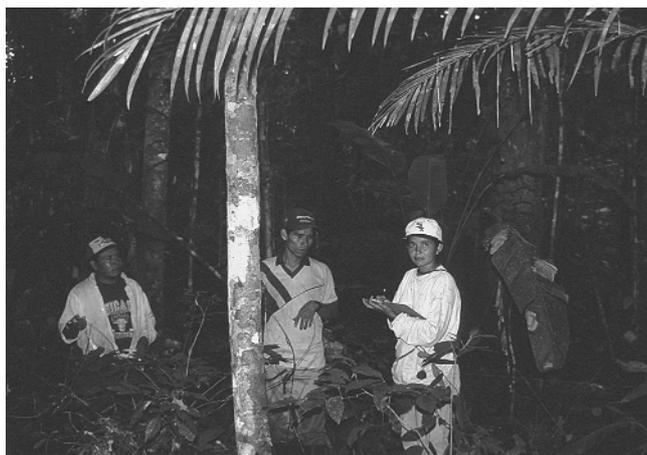
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Introduction • 25





Chapter 2

Changes in forest structure and species composition during secondary forest succession in the Bolivian Amazon

Abstract

Changes in forest structure and species dominance throughout secondary succession were studied in two sites in the Bolivian Amazon, using a chronosequence. Secondary forests ranging in age from 2 to 40 years, as well as mature forests were included, making a total of 14 sites. Fifty plants per vegetation layer (understory, subcanopy and canopy) were sampled using a transect of variable area. Total stem density, basal area, and species diversity were calculated at the stand level, while species dominance was calculated for each layer separately. A correspondence analysis was performed, and the relationship between relative abundance of the species and stand age was modeled using a set of hierarchical models.

Height of the canopy and basal area increased with stand age, indicating that secondary forests attain a forest structure similar to mature forests relatively rapidly. A total of 250 species were recorded, of which less than 50 % made up 86.5 % of the sampled individuals. Species diversity increased with stand age, while species dominance varied with the layer considered, the canopy being the one with the highest values of species dominance. The results of the correspondence analysis indicated that species composition varied with stand age, layer of the forest and site. These results indicated that the species composition of mature forests is recovered at different rates in the different forest layers, the slowest being the canopy layer. Species showed different patterns in abundance over time, supporting the current model of succession.

Introduction

In the neotropics areas covered by tropical rain forest are cleared, cultivated for 1 - 3 years, and afterwards abandoned. These areas are rapidly recolonized by plants through secondary succession. As succession progresses, light availability at the forest floor decreases (Saldarriaga 1994, Chapter 4) due to light interception by the regrowing vegetation. This change in light availability influences the establishment of tree species, and therefore, determines the sequence in which species appear in an area undergoing succession (e.g. Finegan 1984).

The first one hundred years of neotropical secondary forest succession has been described in terms of three phases, each of them characterized by a different set of species. The first phase of succession is short, and is dominated by herbs, shrubs and climbers, which establish soon after disturbance and disappear under the shade of the emerging pioneer tree species. The second phase of succession is dominated by pioneer tree species. These species are able to rapidly develop a closed canopy and dominate the second phase for 10 - 20 years, depending on the lifespans of the species. As they die-off, they are replaced by long-lived pioneer tree species. These species are hypothesized to have a wider range of requirements for their establishment than pioneers, with some species establishing only in young successional stages (Guariguata 2000) and others being able to establish in later stages as well (Chapter 4). The long-lived pioneer species are the dominant ones during the third phase of succession, which may last for 75 - 100 years depending on the lifespans of the species. The more shade tolerant species are thought to colonize the site continuously during the last two phases of succession (Budowski 1965, Gomez-Pompa & Vázquez-Yanes 1981, Finegan 1996, 1997). Although it is fairly well known when different groups of species dominate the canopy during succession, data are lacking regarding when these species actually enter into the system. In this study I relate the abundance of common species found in secondary forests in the Bolivian Amazon to the age of the forest to determine the patterns in which species appeared during succession. This was done using a hierarchical set of models developed to describe the relationship between species abundance/presence and (a)biotic factors (Huisman et al. 1993).

To understand successional pathways and predict future changes in canopy composition, one may analyze the species composition of different forest structural layers. Four layers are typically found in tropical rain forests, while

in secondary forests only three layers are present (canopy, subcanopy and understory). The species composition of the understory layer represents the species pool from which eventually species are recruited to the canopy layer. Therefore, the species composition of the understory may be a good predictor of the future species composition of the canopy (Oldeman 1990). Species composition patterns observed during succession are commonly based on changes observed in the canopy layer of secondary forests (e.g., Finegan 1996, Richards 1996). Secondary forests that are 5 - 18 years old have their canopies dominated by a small number of pioneer species; consequently, the species diversity is expected to increase as the pioneer tree species begin to die-off, and other species reach the canopy. In the understory layer a lower dominance of species is expected because recruitment of other species than pioneers occurs already in early successional stages (Uhl et al. 1981, Swaine & Hall 1983, Purata et al. 1986, Uhl 1987). There was a higher species diversity among saplings in secondary forests of Costa Rica (16 - 18 years old, Guariguata et al. 1997) and French Guyana (19 years old, Toriola et al. 1998) than among canopy trees. In this study I looked at species dominance in different structural layers in secondary forests ranging in age from two to 40 years.

In this study I sampled the vegetation of secondary forests differing in age, as well as the vegetation of mature forests, in two distant sites of northern Bolivia to evaluate whether they show similar patterns of succession. The objectives of the study were 1) to describe changes in forest structure and species diversity in secondary forests over time; 2) to evaluate the species composition of different size classes and of secondary forests differing in age; and finally, 3) to determine the relation between the abundance of common species and age of secondary forests to establish when different species groups enter during succession.

Methodology

The study was carried out in two sites in the Bolivian Amazon. One of the sites was the forest reserve El Tigre and the neighboring community area of Campo Central (11° 59'S, 65° 43'W), hereafter referred to as Reserve El Tigre. This site is located about 45 km east of the town of Riberalta, and receives an annual rainfall of 1780 mm with a dry season from May to September (Beekma et al. 1996). The other site was the community area El Turi (11° 45'S, 67° 20'W), which is located at the border of the river Manupare, about 150 km southwest of Riberalta. There are no climatological

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data for this area but it is unlikely that a large difference with Reserve El Tigre exists (Cobija located 300 km northwest of Riberalta has an annual rainfall of 1833 mm, Beekma et al. 1996). The vegetation of both sites consists mainly of lowland tropical moist forest, with patches of secondary forests differing in successional stage and agricultural fields. Secondary forest stands are the result of slash and burn agriculture and fallow.

In each site, secondary forests of different ages were selected, so that a chronosequence was obtained. The chronosequence included young secondary regrowth (2 years after abandonment) to old secondary forests (approximately 40 years after abandonment). Estimates of the age of the secondary forests were obtained from long term residents of the two communities. During the interviews dates provided by the informants were checked with known historical events. In total twelve secondary forests (six per site) and two stands of mature forests (without signs of recent human disturbance) were included in the study. All secondary forest stands had been used for agriculture only once for 2 - 3 years, and their mean size was 2.2 ha (range 1 - 7 ha).

In the center of each stand a transect of variable area was established, about 10 - 20 m inside the edge of the stand. The transect of variable area is a technique specifically developed for rapid assessment of the species composition of plant communities (R. Foster, personal communication). The basis of this method is to sample a fixed number of individuals instead of a fixed area. In this study we sampled in each stand a total of 150 individuals divided into three size categories: saplings (1 m height and up to 1 cm diameter at breast height, DBH), juveniles (1 to 5 cm DBH in stands < 5 years old, 1 - 10 cm in the stands \geq 5 years old) and trees (\geq 5 cm DBH for stands < 5 years old, \geq 10 cm DBH in the stands \geq 5 years old). The size limit between the juvenile and tree categories varies among stands because trees \geq 10 cm DBH are very uncommon in secondary forests < 5 years old.

The length of the transect of variable area is determined by the size category with the lowest density (R. Foster, personal communication). Therefore, I searched first for trees within a distance of 5 m at each side of the central transect line (i.e. transect width of 10 m). To assure that all size categories were represented along the whole transect, the transect was divided into sections of ten trees each (R. Foster, personal communication). The first ten trees were searched, identified by a local guide or given a morphospecies name, and measured in diameter and height. For the morphospecies a sample was collected for later identification. The distance from the tenth tree to the starting point of the transect was measured with a Walktax® Distance Measurer

(Forestry Suppliers Inc., USA), and the tenth tree was marked with red plastic. From the marked point onwards I searched for the next ten individuals, and repeated this procedure until 50 individuals had been sampled. Then while walking back to the beginning of the transect, I sampled the other two size classes. In each transect section only 10 saplings and juveniles were sampled within 1 and 2.5 m at each side of the central transect line, respectively (i.e. transect width of 2 and 5 m). The lengths of the transect sections needed to sample individuals of the smaller size categories were carefully measured. In the case of the saplings, the transect section was not always large enough to include 10 individuals, therefore, the sample sizes for this size class is not necessarily equal to 50 individuals. For total area sampled per stand and per size category, and total number of individuals sampled see Table 1. Hereafter, the sapling, juvenile and tree size categories are referred to as understory, subcanopy and canopy layers.

Vouchers and samples collected during the establishment of the transects were dried. Vouchers and samples were identified using various guides (Sleumer 1987, Gentry 1993, Killeen et al. 1993, Anonymous 1997, R. Foster & Wachter 1997, Reynel & Penington 1997, Vasquez 1997) and by comparing samples with identified material at the Herbario Nacional (La Paz, Bolivia) and at the Field Museum of Natural History (Chicago, USA). Identified

Table 1. Age, total number of individuals sampled, and the sample area per structural layer are given. See text for definition of size classes. Age is given in years since the start of the fallow. MF = mature forest.

Site	Age (y)	Sample Size	Area sampled (m ²)		
			Understory	Subcanopy	Canopy
El Turi	2 y	140	47	108	350
	4 y	145	106	176	700
	14 y	150	80	78	1260
	25 y	150	136	123	1370
	28 y	136	107	112	750
	40 y	137	119	200	645
	MF	149	140	117	1082
Reserve El Tigre	3 y ¹	100	76	80	
	5 y	134	98	193	559
	8 y ²	100		210	1594
	10 y	140	143	153	610
	11 y	150	221	185	730
	25 y	150	59	121	1160
	MF	146	93	82	510

¹ only two categories were included in this inventory (understory: 1 m height to up 1 cm dbh, and subcanopy \geq 1 cm DBH). The latter category was later on divided into two (1 - 5 cm DBH, and \geq 5 cm DBH).

² the understory layer was not included in this inventory.

vouchers and samples have been deposited at the herbarium of the Universidad Técnica del Beni. Vouchers that could not be identified were given a morphospecies name.

Analysis

The following stand characteristics were calculated: density (number of individuals >1 m height ha^{-1}), basal area (including all individuals ≥ 1 cm DBH, in $\text{m}^2 \text{ha}^{-1}$), total number of species, and the Shannon diversity index ($H' = -\sum p_i (\ln p_i)$, where p_i is the proportion of individuals found in the i^{th} species). The Shannon diversity index was calculated pooling all individuals sampled in a given stand because estimates of this diversity index are more reliable when they are based on more than 100 stems in the case of areas with high diversity (Condit et al. 1998). All these characteristics were correlated with stand age using a Spearman's rank correlation analysis.

To quantify species dominance throughout succession, I followed the recommendations of Krebs (1989) and plotted the \ln relative abundance of species to the species rank order. This was done for each combination of structural layer and stand age. Then a linear regression analysis was used to estimate the slope of the curve, which corresponds to the α of the logarithmic series (Krebs 1989). Steeper slopes correspond to higher species dominance. The slopes obtained were correlated with stand age using a Spearman's correlation analysis.

To study the influence of stand age on the species composition of secondary forests I performed a correspondence analysis using CANOCO (ter Braak & Šmilauer 1998). The 92 species with ≥ 5 sampled individuals were included in the analysis. The abundance of each species was calculated for each site (Reserve El Tigre and El Turi), per stand age (14), and per structural layers (3): understory, subcanopy and canopy, providing a total of 84 samples. The abundance data were square root transformed prior to analysis. The first two axis of the CA were correlated with site, stand age and structural layer.

Secondary forests differing in age vary in species composition. This variation has been related to changes in the environmental conditions as succession proceeds, and differences among species in terms of their requirements and life histories (Finegan 1984, Bazzaz 1991, Finegan 1997). Age of the stand may, therefore, explain the abundance of species. To describe the relationship between species relative abundance and stand age, I used a hierarchical set of five models that are ranked according to increasing mathematical complexity (Table 2) (Huisman et al. 1993). The species relative abundance was calculated by stand age, pooling all the structural layers. All

Table 2. Description of the five models used to relate species relative abundance to stand age (based on Huisman et al. 1993). x = stand age; y = relative abundance; M = maximum value that can be attained ($M=90$ in this study); a, b, c, d = parameters to be estimated.

Model	Description	Formula
I	no significant trend in space or time	$y = M \times (1/(1+e^a))$
II	increasing or decreasing trend where the maximum is equal to the upper bound M	$y = M \times (1/(1+e^{a+bx}))$
III	increasing or decreasing trend where the maximum is below the upper bound M	$y = M \times (1/(1+e^{a+bx})) \times (1/(1+e^c))$
IV	symmetrical response curve	$y = M \times (1/(1+e^{a+bx})) \times (1/(1+e^{c-bx}))$
V	skewed response response curve	$y = M \times (1/(1+e^{a+bx})) \times (1/(1+e^{c+dx}))$

the five response curve models were fitted to each of the species. The simplest possible model explaining the observed pattern was chosen. A more complex model was selected only if it explained a significantly higher amount of variation than a simpler one (Huisman et al. 1993). Only those 53 species that had ≥ 10 individuals in total were included in the analysis. When > 70 % of the individuals of a given species were found only in one of the two sites (i.e., Reserve El Tigre and El Turi), the analysis was done including only the seven stands of that particular site. Species abundance data were arcsine transformed to increase homoscedasticity (Huisman et al. 1993). The age of the mature forest was estimated to be 150 years. No significant differences among r^2 and type of model selected were found when the mature forests was considered to be 100 or 200 years old (data not shown).

Results

Forest structure and species composition

As stand age increased the mean height and the maximum height of the canopy layer increased (Fig. 1 A-B). The same pattern was observed for total basal area (for individuals ≥ 1 cm DBH, Fig. 1 C), which increased from 12.3 $m^2 ha^{-1}$ in the 2 year old regrowth to 36.3 $m^2 ha^{-1}$ in the 40 year old secondary forest. Neither total stem density (Fig. 1 D) nor the stem density of the different layers correlated with stand age.

A total of 250 species were recorded. More than half of the species was represented by 5 or less individuals. The 92 species included in the correspondence analysis represented 86.5 % of the sampled individuals. Some abundant species (with ≥ 30 individuals in total) were present in high numbers

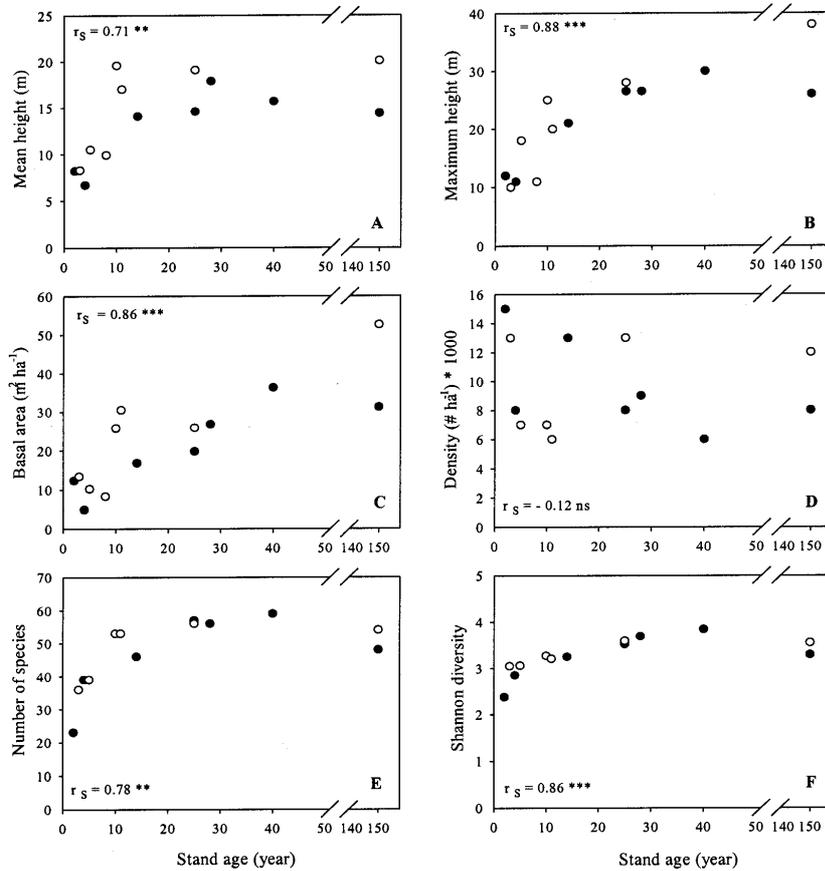


Fig. 1. Structural characteristics and species diversity of secondary forests and mature forests in northern Bolivia. A. Mean height of canopy (≥ 5 cm DBH in stands < 5 years, ≥ 10 cm DBH in stands ≥ 5 years); B. Maximum height of canopy; C. Basal area of all individuals with ≥ 1 cm DBH; D. Density of all individuals ≥ 1 m height; E. Total number of species; and F. Shannon Diversity index. Open circles are from the Reserve El Tigre, filled circles from El Turi. r_s refers to the Spearman's correlation coefficient. *: $P \leq 0.05$, ** = $P \leq 0.01$, *: $P \leq 0.001$.**

in both sites (such as *Cecropia sciadophylla*, *Rinoreaocarpus ulei* and *Bellucia pentamera*), while others were present only in one of the sites (*Senna sylvestris* and *Geonoma deversa* only in El Turi, and *Sclerolobium* sp. 1 only in Reserve El Tigre). Species such as *Ochroma pyramidale*, *Piper* sp. 5, *Geissospermum sericeum* and *Jacaranda copaia* were present in both sites but their abundance differed strongly between sites.

Species diversity and species dominance

Both total species number and the Shannon diversity index increased with stand age (Fig. 1 E - F). In the 2 year old regrowth there were in total 23 species while in the 40 year old secondary forest there were 59. The relation

Table 3. Species dominance (slopes of rank abundance curves) per layer and age. High species dominance is indicated by a steeper negative slope. ET = El Turi, RET = Reserve El Tigre. Stand age is in years since the beginning of the fallow.

Stand age	Understory	Subcanopy	Canopy
2	-0.28	-0.17	-0.32
3	-0.06	-0.25	-0.18
4	-0.08	-0.08	-0.28
5	-0.10	-0.10	-0.27
8 ¹		-0.12	-0.48
10	-0.06	-0.04	-0.55
11	-0.06	-0.07	-0.48
14	-0.09	-0.06	-0.26
25 ET	-0.06	-0.07	-0.10
25 RET	-0.09	-0.05	-0.10
28	-0.05	-0.06	-0.10
40	-0.06	-0.03	-0.07
150 ET	-0.13	-0.08	-0.06
150 RET	-0.04	-0.08	-0.05

¹ the understory layer was not included in this inventory.

between species dominance and stand age varied among size categories (Table 3). The species dominance in the understory was not related to stand age (Spearman's correlation, $r = 0.45$, $p = 0.127$, $n = 13$), while in the case of the subcanopy and canopy the slope of the rank abundance curve became less steep with age (Spearman's correlation, for subcanopy: $r = 0.60$, $p = 0.025$, $n = 14$; for canopy: $r = 0.76$, $p = 0.002$, $n = 14$). The variation in species dominance in the canopy layer was much higher than in the two other layers (Table 3). Dominance was stronger in secondary forests of 8 - 14 years (Table 3), due to high densities of *Cecropia sciadophylla*, *Ochroma pyramidale*, and/or *Stryphnodendron purpureum*.

The variation explained by the first two axes of the CA was only 18.1 % (axis 1 = 10.7 %). The first axis was negatively correlated with stand age (correlation coefficient = -0.66), and positively correlated with the canopy layer (correlation coefficient = 0.55; Fig. 2). This indicates that the main variable explaining differences in species composition is stand age. All canopy samples of secondary forests were located in the right half of the first axis, indicating that the canopies of secondary forests had a different species composition than the canopies of mature forests. In the case of the secondary forests, these were dominated by early successional species. In contrast, the understory and subcanopy layers had species compositions more similar to the ones of mature forests. The second axis was correlated with site (correlation coefficient = 0.81), indicating that the two sites differed in species composition (Fig. 2). The sample scores along the first axis showed that species composition

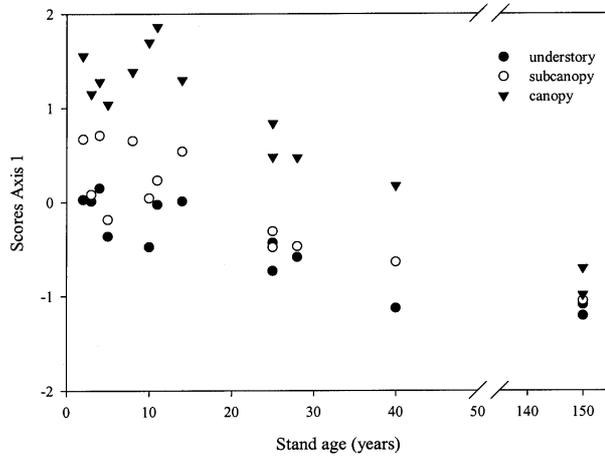


Fig. 3. Variation of the sample scores along the first axis through time.

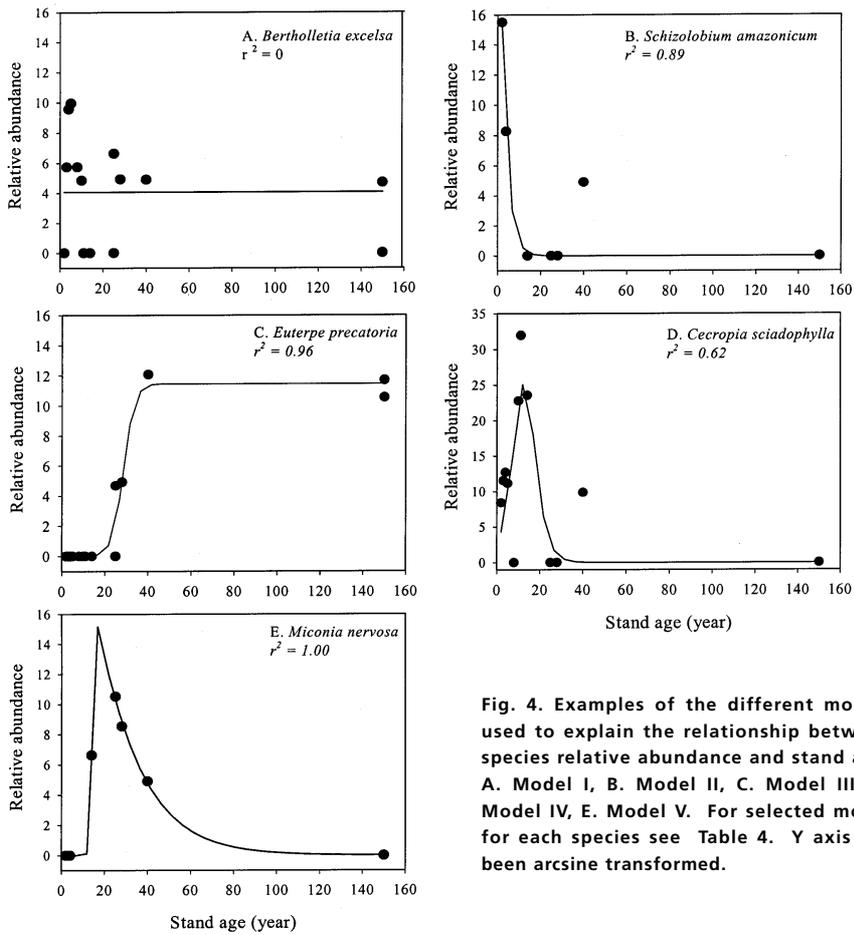


Fig. 4. Examples of the different models used to explain the relationship between species relative abundance and stand age. A. Model I, B. Model II, C. Model III, D. Model IV, E. Model V. For selected model for each species see Table 4. Y axis has been arcsine transformed.

Table 4.

Fits to stand age of the relative abundance of species sampled in secondary forest differing in age and in mature forest in Bolivian Amazon. Species listed had ≥ 10 individuals, and represented 73 % of the total individuals sampled. Family name, the selected model and the r^2 of the model are given. Site refers to the site where species were mostly found (both = equally in both sites, ET = El Turi,

Scientific name	Family	Site	Model	r ²
<i>Apeiba tibourbou</i>	Tiliaceae	both	I	0
<i>Aspidosperma</i> cf. <i>tambopatense</i>	Apocynaceae	both	I	0
<i>Bellucia pentamera</i>	Melastomataceae	both	I	0
<i>Bertholletia excelsa</i>	Lecythidaceae	both	I	0
<i>Calycophyllum megistocaulum</i>	Rubiaceae	both	I	0
<i>Capirona decorticans</i>	Rubiaceae	RET	I	0
<i>Casearia arborea</i>	Flacourtiaceae	ET	I	0
<i>Casearia</i> cf. <i>pitumba</i>	Flacourtiaceae	both	I	0
<i>Cordia</i> cf. <i>ucayaliensis</i>	Boraginaceae	RET	I	0
<i>Galipea</i> cf. <i>jasminiflora</i>	Rutaceae	ET	I	0
<i>Inga thibuadiana</i>	Leguminosae	ET	I	0
<i>Lindackeria paludosa</i>	Flacourtiaceae	RET	I	0
<i>Piper</i> sp. 5	Piperaceae	RET	I	0
<i>Rinoreaocarpus ulei</i>	Violaceae	both	I	0
<i>Tachigali vasquezii</i>	Leguminosae	both	I	0
<i>Xylosma tessmannii</i>	Flacourtiaceae	RET	I	0
palo cepe	Monimaceae	ET	I	0
Saguinto	Myrtaceae	both	I	0
<i>Cecropia ficifolia</i>	Moraceae	both	II -	0.47
<i>Cedrela odorata</i>	Meliaceae	RET	II -	1.00
<i>Geissospermum sericeum</i>	Apocynaceae	ET	II -	0.74
<i>Schizolobium amazonicum</i>	Leguminosae	ET	II -	0.89
<i>Senna silvestris</i>	Leguminosae	ET	II -	0.95
<i>Brosimum alicastrum</i>	Moraceae	both	II +	1.00
<i>Geonoma deversa</i>	Arecaceae	ET	II +	0.89
<i>Tetragastris altissima</i>	Burseraceae	both	II +	0.58

ficifolia, *Schizolobium amazonicum*, and *Senna silvestris* declined with stand age (Table 4). Model III fitted best the response of 13 species (Table 4, Fig. 4); all of them increasing in abundance with stand age (e.g., *Euterpe precatória*, *Pseudolmedia laevis*, *Iryanthera juruensis*). Fourteen species showed an optimum in abundance through time. Species such as *Alchornea triplinervia*, *Cecropia sciadophylla*, *Jacaranda copaia* had their abundance best explained by model IV (Table 4, Fig. 4), while model V best explained the abundance of *Miconia nervosa* and ‘peraquina negra’ (Annonaceae) (Table 4, Fig. 4).

Discussion

Forest structure

From young to older successional stages there was an increase in mean and maximum canopy height (Fig. 1 A - B). Stem density did not correlate to stand age, and there was a large variation in density among stands of similar

continued Table 4

RET = Reserve El Tigre). Species are ordered according to Model type. For more information regarding models see text. Signs following model type refer to an increase (+) or a decrease (-) in relative abundance with time.

Scientific name	Family	Site	Model	r ²
<i>cf. Ixora</i>	Rubiaceae	both	III +	0.44
<i>Hirtella racemosa</i>	Chrysobalanaceae	both	III +	1.00
<i>Inga cf. capitata</i>	Leguminosae	both	III +	0.34
<i>Casearia javitensis</i>	Flacourtiaceae	ET	III +	0.74
<i>Eschweilera coriacea</i>	Lecythidaceae	both	III +	0.63
<i>Euterpe precatoria</i>	Arecaceae	both	III +	0.96
<i>Iryanthera juruensis</i>	Myristicaceae	both	III +	0.92
<i>Iryanthera sp.</i>	Myristicaceae	RET	III +	0.89
<i>Pseudolmedia laevis</i>	Moraceae	both	III +	0.68
<i>Pseudolmedia rigida</i>	Moraceae	RET	III +	1.00
<i>Sclerolobium sp. 1</i>	Leguminosae	RET	III +	0.77
<i>Quiina poeppigiana</i>	Quiinaceae	ET	III +	1.00
<i>pata de michi</i>	Moraceae	both	III +	0.63
<i>Alchornea triplinervia</i>	Euphorbiaceae	both	IV	0.44
<i>Cecropia sciadophylla</i>	Moraceae	both	IV	0.62
<i>Cecropia sp. 3</i>	Moraceae	ET	IV	1.00
<i>Dictyoloma peruviana</i>	Rutaceae	RET	IV	1.00
<i>Inga cf. sertulifera</i>	Leguminosae	ET	IV	0.90
<i>Jacaranda copaia</i>	Bignoniaceae	ET	IV	0.87
<i>Ochroma pyramidale</i>	Bombacaceae	RET	IV	0.99
<i>Rollinia sp.</i>	Annonaceae	RET	IV	1.00
<i>Piper obliquum</i>	Piperaceae	both	IV	0.60
<i>Sorocea cf. trophoides</i>	Moraceae	both	IV	0.59
<i>Stryphnodendron purpureum</i>	Leguminosae	RET	IV	0.92
<i>Trema micrantha</i>	Ulmaceae	ET	IV	1.00
<i>Miconia nervosa</i>	Melastomataceae	ET	V	1.00
<i>peraquina negra</i>	Annonaceae	ET	V	0.97

age (Fig. 1 D). This was also found by Saldarriaga et al. (1988). The understory layer was the densest one, as has been found before (e.g., Guariguata et al. 1997, Okimori & Matius 2000). The basal area increased with stand age, so that secondary forests ≥ 25 years old had attained already on average 70% of the basal area found in mature forests. This trend has also been found in other chronosequences (e.g. Saldarriaga et al. 1988, Tucker et al. 1998, Gomide et al. 1998, Denslow & Guzman 2000), and it indicates that secondary forests attain a structure similar to mature forests relatively rapidly. The time needed for a secondary forest to recover to pre-shifting cultivation values is likely to depend on several factors such as climate, soil fertility, land use history, size of the area, and distance to propagule sources (Uhl et al. 1988, Brown & Lugo 1990, Guevara et al. 1992, Guariguata et al. 1997, Steininger 2000).

Species diversity and species dominance

Species number and the Shannon diversity index increased with time and obtained an optimum after 20–25 years (Fig. 1 E – F). The lower species

diversity found in younger successional stages is related to the high dominance of a few pioneer tree species (such as *Cecropia sciadophylla*, *Dyctyoloma peruviana*, *Ochroma pyramidale*, *Piper* sp. 5, *Senna silvestris*, *Schizolobium amazonicum*, *Stryphnodendron purpureum* and *Trema micrantha*), which is a common feature of secondary forests in general (see Richards 1996 for summary). The abundance of these species decreases with stand age as the pioneer species die-off, and consequently, there is an increase in species diversity as the stand gets older (Saldarriaga et al. 1988). The lower diversity of mature forests is probably due to the fact that at least some of the long-lived pioneer species have died off.

The three plant size categories differed in their species dominance (Table 3). The species dominance in the canopy decreased with age, with the highest value being found in secondary forests 8 - 14 years old. Secondary forests of that age had their canopies dominated by 1 - 3 species, that made up to 94 % of the individuals ≥ 10 cm DBH. The species dominance in the subcanopy layer was high only in the 2 - 3 years old regrowth. It was not as pronounced as in the canopy layer, and it diminished rapidly with time. Probably this is due to the fact that the pioneer tree species that established early in succession can grow very fast to the next size category, or have a very short life cycle. Finally, at the understory layer the species dominance was not correlated with age, suggesting that at this layer there is a more diverse species composition from very early in succession onwards. A similar result was found in East Kalimantan, species number increased throughout succession in the tree (≥ 10 cm DBH) and pole (2 - 10 cm DBH) categories but not in the seedling (< 1.5 m height) and sapling (> 1.5 m height - 2 cm DBH) categories (Okimori & Matius 2000). The lower dominance values found for the understory and subcanopy layers are in accordance with the current model of tropical succession (Gomez-Pompa & Vazquez-Yanes 1981, Finegan 1996): Species from different light requirements are recruited at early successional stages (< 5 years, Uhl et al. 1981, Uhl 1987); long-lived pioneer species are able to grow and survive under the canopy of the faster growing pioneer tree species (Chapter 5); and shade tolerant species are recruited continuously throughout succession (Swaine & Hall 1983). This results in a larger species diversity and lower dominance in the lower layers compared to higher ones (Saldarriaga et al. 1988, Toriola et al. 1998).

The results of the correspondence analysis indicated that age was an important determinant of the species composition of secondary forests. The species composition of secondary forests became more similar to the composition of mature forests as the secondary forest got older (Fig. 2). The rate at which this happened depended, however, on the layer considered. The

species composition of the understory and subcanopy layers approached the species composition of mature forests more rapidly than the canopy layer did (Fig. 3). This was caused by the fact that long-lived pioneer and shade tolerant species recruit continuously to the lower layers already from early successional stages onwards (e.g., Uhl 1987); apparently their establishment being facilitated by the shade of the pioneer trees (cf. Connell & Slatyer 1977). The species composition of the canopy changed at a lower rate because this layer was dominated for a long period of time by pioneer and long-lived pioneer tree species. Pioneer tree species establish very early in succession (Uhl 1981, Uhl 1987). They have very high growth rates (e.g., Swaine & Hall 1983, Bazzaz 1991), and are able to suppress other species very rapidly (Rose 2000), which enables them to dominate the canopy and temporarily inhibit the pace of succession (cf. Connell & Slatyer 1977). Pioneer tree species have a short lifespan, and die-off after 10 - 20 years. Subsequently, long-lived pioneer species are able to recruit to the canopy. Because of the long lifespan (50 - 100 years) of the long-lived pioneer species (Guariguata et al. 1997, Terborgh et al. 1997), shade tolerant species will become dominant only much later in succession (Finegan 1996). Consequently, species composition of the forest canopy shows a much lower rate of recovery than forest structure does (e.g. Guariguata et al. 1997), and it may take more than 100 years to be similar to the composition of mature forests.

The second axis of the correspondence analysis had a high correlation with site, indicating that El Turi and the Reserve El Tigre differed considerably in species composition (Fig. 2). The dissimilarity found can be partly attributed to the geographic distance between sites and to the fact that stands of the Reserve El Tigre tended to be closer to other secondary forests whereas stands in El Turi were dispersed in a matrix of mature forest (M. Peña - Claros, personal observation). The fact that site was only related to the second axis of the correspondence analysis indicated that successional patterns were similar, even for forests that are located far apart as has been reported before (Finegan 1996, Richards 1996).

Species abundance

Species showed different patterns in abundance over time (Table 4, Fig. 4). These results are also in accordance with the current model of tropical succession, which states that differences among species in terms of light requirements, growth rates and lifespans play an important role in determining the course of succession (Gomez-Pompa & Vazquez-Yanez 1981, Finegan 1984, Bazzaz 1991). Pioneer tree species need high light for germination (Swaine & Whitmore 1988), although they are not able to germinate in areas

exposed to full sunlight (Uhl 1987, Kyereh et al. 1999, Chapter 4). Sites next to trunks, underneath slash, and under the shade of trees surrounding the agricultural fields seem to be preferred for germination of even very early successional tree species such as *Trema micrantha* or *Cecropia ficifolia* (M. Peña - Claros, personal observation). Pioneer tree species showed an optimum in abundance very early in succession (2 - 4 years, *Schizolobium amazonicum*, *Cecropia ficifolia* and *Dyctiloma peruviana*), or when a closed canopy already existed (8 - 12 years, *Cecropia sciadophylla* and *Ochroma pyramidale*). Long-lived pioneer tree species were present also from early successional stages onwards. They showed a peak in abundance later on in succession, replacing pioneer tree species in the canopy of secondary forests and remaining there for a long period of time (*Jacaranda copaia*, *Inga* cf. *sertulifera*). Finally, shade tolerant species varied on the moment in which they entered into an area undergoing succession, some species were present already in the 2 - 3 year old secondary forests while others appeared only in secondary forests > 20 years old. The abundance of shade tolerant species increased with time (e.g., *Euterpe precatoria*, *Eschweilera coriacea*, *Pseudolmedia laevis*). Other species did not show any relationship with stand age (e.g., *Bertholletia excelsa*, *Capirona decorticans*), suggesting that these species are able to get established at different light conditions and that their recruitment was restricted by other factors such as a nearby seed sources and seed predation. Interestingly, among the 18 species that showed this type of response were seven species that had been previously classified as intermediate or as long-lived pioneer species based on experimental data, species distribution, and field observations (van Ulft 1998, Poorter 1999, Poorter in press, N. Divico personal communication). This supports the idea that the establishment of long-lived pioneer species is not necessarily restricted to very early successional stages and that they are able to survive in the shaded understory of secondary forests (Finegan 1996, Chapter 4 and 5). Saplings of these species are likely to benefit from the increase in light level caused by the death of pioneer trees forming the canopy (cf. Mesquita 2000).

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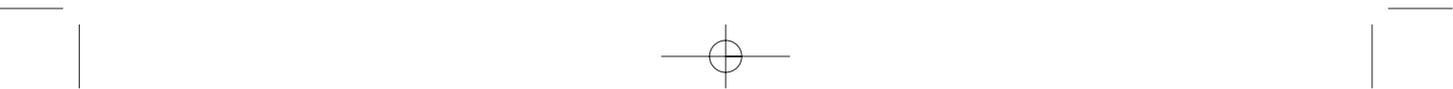
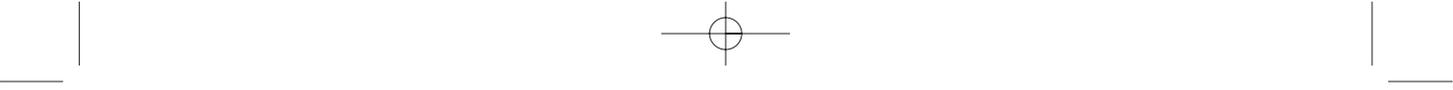
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Chapter 3

The effect of successional stage on seed removal of tropical rainforest tree species

with Henneleen de Boo

Abstract

Seed removal was evaluated at the macro and microhabitat in areas differing in successional stage in the Bolivian Amazon. The successional stages consisted of secondary forests of 2, 10 and 20 years and primary forest. Seeds of nine tree species were artificially dispersed into the different successional stages and the number of seeds removed was evaluated during seven weeks. Several stand characteristics were evaluated at the sites where seeds were dispersed. Seed removal at the end of the experiment varied from 50 to 100 % depending on the species, and from 74 to 90 % depending on successional stage. In general, the removal rate decreased with an increase in age of successional stage. Different microhabitat characteristics explained the removal rate of four species but did not explain the pattern in seed removal rate observed. The higher seed removal rate in young secondary forests seems to be related to the density of seed removal agents, which apparently both in the case of ants and rodents decreases with forest age. The results support the idea that post-dispersal seed removal plays an important role in the establishment of trees in abandoned agricultural areas.

Introduction

Tree establishment in areas used for slash-and-burn agriculture is highly dependent on seed dispersal (Uhl 1987), due to the fact that the soil seed bank has been largely reduced during the burning and farming of the area (Uhl et al. 1981, Uhl 1987). Consequently, post-dispersal seed removal may play an important role in determining the tree species composition and tree density of an area undergoing succession (De Steven 1991, Hammond 1995, Meiners & Stiles 1997, Myster & Pickett 1993, Uhl et al. 1988, Whelan et al. 1991). The tree species composition can be influenced by seed removal rates if the seed removal agents have a preference for seeds of certain species over others. Moreover, seed removal agents will finally determine how many seeds of the seeds dispersed into an area are actually available for germination (Uhl 1987). Although several studies have studied seed removal rates in closed canopy forest in comparison to gaps, forest edges or pastures (e.g. Dirzo & Dominguez 1986, Holl & Lulow 1997, Schupp 1988, Schupp & Frost 1989, Sanchez-Cordero & Martínez-Gallardo 1998), very few studies have assessed seed removal rates in secondary forests differing in successional stage (but see Hammond 1995, Uhl 1987).

As succession progresses in an area, several changes occur in terms of forest structure, stem density and plant species composition (Finegan 1984 and 1996, Uhl 1987). Because the animal community responds to these changes in the vegetation (Emmons 1982), the composition and abundance of seed removal agents will also vary according to successional stage. Rodents and ants have been reported as the most important seed removal agents in areas undergoing succession (e.g. Mittelbach & Gross 1984, Whelan et al. 1991, Nepstad et al. 1996, Sanchez-Cordero & Martínez-Gallardo 1998). Rodents seem to prefer habitats with more cover because cover provides them shelter from predators. Predation risk for rodents has been shown to vary as a function of several environmental and stand characteristics, such as stand density, type of groundcover (Bowers & Dooley 1993, Brown 1988, Dueser & Shugart 1978, Gill & Marks 1991), and amount of canopy cover (Cassini & Galante 1992, Lagos et al. 1995). There is little information available on the habitat preference of ants, although higher ant densities have been reported for younger successional stages than for older ones (e. g. Vasconcelos & Cherret 1995).

Seed removal agents have been shown to prefer seeds of certain species to all the seeds available in the community, limiting in that way the

establishment of the preferred species (cf. Meiners & Stiles 1997). This preference may be related to seed characteristics such as seed size, nutrient content, local abundance, and handling time (Meiners & Stiles 1997). Some authors have found a negative relationship between seed removal rate and seed size (Nepstad et al. 1996, Osunkoya 1994, Uhl 1987), which implies that large seeded species would have a higher chance of being present in secondary forests than small seeded species. Others studies have found, however, no relationship between removal rate and seed size (Holl & Lulow 1997, Meiners & Stiles 1997, Myster & Pickett 1993).

The objective of this study was to assess the rate of seed removal in forests differing in successional stage, ranging from very young forests (2 year old) to very old ones (mature forest). Our hypotheses were 1) seed removal rate will decrease with age of the successional stage; 2) given that stand characteristics vary with successional stage, the seed removal rate observed will depend on stand characteristics. We expect that removal rate will be higher in microhabitats with low litter thickness, high stem and liana density, and high plant cover than in microhabitats with opposite characteristics; and 3) small seeded species will have a higher seed removal rate than large seeded species (see Fig. 1 for schematic model of the hypotheses). In this paper, we used the term “seed removal” instead of “seed predation” because we did not assess the final fate of the seed after being removed from the seed depots (predated or dispersed to another site). The probability, however, that most seeds removed will be finally predated is high. Only about 6.4 % of the seeds removed by ants are deposited intact on refuse piles (Levey & Byrne 1993), and seeds cached by rodents have also a high probability of being predated later on (Price & Jenkins 1986).

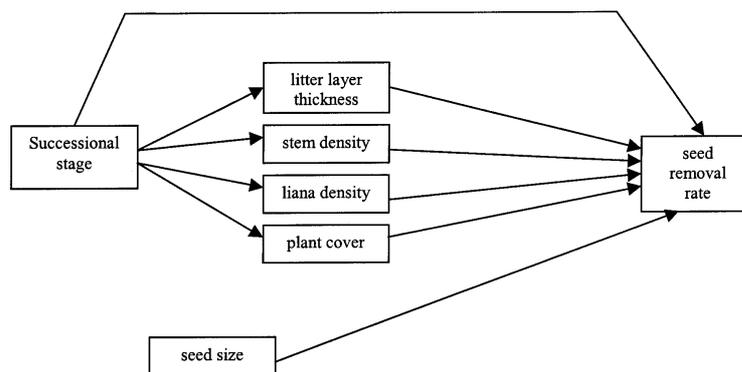


Fig. 1. Model showing the different factors that may affect the removal rate of seeds in successional stages differing in age.

Methodology

Research site and study species

The study was carried out in the Bolivian Amazon in the forest reserve El Tigre (11°59'S, 65°43'W) and in nearby areas owned by local farmers (< 5 km from El Tigre). El Tigre is the research and training center of the Programa de Manejo de Bosques de la Amazonía Boliviana (PROMAB), and is located 45 km east of the town of Riberalta. The area receives an annual rainfall of 1780 mm with a dry season (< 100 mm/month) from May to September (Beekma et al. 1996). The vegetation of El Tigre and surrounding areas consist mainly of lowland tropical moist forest, with some patches of secondary forests differing in successional stage and agricultural fields. Secondary forest patches are the result of slash-and-burn agriculture and fallow, and often have an area of 1 ha.

Nine tree species were included in the experiment. All of them occur naturally in the area, and differ in their life history strategy, seed weight, dispersal mode and removal agent (Table 1). Henceforth, species will be referred to only by generic name.

Experimental design

The study was carried out in 4 successional stages: secondary forests of 2, 10 and 20 years and mature forests. Two sites were selected per successional stage. Site selection was based on similarities in vegetation structure between sites of the same successional stage. Site age was determined by interviewing the owners of the sites and long term residents of the area.

In each site, five transects were established in the center of the secondary forest, each transect at least 10 m apart from each other. Along the transects, nine seed depots were laid out, each seed depot spaced 8 m apart. The seed depots had a triangular shape (20 cm per side) and were made of green colored nylon mosquito netting with a mesh of 1 mm. To prevent seeds from being washed away from the seed depot during heavy rains, the edges of the triangle (3 cm) were folded upright. Seed depots were fixed to the ground at each corner by cramps made of 12 cm long pieces of iron wire. Species were randomly allocated to the seed depots of a given transect, on the condition that seeds of the same species were not next to each other in two adjacent transects. In a trial experiment, seed depots did not have a positive or negative influence on the foraging behaviour of the animals. Seeds placed directly on the forest floor showed the same removal rate as seeds placed in the seed depots (data not shown).

Table 1. List of tree species used in the experiment. Family name, life history strategy, seed dry weight (mean \pm SD), dispersal mode, and removal agent are given. P = Pioneer, LLP = Long-lived Pioneer, C = Climax.

Scientific name	Family	Strategy	Dry weight (g) ¹	Dispersal mode	Removal agent ⁴
<i>Bertholletia excelsa</i>	Lecythidaceae	LLP	6.508 \pm 1.476	zoochorous	rodents
<i>Buchenavia punctata</i>	Combretaceae	C	1.712 \pm 0.197	zoochorous	rodents
<i>Cecropia sciadophylla</i>	Moraceae	P	0.0014	zoochorous	ants
<i>Cedrela odorata</i>	Meliaceae	LLP	0.036 \pm 0.013 ²	anemochorous	ants
<i>Enterolobium contortisiliquum</i>	Mimosaceae	C	4.060 \pm 0.498	zoochorous	rodents
<i>Inga</i> spp.	Mimosaceae	LLP	³	zoochorous	rodents + ants
<i>Jacaranda copaia</i>	Bignoniaceae	LLP	0.005 \pm 0.003 ²	anemochorous	ants
<i>Schizolobium amazonicum</i>	Caesalpinaceae	P	0.921 \pm 0.148	zoochorous	rodents + ants
<i>Virola sebifera</i>	Myristicaceae	C	1.410 \pm 0.191	zoochorous	rodents

¹ Seeds were dried in an oven for two days (80 °C) before weighing.

² Seed without wings.

³ Data not available due to restriction in number of seeds.

⁴ Based on literature and personal observations.

Seeds from all species except *Cedrela* and *Schizolobium* were collected in the same area during their natural dispersal period. Fruit flesh was removed in all cases but *Inga*, which seeds were offered with a very thin layer of fruit pulp. Seeds of *Cedrela* and *Schizolobium* were obtained from the Centro de Investigación Agrícola Tropical, Santa Cruz, Bolivia. Only undamaged seeds were used in the experiment. Twelve seeds of a given species were evenly distributed in the corresponding seed depot. In the case of *Cecropia*, 50 seeds were placed per depot because of its small seed size. Depots were checked after 2, 7, 14, 21, 35 and 49 days of seed placement. At each evaluation day the number of seeds inside and within 10 cm of the seed depot were counted as seeds still present. Seeds eaten in the depot were considered as removed seeds. Litter falling into the seed depots was removed periodically. Walking paths constructed between two transects (three per site) were used during the check up; thus, reducing damage to the surrounding vegetation.

Several stand characteristics were evaluated in a 1 m radius around half of the seed depots at each site, providing a total of 179 depots. The stem density was estimated by counting all plants > 10 cm in height. In the case of multi-stemmed plants each stem was counted individually. The liana density was evaluated separately from stem density by counting all the lianas rooted in the circle or passing through it. Lianas are an important life form in early successional stages and give a more dense structure to the forest. In addition, the area of the circle covered by herbs and other plants < 30 cm in height (referred hereafter as plant cover, in %) and the area covered by dead *Cecropia*

leaves were estimated (in %). The area covered by dead *Cecropia* leaves (referred hereafter as *Cecropia* litter cover) was evaluated because *Cecropia* litter is a conspicuous feature in the understory of successional stages dominated by this species. The leaf litter thickness was evaluated in eight different places of the circle by determining the amount of leaf layers intersected by a knife point. Stem and liana densities were calculated as number of individuals per m². The leaf litter thickness of a given circle was estimated by calculating the median value of the eight points measured per circle.

Data analysis

Differences in stem density among successional stages were analysed with a one-way ANOVA. The Student-Newman-Keuls test was used as post-hoc test. Data on liana density, plant cover, *Cecropia* litter cover, and leaf litter thickness data had unequal variances, so for these variables Kruskal Wallis tests were used with successional stage as factor. To find differences between pairs of successional stages, the Kruskal Wallis test was performed several times. The p-value was corrected accordingly using the Bonferroni correction (p-value: 0.0083).

Seed removal data were analysed with a survival analysis (Fox 1993). The effect of successional stage on seed removal rate was determined for all species together and for each species using Cox regression. Simple contrasts were carried out to find significant differences among the different successional stages. There were six possible contrasts; consequently, the p-value was corrected using a Bonferroni correction (p-value for contrasts is 0.0083).

To evaluate the effect of microhabitat on seed removal, the seed removal rate was calculated per seed depot. For each individual seed depot, the removal rate was estimated by regressing the ln-number of removed seeds ($x + 1$) against time. The removal rates obtained per seed depot were then regressed against the corresponding stand characteristics, using a forward stepwise multiple regression analysis. This analysis was also done per species and overall species.

The effect of seed size on removal rate was analysed at two levels. First, the species specific removal rate averaged over all successional stages was regressed on seed weight. Second, we regressed the specific removal rates of a given successional stage against seed weight. Removal rate was calculated per seed depot as indicated in the above paragraph.

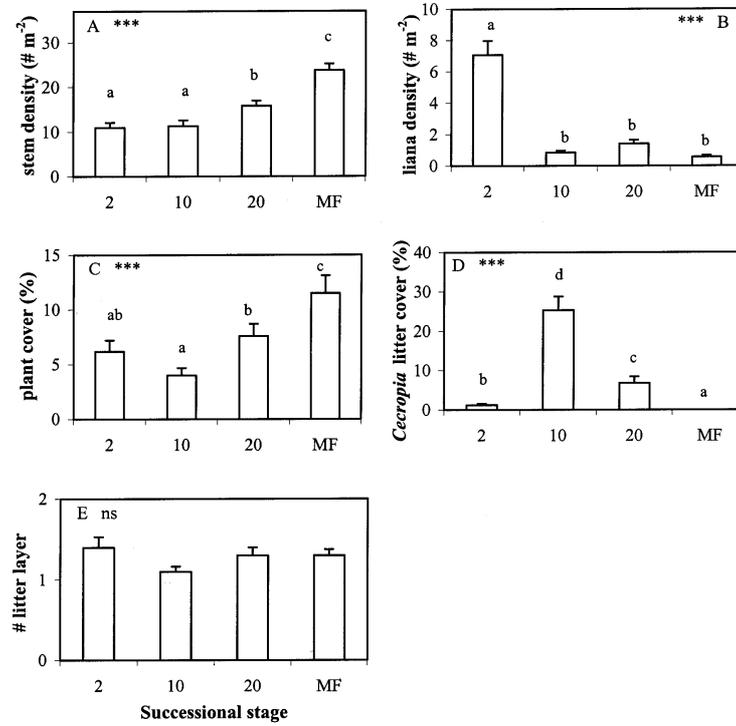


Fig. 2. Stand characteristics per successional stage. Successional stages with different letters are significantly different at p level 0.05 in the case of stem density, and at p level 0.0083 in the case of all other stand characteristics. Data given are mean \pm SE. ns = non-significant, *** P < 0.001.

Results

All stand characteristics but leaf litter thickness varied with successional stage (Fig. 2). Stem density was lower in the 2 and 10 year old secondary forests and higher in the mature forest (Fig. 2A), while liana density showed the opposite trend (Fig. 2B). The plant cover was lowest in the 10 year old secondary forest and highest in the mature forests (Fig. 2C). The *Cecropia* litter cover was significantly higher in the 10 year old secondary forests, and no dead *Cecropia* leaves were found in the mature forest (Fig. 2D).

After seven weeks the seed removal varied from 48.3 % for *Buchenavia* to 99.8 % for *Cedrela*, and from 74 % for the mature forest to 90 % for the 2 year old secondary forest (Table 2). For all species but *Bertholletia* the successional stage had an effect on seed removal rate (Table 2, Fig. 3). Most species experienced the highest removal rate in the 2 year old secondary forests, while *Cecropia* did in the 10 year old secondary forest. The lowest removal rate was found in the mature forest for *Buchenavia*, *Cecropia*, *Enterolobium*, *Inga*, *Jacaranda*, and *Schizolobium*. *Cedrela* had the lowest

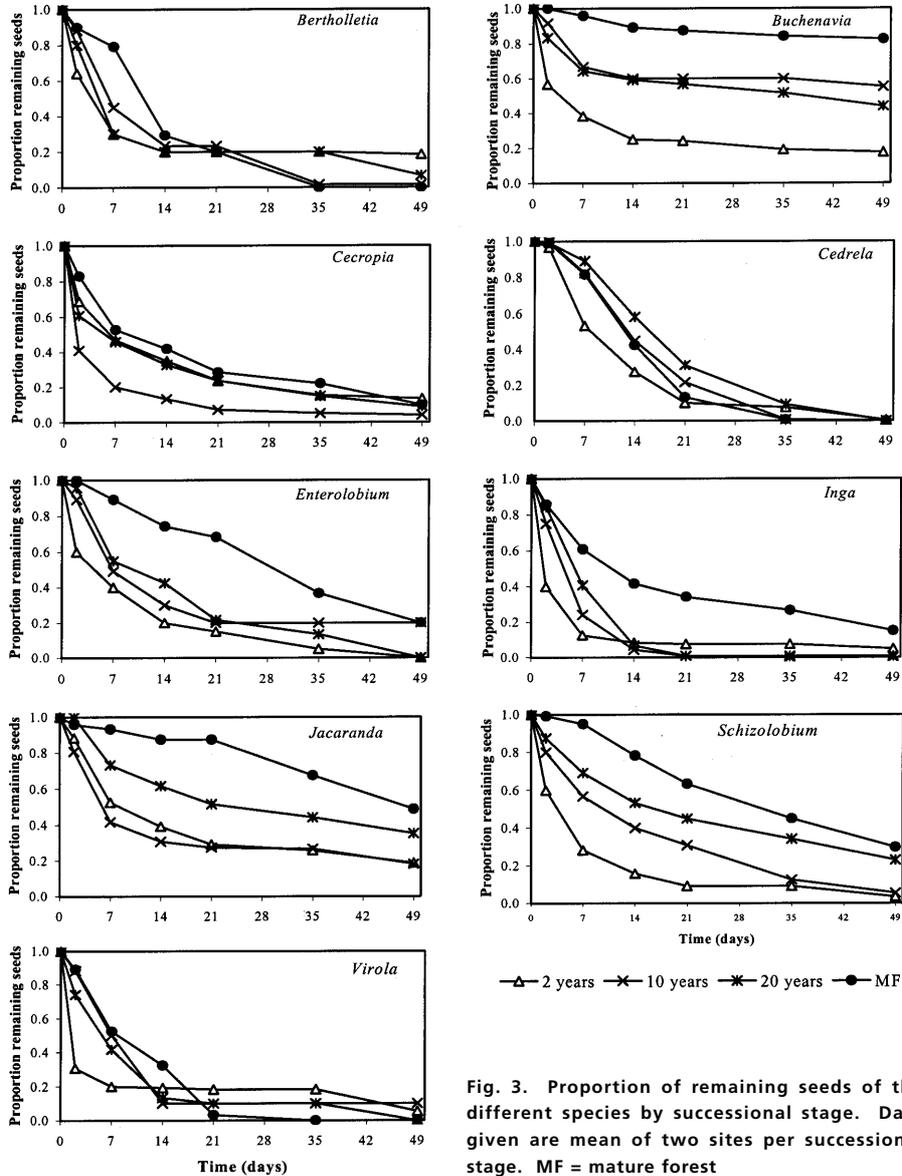


Fig. 3. Proportion of remaining seeds of the different species by successional stage. Data given are mean of two sites per successional stage. MF = mature forest

removal rate in the 20 year old secondary forest and *Virola* in the 10 year old secondary forest (Table 2, results of contrasts).

The seed removal rate of *Bertholletia*, *Buchenavia*, *Inga* and *Virola* were only partially explained by the different microhabitat characteristics (Table 3). The removal rate of *Bertholletia*, *Inga* and *Virola* decreased as the leaf litter

Table 2. Results of the Cox regression analysis testing for effect of successional stage on the removal rate over all species and per species. Also shown are the results of the contrasts among different successional stages and the removal percentage per species and per successional stage at day 49 (end of experiment). Successional stages in a given row followed by the same letter are not significantly different (at $p = 0.0083$). 2 y = 2 year old secondary forest, 10 y = 10 year old secondary forest, 20 y = 20 year old secondary forest, MF = mature forest.

Species	p value	Successional stages				Removal percentage
		2 y	10 y	20 y	MF	
All species	< 0.0001	a	a	b	c	85.1
<i>Bertholletia</i>	0.6292					92.3
<i>Buchenavia</i>	< 0.0001	a	b	b	c	48.3
<i>Cecropia</i>	< 0.0001	b	a	b	b	89.0
<i>Cedrela</i>	0.0011	a	ab	b	ab	99.8
<i>Enterolobium</i>	< 0.0001	a	b	b	c	88.5
<i>Inga</i>	< 0.0001	a	ab	b	c	93.5
<i>Jacaranda</i>	< 0.0001	a	a	b	c	65.2
<i>Schizolobium</i>	< 0.0001	a	b	c	c	81.0
<i>Virola</i>	0.0177	a	b	ab	ab	95.4
Removal percentage		89.6	86.3	84.9	74.0	

thickness, the *Cecropia* litter cover and the liana density increased, respectively (Table 3, Fig. 4). The removal rate of *Buchenavia* varied with liana density and plant cover (Table 3).

No relationship between average seed removal rate and seed mass was found (Linear regression, $p = 0.77$). Neither was there a relationship between seed removal rates of specific successional stages and seed mass (Linear regression; for 2 year secondary forest: $p = 0.19$; for 10 year secondary forest: $p = 0.97$, for 20 year secondary forest: $p = 0.54$, and for mature forest: $p = 0.71$).

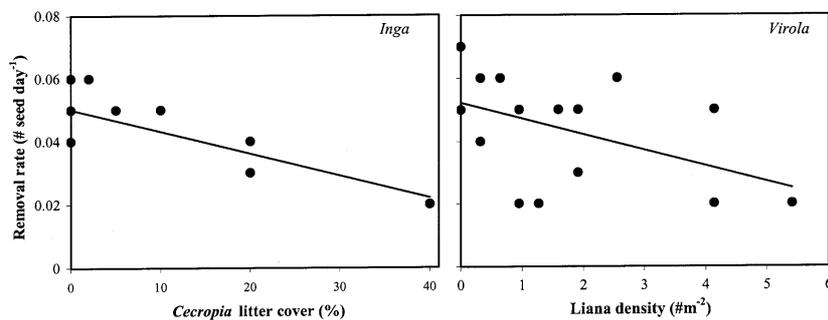


Fig. 4. Examples of the relationship between removal rate and stand characteristics. The removal rate of *Inga* and *Virola* is related to *Cecropia* litter cover and liana density, respectively. For equation and r^2 see Table 3.

Table 3. Effect of microhabitat characteristics on the removal rate per species and over all species. A forward stepwise multiple regression analysis was performed. The slopes for the different stand characteristics included in the regression models are given. ns = non-significant.

Species	N	stem density	liana density	<i>Cecropia</i> litter cover	plant cover	leaf litter thickness	r ²	p value
<i>Bertholletia</i>	27	-	-	-	-	- 0.0107	0.184	0.025
<i>Buchenavia</i>	17	-	0.0271	-	-0.00056	-	0.580	0.002
<i>Cecropia</i>	25	-	-	-	-	-		ns
<i>Cedrela</i>	18	-	-	-	-	-		ns
<i>Enterolobium</i>	22	-	-	-	-	-		ns
<i>Inga</i>	15	-	-	-0.00053	-	-	0.443	0.009
<i>Jacaranda</i>	14	-	-	-	-	-		ns
<i>Schizolobium</i>	23	-	-	-	-	-		ns
<i>Virola</i>	19	-	-0.0045	-	-	-	0.280	0.035
All species	180	-	-	-	-	-	-	ns

Discussion

Seven weeks after seeds had been artificially dispersed, 85 % had been removed. The removal ranged from almost 50 to 100 % depending on the species, and from 74 to 90 % depending on the successional stage (Table 2). This range is similar to the values reported for other tropical regions (e.g., secondary forests of different ages and primary forest: 98.4% over 2 months (Hammond 1995); 2 year old secondary forests and gaps in primary forest: 35 - 100 % over 4 months (Uhl 1987); closed canopy forests vs. gaps: 97 % over 20 weeks (Cintra & Horna 1997); pastures and gaps in primary forest: > 80% for eight of 11 species over 50 days (Nepstad et al. 1996); pastures, gaps in primary forest, forest edge, and canopy closed forest: 59% over one month (Osunkoya 1994)). Most of the depots were visited within the first 7 days of the experiment, so that after only one week just 34 % of all depots had all seeds present (Fig. 3). For species with low removal rates (*Buchenavia* and *Jacaranda*, see Table 2), it seems that depots were not detected or were detected but seeds ignored (15 % of all depots containing *Buchenavia* and 7.5 % of those containing *Jacaranda* still had all seeds present at the end of the experiment). The low removal of *Buchenavia* could be due to the fact that the seeds were offered without fruit pulp and that the seeds have a very thick pericarp.

In general, removal rate decreased as the age of the forests increased. For all species except *Bertholletia* the removal rate varied among successional stages (Table 2, Fig. 3). This result can be related to differences in abundance of removal agents, i. e. ants and rodents. The pattern of a higher removal rate

in younger stages (2 and 10 year old) than in older ones (20 years old and mature forest) observed for seed removed by ants (*Cecropia*, *Cedrela* and *Jacaranda*) is likely to be due to differences in ant density among successional stages. A higher abundance of ants in general, and of granivorous ants in particular (such as *Atta*, *Solenopsis*, *Wasmannia*; Kaspari 1995, Vasconcelos & Cherret 1995), has been found in younger secondary forests as compared to older ones. Studies done in our research site have also found the pattern described above (Robert Dunn, personal communication). The higher ant abundance in younger secondary forests has been related to a higher productivity and a higher abundance of open areas for nest establishment in these forests than in older successional stages (Vasconcelos & Cherret 1995).

Removal rates of seeds removed by rodents have been related to the density and the behaviour of rodents (e. g. Osunkoya 1994, Asquith et al. 1997, Manson & Stiles 1998, Sanchez-Cordero & Martinez-Gallardo 1998) and to stand characteristics (e. g. Hammond 1995, Whelan et al. 1991, Manson & Styles 1998). In this study all species removed by rodents but *Bertholletia* were removed at a higher rate in the younger successional stages than in the older ones (Table 2), suggesting that there is a higher density of rodents in younger stages than in older ones. Densities of mammal footprints, however, were not significantly different among the different successional stages (H. de Boo, unpublished data). The evidence available so far is the literature on rodent density in different successional stages is scarce and sometimes contradictory. It has been reported that there is no difference in terms of mammal abundance and species richness between 6 year old secondary forests and mature forests (Medellin & Equihua 1998), that there is a higher abundance of rodents in pastures when compared to mature forests (Nepstad et al. 1996), and that pastures have lower abundance of non-flying mammals than forest, forest edges and plantations (Estrada et al. 1998).

Rodents seem to prefer habitats that allow them to reduce the risk of being predated (e. g. Manson & Stiles 1998). Lower seed removal rates in older successional stages than in younger ones have been related to the thickness of the litter layer. The line of reasoning is that the older the successional stage the higher the amount of litter, and therefore, the higher the chances of the seeds not to be found by seed removal agents (Hammond 1995). In this study, however, leaf litter thickness did not increase with age of the forest (Fig. 2E). Other studies have found an increase in seed removal rate with an increase in stem and liana density, vegetation structure and ground cover (Myster & Pickett 1993, Osunkoya 1994, Manson & Styles 1998). In this study, however, the lowest seed removal rate was found in the mature forest

(Table 2), which had the highest stem density and the highest plant cover of all successional stages (Fig. 2A and 2D). Based on these results, the general trend observed is apparently mainly due to a decrease in liana density as the forest age increases (Fig. 2B). Young successional stages are characterized by a high abundance of lianas, which gives a more dense structure to the forest. Rodents may have a smaller risk of being predated while foraging in these areas than in older successional stages, and therefore, the seed removal rate is higher than in older successional stages.

The seed removal rate observed could only be partly explained by microhabitat characteristics in the case of *Bertholletia*, *Buchenavia*, *Inga* and *Virola* (Table 3, Fig. 4). Apparently seeds of *Bertholletia*, *Inga* and *Virola* had higher probabilities of surviving when dispersed in microhabitats that reduce their chances of being found, i.e. microhabitat that had higher leaf litter thickness, more *Cecropia* litter cover and higher liana density, respectively. On the other hand, *Buchenavia* seeds had a higher chance of surviving in areas with low liana density and high plant cover (Table 3). These different microhabitats are not unique to a given successional stage; i.e. there is microhabitat heterogeneity within a successional stage. Our results clearly demonstrate that microhabitat per se can not explain the general trend that younger stages of succession have a higher removal rate than older ones. This heterogeneity, however, may play a crucial role in the regeneration of secondary forests because it may allow seeds of preferred species to escape removal (sensu Mittelbach & Gross 1984).

Seeds of *Bertholletia*, *Buchenavia* and *Virola* are more likely to be removed by rodents than by ants because of their seed size (Table 1). The fact that only their seed removal rates were partly explained by microhabitat characteristics suggests that the stand characteristics evaluated in this study may not serve as cues for seed removal by ants. This is probably related to differences in the way that rodents and ants perceive their environment because of body size constraints (Kaspari & Weiser 1999). Another explanation for these results could be the difference in foraging behavior between ants and rodents. For many ants, the discovery of seeds is mainly dependent on whether the seeds are within the vicinity of the foraging trails (Mull & Macmahon 1997), while in the case of rodents it is mainly dependent on territorial behavior and predator avoidance (Bowers & Dooley 1993).

Seed removal rate was not related to seed mass, as has been reported by other studies (e.g. Holl & Lulow 1997). Seeds were removed by different seed removal agents (Table 1) that use different strategies for seed removal and that

may differ in their densities. In the case of seeds removed by ants, the relationship becomes unclear because big seeds are likely to attract bigger ants as well as mass recruiting species (Robert Dunn, personal communication). Consequently, small and large seeds may have an equal chance of being removed. In the case of seeds removed by rodents, no relation was found between seed removal rate and seed mass even when only rodent-removed species were considered (data not shown).

As predicted in our model (Fig. 1), seed removal rate decreases as the age of the successional stage increases (Table 2). It is not, however, influenced by stand characteristics (Table 3) or by seed size. This suggests that other stand characteristics than the ones measured in this study are determining the effect of successional stage on seed removal rate. In the case of seeds removed by ants, the effect of successional stage on seed removal may be explained by a decrease in ant density with an increase in age of successional stage (e. g. Kaspari 1995, Vasconcelos & Cherret 1995, R. Dunn, personal communication). In the case of seeds removed by rodents, the effect of successional stage on seed removal rate may as well be explained by the density of the removal agent. If we assume that the abundance of rodents is higher in areas with more dense vegetation because the risk of being predated decreases, then we can expect a higher removal rate in younger successional stages than in older ones. Additionally, we can expect that in the older successional stages there would be a greater selectivity of resources (less preferred species would have lower seed removal rates than highly preferred species) because rodent density would be lower (P. Jansen, personal communication).

The results of this study support the idea that post-dispersal seed removal plays a role in the establishment of trees in abandoned agricultural areas. Seed removal rates decrease with an increase in forest age, so that seeds dispersed to younger stages of succession have lower chances of surviving than seeds dispersed to older ones. This has different implications for tree species differing in shade tolerance. Shade tolerant species are known to establish themselves slowly in areas undergoing succession. This may be due to the fact that they have other establishment requirements than pioneer species (Uhl 1987, Finegan 1984) or that their seeds arrive to the area in smaller quantities than the seeds of pioneer species (Uhl et al. 1981, Uhl 1987). The latter case combined with a higher seed removal rate in younger stages of succession may explain better the low density of forest tree seedlings found in young successional stages (Uhl et al. 1981). Pioneer and long-lived pioneer species, on the other hand, get established in higher densities in younger successional stages. These species need to be dispersed to early stages of succession to encounter the high light

levels necessary for their establishment (Kyereh et al. 1999, Guariguata 2000, Chapter 4). Therefore, they should be able to overcome the high seed removal rates typical of younger stages of succession. A massive seed production, a seed production throughout the year, a high seed dispersal rate, and/or a quick germination after dispersal may help compensate the high seed removal values found in early stages of succession.

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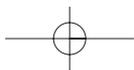
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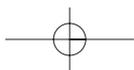
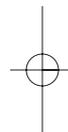
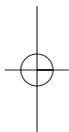
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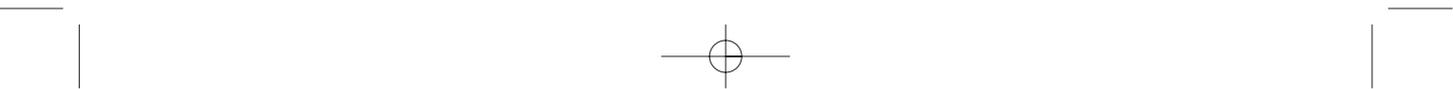
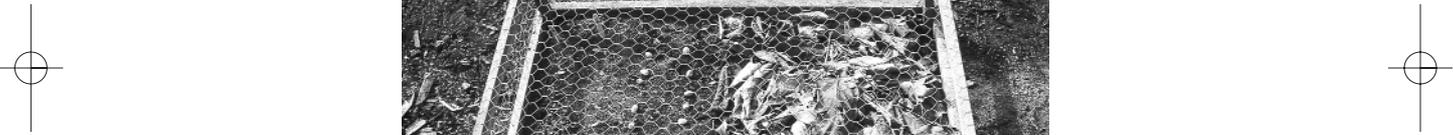
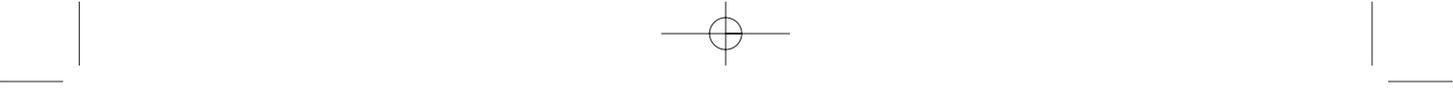
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Chapter 4

Is the regeneration of light demanding species restricted to early stages of secondary forest succession?

Abstract

The germination, early survival, and growth requirements of light demanding tree species of the tropical rain forests of the Bolivian Amazon were studied in areas differing in successional stage. The successional stages consisted of agriculture fields, 2, 10 and 20-year-old secondary forests, and primary forest. Seeds of two pioneer and of four long-lived pioneer tree species were sown in the different successional stages and were subjected to two litter treatments: "with litter" and "without litter". Germination, survival and height growth rate were monitored periodically for 13 to 19 months depending on the species. Canopy openness and litter thickness were evaluated in all successional stages. Canopy openness decreased and litter thickness increased as succession proceeded. Species did not germinate well in the agricultural fields, and had in general higher germination rates in the older successional stages than in the younger ones. Litter had a negative effect on the germination of some of the species. Pioneer species survived better in the younger stages of succession, while the long-lived pioneer species realized the highest survival and height growth rate in different successional stages, according to their shade tolerance. The results indicate that the limiting process for the regeneration of long-lived pioneer is not necessarily germination but mortality and growth. Consequently, early colonization of areas undergoing succession is not obligatory for long-lived pioneer species in order to be present in older stages of succession.

Introduction

During the cycle of slash-and-burn agriculture, areas covered by tropical rain forest are cleared, cultivated and abandoned after a few years. These areas are rapidly recolonized by plants through secondary succession. Due to the regrowing vegetation, several changes in the environmental conditions of the area occur as succession progresses. Among these changes are a decrease in the light availability aboveground (Finegan 1996) and an increase in the litter cover. Both light availability and litter cover may play an important role in the establishment of tree species.

The first one hundred years of neotropical secondary forest succession has been described in terms of three phases, which are distinguished by the dominance of a given group of plants. The first phase of succession is dominated by herbs, shrubs and climbers, which establish quickly after disturbance and disappear under the shade of the emerging pioneer tree species. The pioneer tree species are able to develop a canopy very quickly and will dominate the second phase for 10 - 20 years depending on the species lifespan. As they die off, they are replaced by long-lived pioneer tree species. These latter species are the dominant ones during the third phase of succession, which may last for 75 - 100 years depending on the lifespan of the species. The colonization of the site by more shade tolerant species is very likely to be continuous during the last two phases (Budowski 1965, Gomez-Pompa & Vázquez-Yanes 1981, Finegan 1996, Finegan 1997).

At early stages of succession in slash-and-burn areas pioneer and long-lived pioneer tree species get established in higher abundance than shade tolerant species (Uhl et al. 1981, Purata et al. 1986, Uhl 1987). This may be due to the fact that seeds of pioneer and long-lived pioneer tree species are present in higher abundance in the seed bank and/or arrive to the area in larger quantities than seeds of shade tolerant species (Uhl et al. 1981, Uhl 1987, Saulei 1988). Another reason may be that these species groups have different requirements for their establishment (Finegan 1984, Swaine & Whitmore 1988). The establishment of pioneer and long-lived pioneer tree species is thought to be restricted to very young secondary forests because of their high light requirement for germination, survival, and growth (Budowski 1965, Swaine & Whitmore 1988, Finegan 1996, Kabakoff & Chazdon 1996, Walters & Reich 1996, Whitmore 1997). Seeds arriving later on in succession are therefore not expected to germinate. Within the group of long-lived pioneer species there is a larger range of life history strategies than within the

group of pioneer tree species (Finegan 1996). Therefore, establishment of long-lived pioneer species during later phases of succession might be possible.

Leaf litter may represent a physical barrier to reach the light for seedlings emerging from the seed bank, or to reach the soil for seedlings emerging from seeds recently dispersed to the site on the litter layer. Beyond the initial stage of seedling establishment, however, litter may have primarily a positive effect on seedling survival by avoiding soil water loss. This is especially important for seedlings growing in relatively open areas or in seasonal forests (Winn 1985, Molofsky & Augspurger 1992, Vázquez-Yanez & Orozco-Segovia 1993, Hoffman 1996).

In this study, I evaluated if the establishment of two pioneer and four long-lived pioneer tree species was restricted to the early stages of succession, as predicted by the current model of tropical secondary succession (Finegan 1996). Changes in canopy openness and litter cover with succession were determined for a series of successional stages, varying from very young stages (agricultural fields) to very old ones (mature forests). The effect of canopy openness and litter cover on germination, survival and early growth of pioneer and long-lived pioneer tree species was evaluated for a period of 19 months.

Methodology

Study area and study species

The study was carried out in the northern Bolivian Amazon in the forest reserve El Tigre (11°59'S, 65°43'W) and in nearby areas owned by local farmers (< 5 km from El Tigre). El Tigre is the research and training center of the Programa de Manejo de Bosques de la Amazonia Boliviana (PROMAB), and is located 45 km east of the town of Riberalta. The area receives an annual rainfall of 1780 mm with a dry season from May to September (Beekma et al. 1996). The vegetation of El Tigre and surrounding areas consists mainly of lowland tropical moist forest, patches of secondary forests differing in successional stage and agricultural fields. Secondary forest patches are the result of slash-and-burn agriculture and fallow, and have in general an area of 1 ha.

Six tree species were included in the experiment ranging from typical pioneer species (*Cecropia sciadophylla* and *Bellucia pentamera*) to long-lived pioneer species (*Cedrela odorata*, *Inga thibuadiana*, *Jacaranda copaia*, and

Table 1. Species included in this study in order of increasing seed size. Family name, seed mass (mean \pm SD) and life strategy are given. Seed mass is determined differently, some species are weighted individually and others in batches. P = pioneer, LLP = long-lived pioneer.

Species	Family	Seed mass (mg)*	Life strategy
<i>Bellucia pentamera</i>	Melastomataceae	0.12 \pm 0.01 ^a	P
<i>Cecropia sciadophylla</i>	Moraceae	1.8 \pm 0.08 ^b	P
<i>Jacaranda copaia</i>	Bignoniaceae	8.4 \pm 1.4 ^c	LLP
<i>Cedrela odorata</i>	Meliaceae	19.9 \pm 0.7 ^c	LLP
<i>Inga thibaudiana</i>	Mimosaceae	166 \pm 40 ^c	LLP
<i>Tachigali cf. vasquezii</i>	Caesalpinaceae	404 \pm 30 ^c	LLP

^a To estimate the mean weight, 20 groups of 100 seeds each were weighed, and then the mean per seed calculated.

^b To estimate the mean weight, 20 groups of 40 seeds each were weighed, and then the mean per seed calculated.

^c Seed mass is based on the mean weight of 20 fresh seeds weighed individually.

Tachigali cf. vasquezii; Table 1). All species occur naturally in primary and/or secondary forests in the region, and reach the canopy when mature. Henceforth, species will be referred to only by generic name.

Experimental design

The study was carried out in five successional stages: agricultural fields still in use, secondary forest of 2, 10 and 20 years old, and primary forest. Two sites were selected per successional stage. Site selection was based on similarities in vegetation structure between sites of the same successional stage. In each site two blocks were laid out at least 10 m apart.

In each block, several 60 x 90 cm cages of chicken wire (opening of 2.5 cm) were placed. In one half of the cage, seeds were sown in rows, perpendicular to the length of the cage, directly on the leaf litter (“with litter” treatment). In the other half of the cage, all litter was removed (“without litter” treatment), and seeds were sown directly on the forest floor. The cages prevented seed predation and removal by mammals. At the most 2 species were included in the same cage, so that a total of 7 cages per site were used during the experiment (14 per successional stage). To include the “with litter” treatment in the agricultural fields, litter from a nearby 20 year old secondary forest was collected, and several layers of litter were put in the corresponding half of the cages. Leaves falling into the “without litter” treatment were removed initially weekly and biweekly later on. Leaves falling on the top of the cage were either included in the “with litter” treatment or removed, depending on the half of the cage in which they had fallen.

Table 2. Seed number of the different species used in the experiment, length of the evaluation period for germination and growth, month and year in which the experiment began for the different species, and germination percentage (%).

Species	Seed number (#)	Germination (days)	Growth (days)	Beginning experiment	Germination percentage
<i>Bellucia</i>	8000	200	322	October '97	0.7
<i>Cecropia</i>	8000	200	322	October '97	0.6
<i>Cedrela</i>	800	91	413	November '97	56
<i>Inga</i>	720	56	322	December '97	59
<i>Jacaranda</i>	800	140	238	March '98	1.3
<i>Tachigali</i>	300	91	385	March '98	37

Seeds from all species were collected in the same area and their fruit flesh was removed. Only undamaged seeds were selected for the experiment. Seeds were sown during the natural dispersal period of the study species (between October 1997 and March 1998; Table 2), so that they would encounter similar environmental conditions as when naturally dispersed. The number of seeds used in the experiment was dependent on seed availability and seed size. In the case of *Inga* 18 seeds, and in the case of *Cedrela* and *Jacaranda* 20 seeds were included for each combination of treatment, site and block. Because of scarcity of seeds, *Tachigali* was sown only in one block per site (15 seeds per treatment). Finally, due to the very small seed size (Table 1), *Cecropia* and *Bellucia* were sown in batches of 40 seeds into PVC rings. The PVC rings (five rings per treatment) were pressed slightly into the litter layer and soil and were used to prevent seeds from being washed away. For total number of seeds per species see Table 2.

Seeds were checked for germination and developmental status (presence of radicle, cotyledons, and leaves) every week at the beginning of the experiment and every 2 weeks later on. For a given species, germination was evaluated until a steady level in the percentage germinated had been reached; therefore, the length of the evaluation period differed among species (Table 2). Every germinated seed was labeled and its survival monitored during each check up. Once the germination was not evaluated anymore, seedling height was measured. Seedling survival and height were remeasured once more during the following wet season (March 1999). To calculate the height growth rate (HGR, cm/day), I divided the height difference between the 2 measurements by the length of the time period evaluated (Table 2).

Canopy openness was estimated using hemispherical photographs. In March 1998 hemispherical photos were made under overcast sky conditions

at a height of 1 m above each cage (70 cages in total). Photographs were made with a Canon AE-1 camera with a 7.5-mm fish-eye lens. Negatives were scanned using a Sony XC-& CE black and white CCD camera attached to a VIDAS image analysis system (Kronton/Zeiss, Eching, Germany) and analyzed with Winphot 5 (ter Steege 1997).

The leaf litter thickness was evaluated twice, at the end of the dry season (October 1997) and at the end of the wet season (April 1998), at 1 m intervals along 100 m transects in the different sites used for the experiment. The thickness of the leaf litter was determined as the amount of leaf layers intersected by a knife point (Molofsky & Augspurger 1992).

Analysis

Canopy openness was analyzed with a one way ANOVA with successional stage as factor. Litter thickness was analyzed with a two way ANOVA with successional stage and season as factors. The Least Significant Difference (LSD) was used as post-hoc test. Both variables were $\log(x+1)$ transformed prior to the analysis to increase homoscedasticity.

Germination and survival data were analyzed with a survival analysis (Fox 1993). Differences in germination and survival patterns among the different successional stages and litter treatments were determined for each species using Cox regressions. The analysis was done for each species separately because total seed number was not the same (Table 2). For *Cecropia*, *Cedrela*, *Inga*, and *Tachigali* successional stage and litter were used as factors. Simple contrasts were carried out to find significant differences among the different successional stages. There were 10 possible contrasts; consequently, the P value was corrected using a Bonferroni correction (P value for contrasts is 0.005). *Bellucia* and *Jacaranda* had very few seeds germinating; therefore, the analysis was done differently. For *Jacaranda*, I considered only litter as a factor because this species germinated only in the 2-year-old secondary forest. For *Bellucia* I grouped the successional stages into two classes: young (agricultural fields and 2 year old secondary forest) and old (10 and 20 year old secondary forests and primary forests) successional stages.

The HGR data were squared root transformed $((x + 1)^{-2})$ to increase homoscedasticity. A two way ANOVA was then carried out with successional stage and litter as factors and canopy openness as a covariate. Canopy openness was used as a covariate to control for the effect of light on the height growth rate. Simple contrasts were carried out to find significant differences among

the different successional stages. There were 6 possible contrasts, thus the P value was corrected accordingly (P value for contrasts is 0.0083). Only *Cedrela*, *Inga* and *Tachigali* were included in the analysis because they had more than 5 seedlings per successional stage. The agricultural field was excluded from the analysis because of the very low number of seedlings surviving there (see Results).

Results

Abiotic factors

Canopy openness varied with successional stage (ANOVA, $F_{4, 62} = 125.6$, $p < 0.001$). Younger successional stages had higher canopy openness than older ones (Table 3). Canopy openness decreased from 53 % in the agricultural field to 4 % in mature forest.

The number of leaf layers in the litter varied significantly between seasons (ANOVA, $F_{1, 1926} = 67$, $p < 0.0001$) and among successional stages (ANOVA, $F_{4, 1926} = 448$, $p < 0.0001$). There was a thicker litter layer at the end of the dry season than during the wet season. The only exception to this were the agricultural fields, which were burnt during the dry season and accumulated litter afterwards during the wet season. Older successional stages tended to have a thicker litter layer than younger successional stages (Table 3).

Germination

In general, the germination percentage of the species differed strongly. It ranged from 0.6 to 1.3 % for *Bellucia*, *Cecropia* and *Jacaranda* while for *Tachigali*, *Cedrela* and *Inga* it ranged from 37 to 59 % (Table 2).

Table 3. Canopy openness (%) and litter thickness (number of leaf layers) in the different successional stages. For canopy openness, mean (and SD) is given based on hemispherical photos taken above 14 cages per successional stage. For litter, mean (and SD) are given based on measurements done every 1 m along two 100 m transects per successional stage. Values in the same column followed by different letters are significantly different at a P-level of 0.05.

Successional stage	Canopy openness	Litter thickness	
		Dry season	Wet season
Agricultural field	53.4 (10.9) ^a	0.1 (0.4) ^a	0.6 (0.8) ^a
2 year old secondary forest	9.1 (4.5) ^b	2.8 (1.9) ^b	2.6 (1.2) ^d
10 year old secondary forest	4.7 (0.9) ^c	2.3 (1.3) ^b	1.9 (1.2) ^b
20 year old secondary forest	4.6 (1.7) ^c	3.2 (1.8) ^c	1.8 (1.2) ^b
Primary forest	3.8 (1.4) ^c	4.5 (2.1) ^d	2.1 (1.1) ^c

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Table 4. Results of Cox regression analysis testing for effect of successional stage and litter on germination rate of 6 tree species. AF = agricultural fields, 2y = 2 year old secondary forest, 10y = 10 year old secondary forest, 20y = 20 year old secondary forest, PF = Primary forest, NL = without litter, WL = with litter. ns = non-significant.

Species	Successional stage					Litter		
	P value	Contrast					P value	Contrast
		AF	2y	10y	20y	PF		
<i>Bellucia</i>	ns						< 0.0001	NL > WL
<i>Cecropia</i>	0.0027	ab	ab	ab	a	b	ns	
<i>Jacaranda</i>	*						ns	
<i>Cedrela</i>	< 0.0001	a	b	d	bc	cd	0.0086	NL > WL
<i>Inga</i>	< 0.0001	a	b	c	b	c	0.0113	NL > WL
<i>Tachigali</i>	ns						ns	

* species only germinated in the 2 year old secondary forest, so only litter effect was tested.

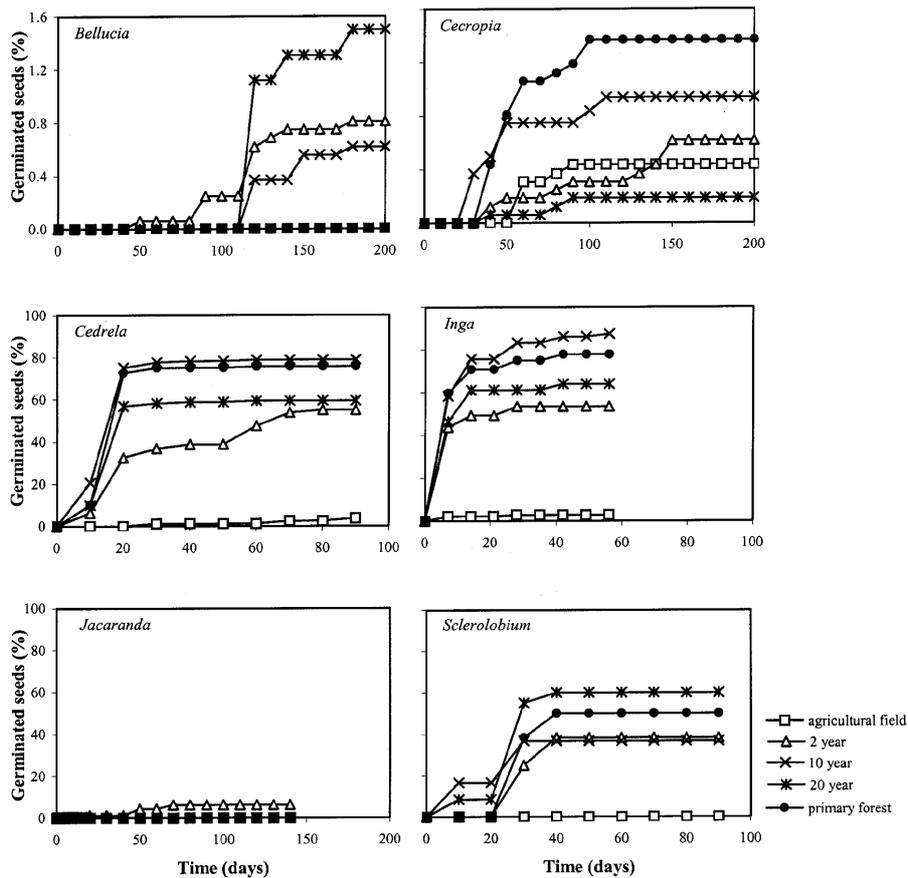


Fig. 1. Germination rate of six different tree species by successional stage. Data given are mean over litter treatment. The two pioneer species, *Bellucia* and *Cecropia*, have different y-axis than the rest of the species. X-axis varies according to the evaluation period (see Table 2).

The germination rate of the species was influenced by successional stage (*Cecropia* and *Jacaranda*), litter (*Bellucia*), or both factors (*Cedrela* and *Inga*). *Tachigali* was the only species not affected by any factor (Table 4). *Cecropia*, *Cedrela* and *Inga* had their highest germination rates in the primary forest and in the 10-year-old secondary forest, while *Jacaranda* only germinated in the 2-year-old secondary forest (Fig. 1). Germination at the agricultural field was very low for all species. The presence of litter reduced the germination rates of *Bellucia*, *Cedrela*, and *Inga* (Table 4).

Survival

From all 1080 emerged seedlings, 54.2 % had died by the end of the experiment. The survival percentage varied from 0 % (*Bellucia*) to 79 % (*Tachigali*).

The survival rate of the seedlings depended on successional stage (*Bellucia*, *Cecropia*, *Inga* and *Jacaranda*) or on a combination of successional stage and litter (*Cedrela*). *Tachigali* was not affected by any of these factors (Table 5). The species response to successional stage varied among species (Fig. 2). *Bellucia* and *Cecropia* had higher survival rates at the younger successional stages. In the case of *Cecropia*, the only seedlings surviving until the end of the experiment were those in the agricultural field sites, while no *Bellucia* seedling survived until the end of the dry season (September 1998). *Inga* seedlings did not survive in the agricultural field but had higher survival rates in the 10 and 20-year-old secondary forest sites than in the 2-year-old secondary forest. *Cedrela* had the highest survival rate in the 2-year-old secondary forest, and it survived better in the “with litter” treatment. Fifty percent of the emerged *Jacaranda* seedlings survived until the end of the experiment.

Growth

The mean HGR of the three species evaluated was affected by successional stage. Litter only affected the HGR of *Inga* (Table 6). *Cedrela* had the highest HGR in the 10-year-old secondary forest and the lowest HGR in the 2-year-old secondary forest. Its HGR in the other successional stages were intermediate (Fig. 3). *Inga* grew faster in height in the 2-year-old secondary forest and slower in the primary forest. In general, *Inga* plants growing in the “without litter” treatment had a significantly higher HGR than in the “with litter” treatment (Fig. 3). *Tachigali* had a significantly higher HGR in both the 2 and 10-year-old secondary forest and a significantly lower HGR in the mature forest. The effect of litter on its HGR varied with successional stage and had a markedly positive effect in the 10-year-old secondary forest.

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Table 5. Results of Cox regression analysis testing for effect of successional stage and litter on survival rate of seedlings. AF = agricultural fields, 2y = 2 year old secondary forest, 10y = 10 year old secondary forest, 20y = 20 year old secondary forest, PF = Primary forest, NL = without litter, WL = with litter. ns = non-significant.

Species	P value	Successional stage					Litter	
		AF	Contrast				P value	Contrast
			2y	10y	20y	PF		
<i>Bellucia</i>	< 0.0001		younger > older				ns	
<i>Cecropia</i>	0.001	c	bc	ab	abc	a	ns	
<i>Jacaranda</i>	*						ns	
<i>Cedrela</i>	< 0.0001	ab	b	a	a	a	0.0106	WL > NL
<i>Inga</i>	< 0.0001	a	b	c	c	bc	ns	
<i>Tachigali</i>	ns						ns	

* species only germinated in the 2 year old secondary forest, so only litter effect was tested.

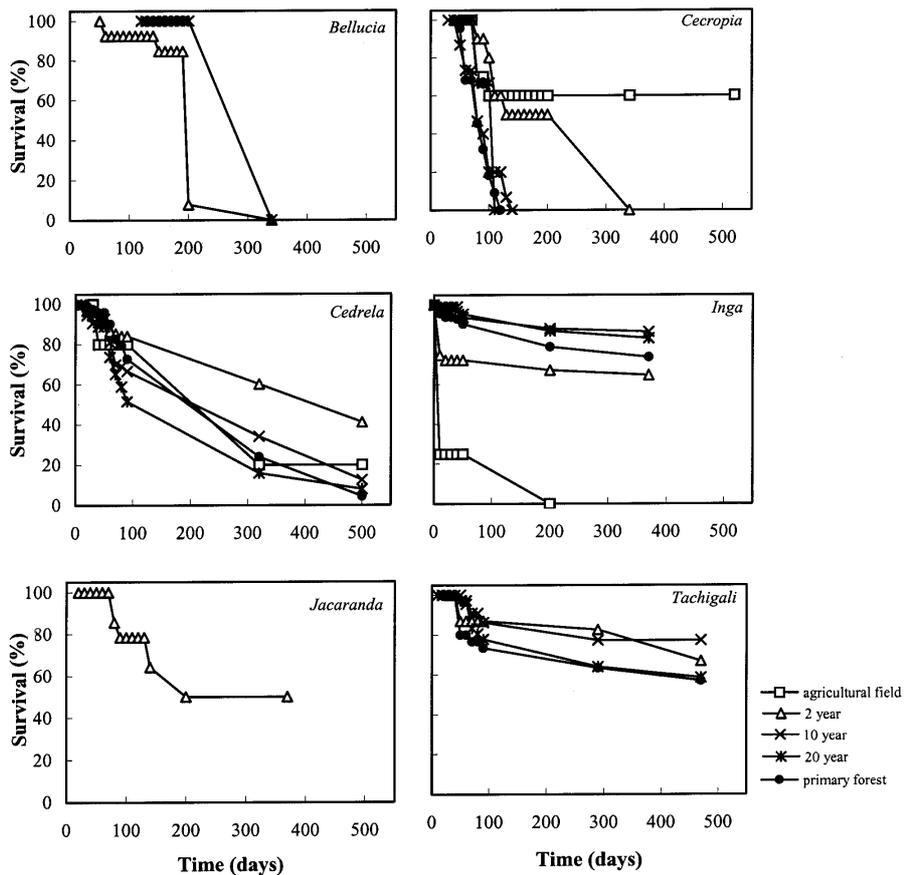


Fig. 2. Survival rate of emerged seedlings by species and successional stage. Data given are mean over litter treatment.

Table 6. Results of the two way ANOVA per species with square root height growth rate as dependent variable, successional stage and litter as independent variables, and canopy openness as covariate. Sample size for *Cedrela*: 98, for *Inga*: 335, for *Tachigali*: 75.

Source	<i>Cedrela</i>		<i>Inga</i>		<i>Tachigali</i>	
	F	p	F	p	F	p
Canopy openness	8.62	< 0.001	66.39	< 0.001	0.007	0.933
Successional stage	4.28	0.007	16.24	< 0.001	14.49	< 0.001
Litter	2.05	0.156	13.49	< 0.001	2.55	0.115
Successional stage * Litter	0.02	0.995	3.15	0.025	1.02	0.011

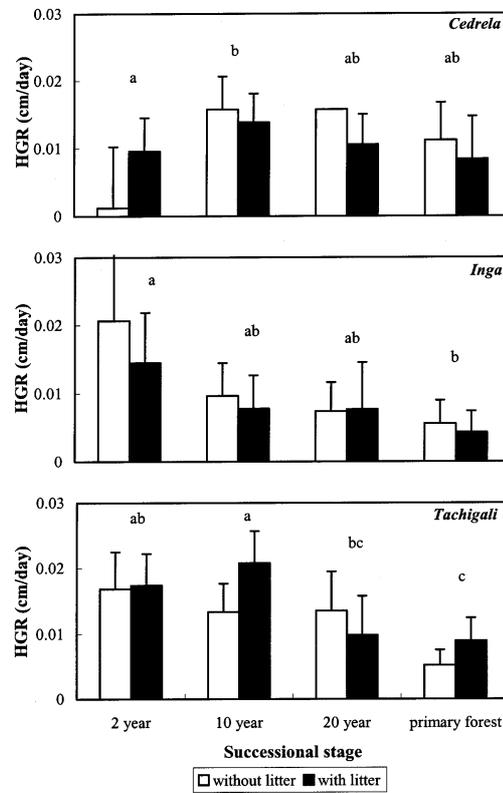


Fig. 3. Height growth rates (HGR) by species, successional stage and litter. Successional stages with different letters are significantly different from each other ($p < 0.0083$). Data are mean + SD.

Discussion

The regeneration of pioneer and long-lived pioneer species in secondary forests is influenced by environmental conditions that vary according to successional stage. As expected canopy openness decreases as succession proceeds due to the development of the vegetation. The agricultural field and

the 2-year-old secondary forest had a wider range in canopy openness than the older successional stages (Table 3). This is due to the fact that the vegetation is more patchily distributed in younger successional stages than in older ones where an even canopy already exists. The older secondary forests and the primary forests do not differ in canopy openness (Table 3). This has also been reported before (Nicotra et al. 1999), and it means that the light availability practically does not change anymore after 10 years of succession.

Leaf litter increased as the age of the forest increased (cf. Uhl & Jordan 1984). The litter layer was thicker during the dry season than during the wet season (Table 3), as has been found before (Songwe et al. 1988). This is due to higher leaf shedding and lower decomposition rates during the dry season. The difference in leaf litter thickness between seasons was greater in the older successional stages than in the younger ones.

Germination

All species had very low or no germination in the agricultural field, probably due to desiccation, as cracks in seeds were observed. Seed viability could not be the reason for the low germination percentages found for some of the species in the present study (Table 2) because seeds coming from the same batches showed higher germination rates under controlled conditions (Hayashida, unpublished data). Open areas are known to have higher temperatures and greater temperature fluctuations than areas covered with vegetation (Bazzaz & Pickett 1980, Uhl et al. 1981). Low germination rates in agricultural fields have also been found in Venezuela (Uhl 1987) and in Ghana (Kyereh et al. 1999). Sites next to trunks, underneath slash, and under the shade of trees surrounding the agricultural fields seemed to be preferred for germination of even very early successional tree species such as *Trema micrantha* or *Cecropia ficifolia* (M. Peña - Claros, personal observation).

All species but *Jacaranda* germinated in all the forest habitats. The germination of *Jacaranda* was restricted to the 2-year-old secondary forest, suggesting that this species needs very specific light levels to germinate, or that it has little capacity of germinating under shade as has been observed elsewhere (Guariguata 2000). *Cecropia*, *Cedrela*, and *Inga* had higher germination rates in the older successional stages than in the 2-year-old secondary forests (Table 4). The results demonstrate that the species studied are able to germinate in the shade, which contradicts the idea that high light levels are always required for the germination of pioneer and long-lived pioneer tree species (Swaine & Whitmore 1988, Whitmore 1997). The ability of pioneer and long-lived pioneer species to germinate in the shade has also

been observed in Malaysia, Ghana and Costa Rica (Raich & Gong 1990, Swaine et al. 1997, Guariguata 2000). The present results suggest that germination is enhanced when some vegetation cover, or shade, exists, and support the hypothesis that facilitation processes play an important role in the succession in tropical areas (Uhl et al. 1981, Ewel 1983, Finnegan 1984).

Litter delayed or reduced the germination of *Bellucia*, *Cedrela* and *Inga* (Table 4); this has been found for other neotropical forest tree species (Molofsky & Augspurger 1992) and for a savanna shrub species (Hoffman 1996). The effect of litter on germination, however, does not have a clear general pattern. It seems to depend on the species considered, the plant development stage and the successional stage of the area (Molofsky & Augspurger 1992, Guariguata 2000).

Survival

The two typical pioneer species, *Bellucia* and *Cecropia*, showed higher survival rates in the younger successional stages than in the older ones, as had been expected (Fig. 2). This pattern was also observed in naturally occurring *Cecropia* seedlings in the 10-year-old secondary forests, which did not survive for more than few weeks after germination (M. Peña-Claros, personal observation). A similar trend was as well found in Ghana. Emerged seedlings of 2 pioneer species had lower survival in the understory than under gap conditions due to their negative growth rates in the understory (Kyereh et al. 1999). These results indicate that pioneer species are restricted to younger stages of succession not because they are not able to germinate in the shade but more because they are not able to grow and survive (Finnegan 1996, Kyereh et al. 1999).

The response of the long-lived pioneer species in terms of survival was species specific. As it has been suggested for long-lived pioneer species (Swaine & Whitmore 1988, Finnegan 1996), *Cedrela* had a higher survival rate in the 2-year-old secondary forests than in the older successional stages (Table 5). On the other hand, *Inga* had a higher survival rate in the older secondary forests than in the 2-year-old ones. This indicates that this long-lived pioneer species is more shade tolerant in terms of survival than *Cedrela* (Table 5). *Tachigali* survival was not affected by successional stage or by litter, which indicates that this species can survive in a broad range of successional stages and light conditions (Table 3 and 5). Similar differences in survival were also found among seedlings of six long-lived pioneer species transplanted into old secondary forests in Costa Rica (Guariguata 2000). Litter had only an effect on the survival of *Cedrela* seedlings, probably by maintaining soil humidity.

Growth

Successional stage and litter (Table 6) influenced height growth rate (HGR). As expected for long-lived pioneer species, the HGR of *Inga* and *Tachigali* was higher in the younger successional stages. On the other hand, *Cedrela* had the lowest HGR in the 2-year-old secondary forest. These results indicate that long-lived pioneer species do not always perform better in the highest light level available and that they differ in their degree of shade tolerance. The results also support the idea that long-lived pioneer species have a wider range of regeneration strategies than pioneer species (Finegan 1996, Guariguata 2000). Consequently, early colonization of an area undergoing succession is not always a pre-requisite for long-lived pioneer species as has been proposed before (Ewel 1983, Swaine & Whitmore 1988, Finegan 1996).

In summary, this study shows that the requirements for germination, survival and early growth of pioneer and long-lived pioneer species are not necessarily the same (Fig. 4). Seeds of pioneer and long-lived pioneer tree species need successional stages with at least some cover to be able to germinate. Yet, in the case of pioneer species the light availability has to be high enough to allow for survival and growth. Seeds of pioneer species dispersed into later stages of succession (> 2 years) are able to germinate but

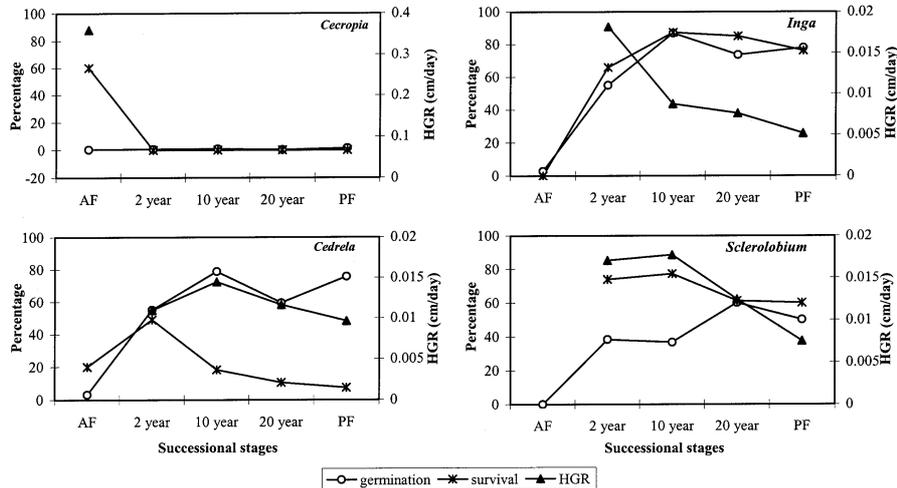


Fig. 4. Germination, survival and height growth rate (HGR) of four of the studied species at the different successional stages. Values given are mean over both litter treatments combined at the end of the experiment. *Cecropia* survival percentage and HGR are mean data based on three seedlings. Note that y-axis extends below zero to show low germination rates. Scale of HGR axis of *Cecropia* is different than for the other species. AF = agricultural fields, PF = primary forest.

seedlings do not survive probably due to low light levels (Fig. 1 and Fig. 2). In the case of long-lived pioneer species, there is a greater variation in light requirements for regeneration than in the case of pioneer species (cf. Finegan 1996). Species which require high light levels for survival (e.g. *Cedrela*; Fig. 4) or for growth (e.g. *Inga*, Fig. 4) may only reach the canopy of secondary forests when establishing during early stages of succession. On the other hand, species that do not have a very specific range of light level for survival and growth (e.g. *Tachigali*, Fig. 4) may get established in a wide range of successional stages. Consequently, the limiting process for the regeneration of long-lived pioneer species is not necessarily germination (cf. Finegan 1996). Instead, mortality and growth act as filters and determine the abundance of seedlings of long-lived pioneer species in later stages of succession. This result also implies that long-lived pioneer species are able to form seedling banks in the understory of secondary forests. Once the pioneer trees forming the canopy begin to die off, these seedlings are likely to profit from the increase in light level and are probably recruited into larger size classes (cf. Mesquita 2000).

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Chapter 5

Forest successional stage affects survival and growth of rain forest tree species differing in shade tolerance

Abstract

The survival and growth of seedlings of tropical tree species was studied in successional stages differing in age in the Bolivian Amazon. Seedlings of nine tree species, ranging from pioneer to shade tolerant species, were planted in three successional stages (1, 10 and 20 years old). Survival and height growth were monitored during two years, after which a destructive harvest was done, which was used for a growth analysis. Successional stage and species had an effect on almost all variables measured. Survival rate decreased with age of the successional stage, as did height growth rate and relative growth rate. This suggests that all species, regardless of their shade tolerance, perform better early than later on in succession. Growth and survival tended to be positively related, indicating that there is no trade-off between these variables. Survival in the 20 year old secondary forests was negatively related to stem mass fraction and positively to leaf mass fraction, while relative growth rate in the 1 year old regrowth increased with net assimilation rate and leaf area ratio. These results support the idea that different plant traits enhance survival at low light and growth at high light. This study suggests that differences in survival and growth among species at different successional stages play an important role in succession.

Introduction

The first one hundred years of secondary forest succession in the tropics have been divided into three different phases, each of them characterised by a given set of plant species (Budowski 1965, Finegan 1996, Finegan 1997). The first phase lasts 1 - 2 years, and it is dominated by herbs, shrubs and lianas, which establish quickly after disturbance. The second one is dominated by pioneer tree species that readily form a continuous canopy. This phase lasts 10 to 20 years. The third phase is dominated by long-lived pioneer tree species that replace the pioneer trees forming the canopy when these begin to die off. This phase can last 75 - 100 years. Shade tolerant species establish continuously during the second and third phases of succession. The underlying mechanisms that cause different species to dominate during different successional stages are not yet well known. It has been proposed that succession is driven by a combination of factors. The environmental conditions of the site (e.g. light availability, soil characteristics), the availability of propagules, and the characteristics of the species (e.g. light requirements, growth rates, lifespan) are likely to play an important role in shaping the course of succession (Finegan 1984, Glitzenstein et al. 1986, Bazzaz 1991, Finegan 1996).

Tree species of tropical rainforest have been classified into pioneer and climax species (here referred to as shade tolerant species). This classification is primarily based on the species light requirements for germination and establishment (Swaine & Whitmore 1988). Pioneer species require high light levels for their germination (Bazzaz 1991) and/or their survival (Agyeman et al. 1999, Chapter 4). Therefore, the recruitment of pioneer species is limited to the very early stages of succession (e.g., Uhl 1987), when light availability is relatively high. On the other hand, shade tolerant species are able to establish and grow under low light conditions (e.g., Popma & Bongers 1988). Accordingly, they are recruited in later successional stages (Finegan 1996). In between these two extremes, there is a large group of species that have intermediate characteristics (Budowski 1965, Denslow 1980). In this study, I refer to this group as long-lived pioneer species. Long-lived pioneer species may establish in early successional stages but they have a considerably longer life-span than pioneer tree species (Budowski 1965). They are thought to require high light levels for their establishment, although species belonging to this group have been reported to be able to germinate and survive under shaded conditions (Guariguata 2000, Chapter 4). Regardless of the stage in

succession in which they get established, seedlings and saplings of long-lived pioneer species should be relatively tolerant to the low light conditions imposed by the canopy of pioneer species.

During the course of succession, the light availability at the forest floor decreases dramatically due to the regrowing vegetation (Saldarriaga 1994, Ellsworth & Reich 1996). Because tree species differ in their shade tolerance, one can expect that species perform differently in terms of survival and growth during different phases or stages of succession. Pioneer species are expected to have a lower survival rate as the age of the secondary forest increases, while the survival of shade tolerant species should be relatively high in all successional stages (cf. Augspurger 1984a). In terms of growth rates, at high and moderately low light levels (higher $> 3\%$ light), tree pioneer species have higher relative growth rates (RGR) than shade tolerant species (Veneklaas & Poorter 1998, and references therein). When the plants are growing in deep shade ($< 2\%$ light), however, irradiance falls below the light compensation point of the pioneer species. Under these conditions shade tolerant species have a higher RGR than pioneer ones (Walters & Reich 1996, Agyeman et al. 1999). Therefore, in early stages of succession seedlings of pioneer species are expected to attain higher growth rates than seedlings of shade tolerant species. In later stages of succession, the response of species will depend on the light level in the successional stage.

Few field experiments have been carried out to try to understand the processes that are involved in the regeneration of tree species in areas undergoing succession. Moreover, very few growth experiments have been carried out completely under field conditions for a long period of time (but see Osunkoya et al. 1993, Rose 2000). In this study I transplanted seedlings of nine tree species differing in shade tolerance to secondary forests in various successional stages and allowed them to grow for two years. My questions were the following: (1) are seedlings of different species restricted to a given successional stage because they can only survive under very specific light conditions?, (2) if seedlings are able to survive in various successional stages, do species growth rates vary with successional stage?, (3) how does the successional stage affect their biomass allocation and morphology?, and (4) what plant traits are correlated with species survival and growth?

Methodology

Research site and study species

The study was carried out in the Bolivian Amazon in the forest reserve El Tigre (11°59'S, 65°43'W) and in nearby areas owned by local farmers (<5 km from El Tigre). El Tigre is the research and training center of the Programa de Manejo de Bosques de la Amazonía Boliviana (PROMAB), and is located 45 km east of the town of Riberalta. The area receives an annual rainfall of 1780 mm with a dry season (<100 mm/month) from May to September (Beekma et al. 1996). The vegetation of El Tigre and surrounding areas consist mainly of lowland tropical moist forest, with some patches of secondary forests that differ in successional stage and agricultural fields. Secondary forest patches are the result of slash and burn agriculture and fallow, and their size is often 1- 2 ha.

Nine tree species were included in the experiment. Species were selected according to shade tolerance, and seed or seedling availability (Table 1). The classification of the species was based on shade tolerance (Poorter 1999), abundance of individuals in different successional stages (van Ulft 1998), and species distribution (N. Divico, personal communication). All species occur naturally in primary and/or secondary forests of the region, and all reach the canopy when mature.

Experimental design

For the study nine sites were selected: two sites that had been abandoned 1 year prior to the beginning of the experiment (hereafter referred to as the 1 year old regrowth), four sites abandoned 8 - 10 years before (hereafter referred to as the 10 years old secondary forest) and 3 sites abandoned 20 - 25 years before (hereafter referred to as the 20 years old secondary forest).

Table 1. List of tree species used in the experiment. Family name, classification based on shade tolerance, and source of plant material are given. P = Pioneer, LLP = Long-lived pioneer, ST = Shade tolerant.

Species	Family	Classification	Source	Abbreviation
<i>Bellucia pentamera</i>	Melastomataceae	P	Seedlings	BEL
<i>Cecropia sciadophylla</i>	Moraceae	P	Seedlings	CEC
<i>Schizolobium amazonicum</i>	Cesalpiniaceae	P	Seeds	SCH
<i>Cedrela odorata</i>	Meliaceae	LLP	Seedlings	CED
<i>Inga thibaudiana</i>	Mimosaceae	LLP	Seeds	ING
<i>Jacaranda copaia</i>	Bignoniaceae	LLP	Seeds	JAC
<i>Tachigali cf. vasquezii</i>	Caesalpiniaceae	LLP	Seeds	TAC
<i>Buchenavia cf. punctata</i>	Combretaceae	ST	Seedlings	BUC
<i>Aspidosperma sp.</i>	Apocynaceae	ST	Seedlings	ASP

Sites of the same age group had similar vegetation structure and history of use. The 1 year old regrowth sites were characterized by patchy vegetation, which reached at the beginning of the experiment a height of 4 - 5 m at the most. The canopy of the 10 years old secondary forest sites was dominated mostly by *Cecropia sciadophylla* trees. The canopy of the 20 years old secondary forest sites was composed by several species, such as *Bellucia pentamera*, *Capirona decorticans*, *Cecropia sciadophylla*, *Croton* sp., *Dendropanax morototoni*, various species of *Inga*, *Jacaranda copaia*, and various members of the Annonaceae family. For site characteristics see Table 2. Henceforth, studied species will be referred to only by generic name.

Two plots of 20 x 24 m were established in each site except in two of the four 10 year old secondary forests. Both of these sites were small, and consequently, only one plot could be fitted in each of them. Plots were established in the center of the site to reduce edge effect, and were at least 20 m apart. In each plot, a grid of 2 x 2 m was laid out. In mid March 1997 a seedling was planted in every cross-point of the grid. Before planting, all other plants <30 cm in height and in a radius of 15 cm at the cross-points of the grid were removed. Thirteen to fourteen seedlings per species per plot were

Table 2. Characteristics of the secondary forests differing in age included in this experiment. Plant density is given in number of stems > 1 cm DBH per ha; litter thickness in number leaves; soil moisture content, organic matter and total nitrogen content in %. Data are mean \pm sd.

Characteristic	1 year old	10 year old	20 year olds
Plant density ¹	2579 \pm 991	666 \pm 133	659 \pm 185
litter thickness dry season ²	2.8 \pm 1.9	2.3 \pm 1.3	3.4 \pm 1.9
litter thickness wet season	2.6 \pm 1.2	2.0 \pm 1.2	2.1 \pm 1.3
soil moisture content - dry season ³	16.8 \pm 2.6	16.7 \pm 2.3	18.5 \pm 2.2
soil moisture content - wet season	28.1 \pm 5.0	29.1 \pm 3.6	30.0 \pm 5.1
soil pH	3.6 \pm 0.3	3.2 \pm 0.3	3.5 \pm 1.2
soil organic matter (%)	2.2 \pm 0.2	2.2 \pm 0.4	2.4 \pm 0.8
soil total Nitrogen (%)	0.15 \pm 0.02	0.16 \pm 0.03	0.16 \pm 0.04

¹ Trees with a diameter at breast height (DBH) > 1 cm were included in the 1 year old regrowth, and trees with a DBH > 10 cm were included in the 10 and 20 year old secondary forest.

² leaf litter layer was evaluated twice (dry season: October 1997 and wet season: April 1998) by counting the number of leaves intercepted by a knife every 1 m along 100 m transects. Transects were located in the different sites used in the experiment

³ soil moisture content (%) was measured four times during the study period (at the end of the dry and wet season). Measurements represent the volumetric soil moisture content over the first 20 cm of the soil, and were done using a time-domain reflectory (TDR) (Trime FM-2, Eijelkamp Agriresearch equipment, Giesbeek, the Netherlands). For each plot, five plants were selected, around which two measurements were taken. For the other soil characteristics, soil samples were taken at five random points in the plots. Samples coming from the same plot were mixed prior to analysis. Analysis was done at the Soil Analysis Laboratory of the Centro de Investigación Agrícola Tropical (CIAT, Santa Cruz, Bolivia).

assigned randomly to the different cross-points. In summary, the experiment contained 3 ages, 4 to 6 plots per age, 9 species per plot and 13 - 15 seedlings per species, making a total of 1899 seedlings. The mean seedling number per species was 211 (range 208 - 214). During the establishment of the grid and during the rest of the study, care was taken not to damage the existing vegetation.

Plants used in the experiment were either germinated in a nursery at intermediate light levels or were collected as recently germinated wildings from the forest (Table 1). Wildings were first planted in the nursery and then transferred to the plots 3 - 4 weeks later. Only seedlings that looked healthy were used in the experiment. Seedling size (see Appendix 1 for initial height), number of leaves and presence of cotyledons varied with species. Seedlings were transplanted from the nursery to the different sites on cloudy to rainy days. In April and May 1997 dead seedlings were replaced by spare seedlings that had been growing in the nursery.

Plant measurements

The experiment lasted two years (722 days). Plants were measured non-destructively in March 1997 and after 3, 6, 12, 18, and 24 months. At each census plant survival, total height, and total number of fully expanded leaves were recorded. From June 1997 onwards (3 months after transplanting) the youngest and fully expanded leaf of each plant was marked with a colored straw to monitor leaf production. Based on these data, I calculated for each measurement interval the seedling survival rate, and the height growth rate (HGR, height increase per day, in cm day^{-1}). The leaf production rate (LPR; number of leaves produced month^{-1} of a given season) was calculated for the wet (October to March) and dry (April to September) season separately.

Two destructive measurements were made during the course of the experiment, at the beginning and at the end of the experiment. In March 1997 thirty seedlings of each species (only 18 seedlings in the case of *Cedrela*) were randomly selected for harvesting from all the seedlings available in the nursery. In March 1999 all plants still alive in the plots were harvested. From each plant, leaf area was measured for all leaves or a subsample using a CI-202 leaf area meter (CID Inc., USA). Plants were separated into leaves and cotyledons, stems and branches, and roots, and dried for 48 hours in a herbarium drier that was kept constantly at 70°C . Afterwards the different plant parts were weighted. Based on these primary data of the second harvest I calculated the following variables (Hunt 1978): root mass fraction (RMF: root mass/ total plant mass, in g g^{-1}), stem mass fraction (SMF: stem and branch

mass/ total plant mass, in g g^{-1}), leaf mass fraction (LMF: leaf and cotyledon mass/ total plant mass, in g g^{-1}), specific leaf area (SLA: leaf and cotyledon area/ leaf mass, in $\text{m}^2 \text{kg}^{-1}$), and leaf area ratio (LAR, leaf area/ total plant mass, in $\text{m}^2 \text{kg}^{-1}$). Additionally, using the two destructive measurements I calculated the relative growth rate (RGR: biomass growth per unit plant biomass and per unit time, in $\text{mg g}^{-1} \text{day}^{-1}$) and the net assimilation rate (NAR: biomass growth per unit leaf area and per unit time, $\text{g m}^{-1} \text{day}^{-1}$). The calculation of NAR is based on the assumption that total biomass and leaf area are linearly related (Evans 1972). This was tested for each combination of successional stage x species. For half of all possible combinations, it was found that a quadratic function described the relationship better than a linear one. Nevertheless, I assumed a linear relationship to calculate NAR. The reasons for doing so were the following: 1. the r^2 of the linear fit were high (mean 0.89, range: 0.30 - 0.99, with only one combination having a value <0.81), and 2. the NAR obtained on the basis of a derived formula for a linear relationship gave, when multiplied with the mean LAR (average LAR of the two destructive harvests), a better estimate of the observed RGR than a NAR calculated with a quadratic relationship.

Abiotic measurements

Canopy openness was estimated using hemispherical photographs. In October 1997 hemispherical photos were made just before sunrise or just after sunset at a height of 0.7 m above the ground in five points of each plot. The five points were systematically chosen to be equally distributed over the plot area and were located in the same position in all plots. Photographs were made with a Canon AE-1 camera with a 7.5-mm fish-eye lens, using an Ilford FP4 film (black and white, 125ASA). Negatives were scanned using a Sony XC-& CE black and white CCD camera attached to a VIDAS image analysis system (Kronton/ Zeiss, Eching, Germany) and analyzed with Winphot 5 (ter Steege 1997) for their canopy openness and total site factor. Canopy openness is the percentage of the canopy that is not covered by leaves or stems. Total site factor is the sum of the direct and indirect light that gets into the area.

Data Analysis

All plants were included only in the analysis of the survival data. For the analysis of all other parameters, a mean value per species per plot was calculated. In other words, plots and not individual plants were considered replicates ($n = 4$ plots for the 1 year old regrowth treatment, and $n = 6$ for the 10 and 20 year old secondary forest treatments). Because plants died during the experiment, the number of plants used to estimate the mean of a given variable varies with species and successional stage. For total plant number per

species, and total number of replicates per treatment at the end of the experiment see Appendix 1. *Cecropia*, *Jacaranda* and *Schizolobium* were not included in the latter analyses because not enough replicates were available (see Appendix 1).

The mean canopy openness was calculated per plot. The data were analyzed using a Kruskal Wallis test with age as a factor because variances were not homogeneous.

Survival data were analyzed with a survival analysis (Fox 1993). Differences in survival patterns among the different successional stages and species were determined using Cox regressions. Additionally, I performed Cox regressions for individual species to test the effect of successional stage on the survival pattern of each species. Simple contrasts were carried out to find significant differences among the different factors, and the p-value was corrected according to the number of possible contrasts (overall test: for age $p = 0.017$, for species $p = 0.0014$; per species test: for age $p = 0.017$).

Plant responses in terms of growth (HGR and RGR), biomass allocation (LMF, SMF, RMF), morphology (LAR and SLA) and whole-plant assimilation (NAR) were tested using a two-way ANOVA with successional stage and species as factors. Plants may show ontogenetic drifts in the allocation and morphology related parameters; therefore, \ln biomass at the end of the study was used as covariate to be able to compare plants at a similar biomass. One condition to perform an ANCOVA is that there should be no interaction between main factors and the covariate. Neither species nor successional stage interacted with \ln biomass. To test the effect of successional stage on the species response a one-way ANOVA was carried out for each species, with successional stage as factor and \ln biomass as covariate (when applicable). HGR, RGR, LAR and NAR were \ln -transformed prior to analysis to increase homoscedasticity.

Leaf production was analyzed using a repeated measurement ANOVA with season as within factor (two dry and two wet seasons), and successional stage and species as between factors. The Bonferroni test was used as post-hoc test. *Cedrela* was not included in this analysis because not enough data of this species were available.

I used Pearson's correlation coefficient to determine how allocation patterns (LMF, SMF, RMF), morphological characteristics (SLA, LAR) and assimilation rate (NAR) affected species mortality and growth. In the case of

mortality, the correlations were done using the data of the 20 year old secondary forest, where survival was lowest. In the case of growth, the correlations were done using the data of the 1 year old regrowth, where growth was highest. To quantify the mortality rate of each species in the 20 years old secondary forest, I regressed the total number of surviving individuals against time. The slope was then used in the correlations. Steeper slopes correspond to high mortality rates, or for that matter to low survival rates. The total number of surviving individuals ($x + 1$) was ln-transformed a priori.

Results

Canopy openness

Average canopy openness varied from 8.9 % in the 1 year old regrowth to 5.9 % in the 20 year old secondary forest (Fig. 1), and did not differ significantly among successional stages (Kruskal Wallis, Chi square = 0.25, $p = 0.88$). The 1 year old regrowth had a higher variation in canopy openness than the 10 and 20 year old secondary forest. With the program used to estimate the canopy openness, I also calculated the total site factor (ter Steege 1997). The total site factor is calculated assuming no cloudy days, and indicates the percentage of irradiance which is received compared to the open. The total site factor was 19, 14 and 11 % for the 1 year old regrowth, the 10 and the 20 year old secondary forests, respectively.

Survival

At the end of the experiment 32 % of the seedlings were still alive. The survival rate varied with successional stage (Cox regression, Wald statistic = 91, $p < 0.001$), so that seedling survival decreased significantly as age of

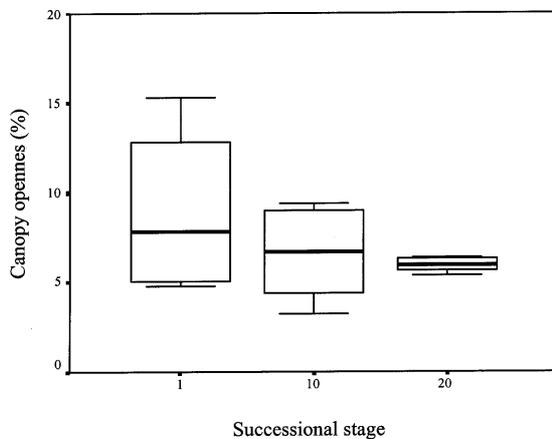


Fig. 1. Canopy openness (in %) in the different successional stages. Boxes indicate the 10th, 25th, 50th, 75th and 90th percentile. Data are mean per plot. Sample size was 4 for the 1 year old regrowth and 6 for the 10 and 20 years old secondary forests.

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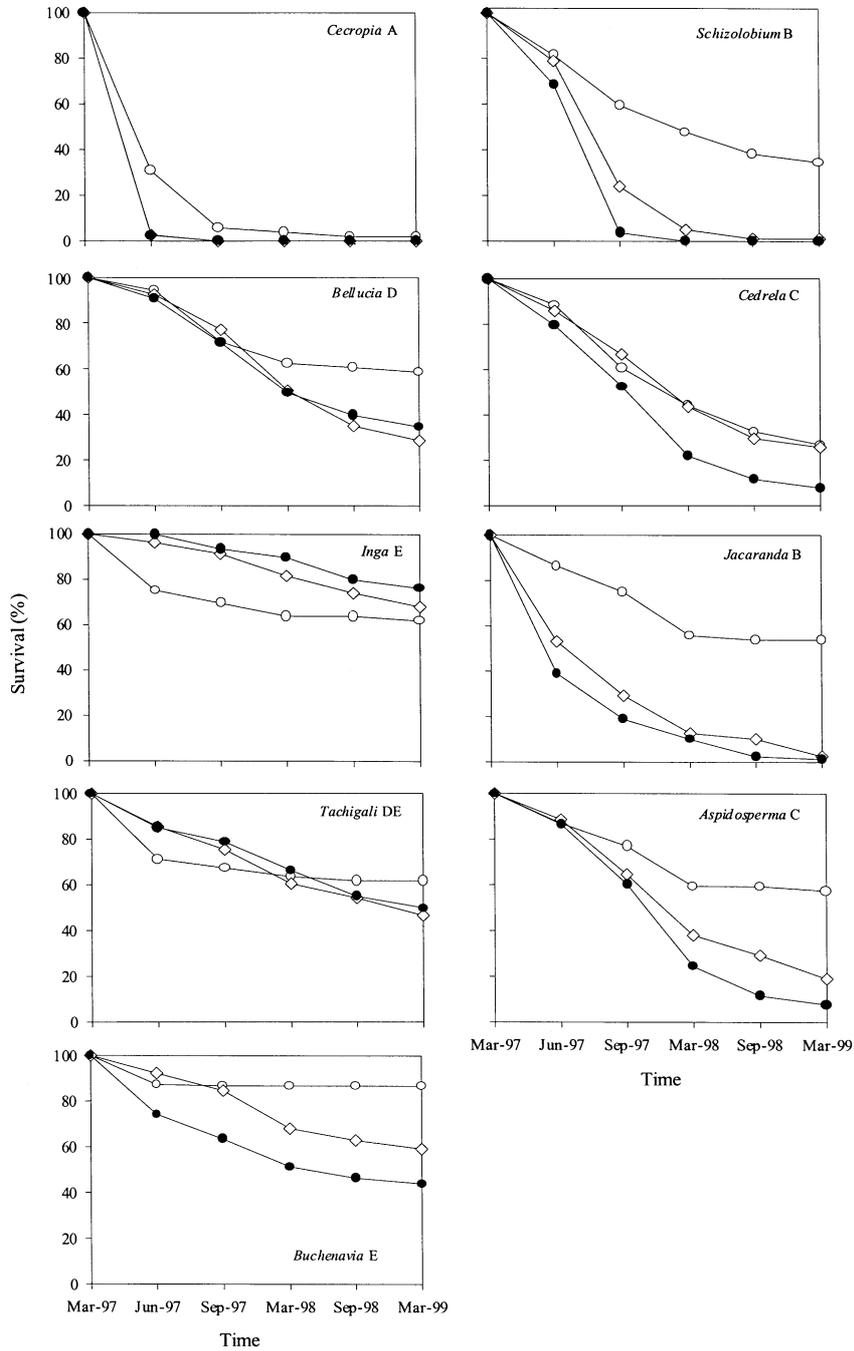


Fig. 2. Survival percentage through time for the different species. Species are ordered according to light requirements (from pioneer to shade tolerant species, see Table 1). Open circle = 1 year old regrowth, open diamond = 10 year old secondary forest, and black circles = 20 year old secondary forest. For *Cecropia* the line of the 10 and 20 years old secondary forest follow the same trajectory. Species names followed by the same letter do not differ from each other ($p > 0.0014$).

successional stage increased (48, 29, and 25 % survival by the end of the experiment in the 1 year old regrowth, the 10 and the 20 year old secondary forests, respectively). The survival rate also varied with species (Cox regression, Wald statistic = 590, $p < 0.001$, Fig. 2). *Cecropia* had the lowest overall survival (0.5 %) and *Tachigali*, *Buchenavia*, and *Inga* the highest ones (51, 61, 70 %, respectively). For most of the species survival decreased as age of the site increased, while for *Cecropia*, *Inga* and *Tachigali* survival did not differ among successional stages (Fig. 2).

Species with a high survival in the 1 year old regrowth did also have a high survival rate in the 10 and 20 year old secondary forests, so that no reversals in terms of survival occurred among the different successional stages (Spearman's correlation; 1 vs. 10: $r = 0.84$, $p = 0.005$, $n = 9$; 1 vs. 20: $r = 0.76$, $p = 0.017$, $n = 9$).

Growth

In general, HGR and RGR decreased as forest age increased (Table 3, Fig. 3). Both HGR and RGR were considerably higher in the 1 year old regrowth than in the 10 and 20 year old secondary forests.

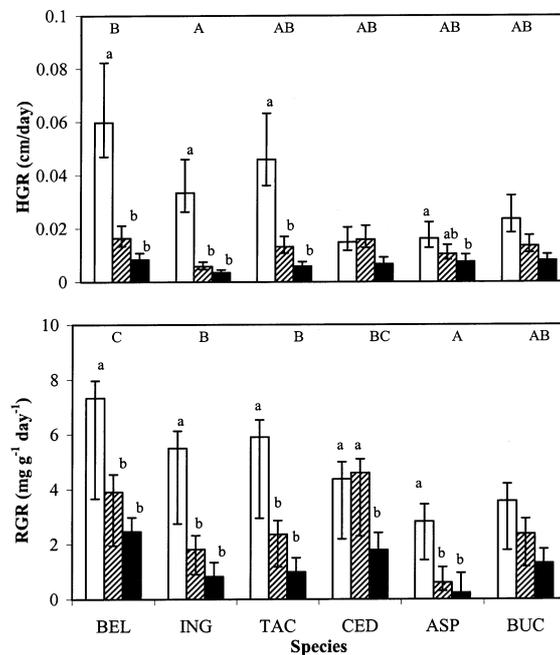


Fig. 3. Height growth rate (HGR) and relative growth rate (RGR) of six tree species growing in different successional stages. Data shown are back-transformed logarithmic means (\pm SE). Among and within species, bars followed by a different letter are significantly different ($p < 0.05$). Within species only significant differences are shown. Open bar is 1 year old regrowth, cross-hatched bar is 10 year old secondary forest, and black bars is 20 year old secondary forest. For species abbreviations see Table 1.

Table 3. Results of two-way ANOVA testing for effect of successional stage and species on variables related to growth (HGR, RGR), biomass allocation (RMF, SMF, LMF), morphology (SLA, LAR) and assimilation (NAR). For the allocation and morphology variables ln biomass at the end of the experiment was used as covariable in the model. F-values, significance (p), slopes (b) and coefficient of determination (r^2) of the model are given. HGR, RGR, LAR, NAR were transformed prior analysis to increase homoscedasticity.

Group	Biomass			Age		Species		Age x Species		r^2
	b	F	p	F	p	F	p	F	p	
HGR				47.4	<0.001	4.0	0.003	2.2	0.027	0.66
RGR				56.3	<0.001	10.9	<0.001	2.2	0.025	0.73
RMF	-0.040	26.1	<0.001	3.6	0.032	9.1	<0.001	0.8	ns	0.70
SMF	0.007	0.9	ns	2.1	ns	16.6	<0.001	2.7	0.008	0.67
LMF	0.048	18.4	<0.001	5.6	0.005	11.8	<0.001	1.8	ns	0.74
SLA	-0.637	0.6	ns	14.6	<0.001	37.2	<0.001	4.9	<0.001	0.84
LAR	0.089	5.5	0.022	20.7	<0.001	8.4	<0.001	5.7	<0.001	0.73
NAR				51.8	<0.001	1.7	ns	0.8	ns	0.63

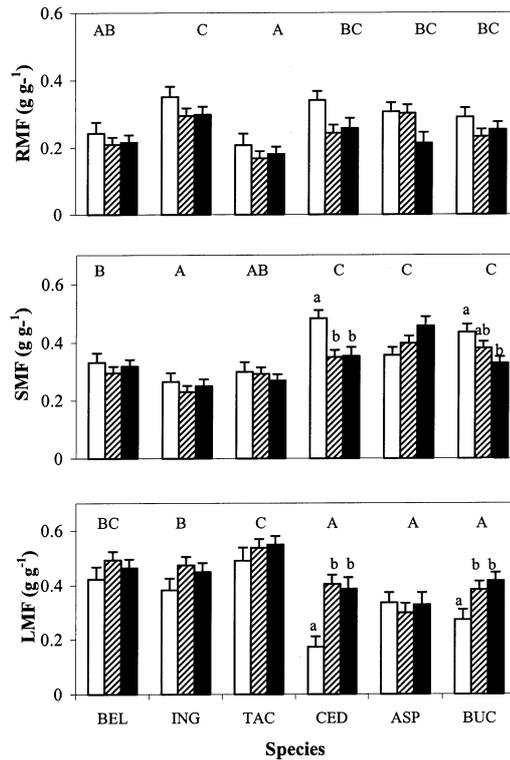


Fig. 4. Biomass allocation (RMF, SMF, LMF) of six tree species growing in different successional stages. Data shown are means \pm SE at a common mass (0.62 g). Among and within species, bars followed by a different letter are significantly different ($p < 0.05$). Within species only significant differences are shown. Open bar is 1 year old regrowth, cross-hatched bar is 10 year old secondary forest, and black bars is 20 year old secondary forest.

Table 4. Leaf production rate (number of leaves month⁻¹) during different seasons per successional stage and species. Data presented are mean ± SE.

	Dry '97	Wet '98	Dry '98	Wet '99
Age				
1 year	0.41 ± 0.03	0.78 ± 0.06	0.49 ± 0.04	0.80 ± 0.11
10 year	0.28 ± 0.03	0.53 ± 0.05	0.25 ± 0.04	0.58 ± 0.10
20 year	0.13 ± 0.03	0.41 ± 0.05	0.15 ± 0.04	0.45 ± 0.11
Species				
<i>Bellucia</i>	0.31 ± 0.04	0.67 ± 0.07	0.27 ± 0.05	0.77 ± 0.14
<i>Inga</i>	0.17 ± 0.04	0.43 ± 0.06	0.22 ± 0.05	0.56 ± 0.13
<i>Tachigali</i>	0.16 ± 0.03	0.35 ± 0.06	0.16 ± 0.04	0.30 ± 0.12
<i>Aspidosperma</i>	0.27 ± 0.04	0.32 ± 0.08	0.34 ± 0.06	0.25 ± 0.16
<i>Buchenavia</i>	0.46 ± 0.03	1.10 ± 0.06	0.50 ± 0.04	1.19 ± 0.13

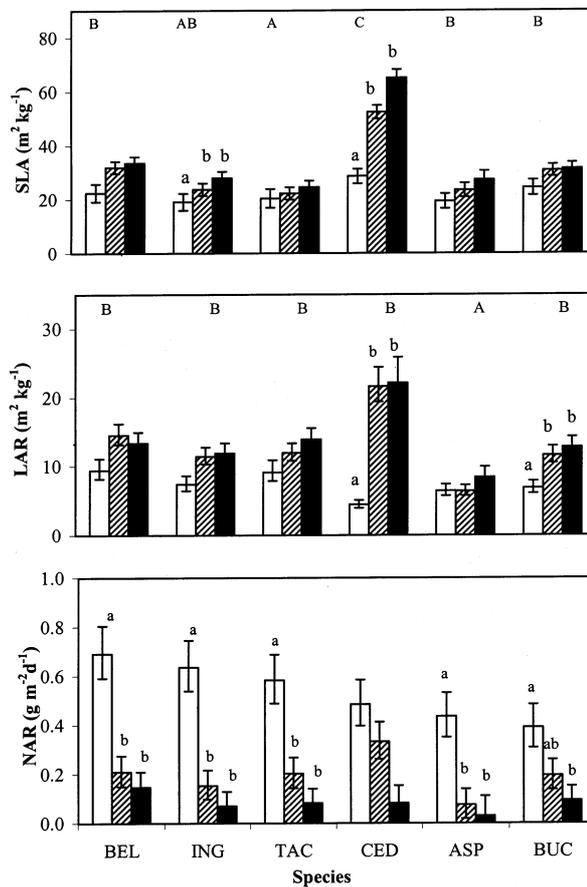


Fig. 5. Morphological characteristics (SLA and LAR) and assimilation rate (NAR) of six tree species growing in different successional stages. SLA data are mean ± SE, while LAR and NAR are back-transformed logarithmic means (± SE). SLA and LAR are estimates at a common biomass (0.62 g). Among and within species, bars followed by different letters are significantly different (p < 0.05). Within species only significant differences are shown. Open bar is 1 year old regrowth, cross-hatched bar is 10 year old secondary forest, and black bars is 20 year old secondary forest.

Table 5. Results of the Pearson's correlation analyses in which the species mortality rates and the relative growth rates were correlated to plant traits. For mortality, data of the 20 years old secondary forests are used (n = 6 species), while for growth data of the 1 year old regrowth are used (n = 8 species). r_s = correlation coefficient, ns = non-significant.

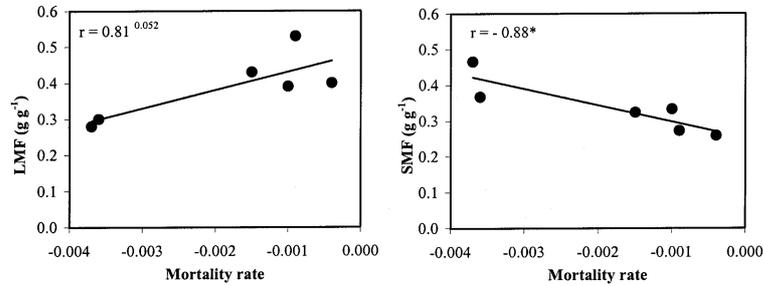
	Mortality rate		Relative growth rate	
	r_s	p-value	r_s	p-value
<i>Allocation</i>				
LMF	0.81	0.052	0.72	0.043
SMF	-0.88	0.020	-0.56	ns
RMF	-0.14	ns	-0.35	ns
<i>Morphology</i>				
SLA	-0.58	ns	-0.19	ns
LAR	-0.20	ns	0.81	0.015
<i>Assimilation</i>				
NAR	0.41	ns	0.75	0.033

Species differed in their HGR and RGR (Table 3). Combining the HGR data over all successional stages, only *Inga* and *Bellucia* differed significantly from each other, all other species were intermediate (Fig. 3). Species responded differently to successional stage (Table 3): some had a higher HGR in the 1 year old regrowth than in the 10 and 20 year old secondary forest (*Bellucia*, *Inga*, *Tachigali*, *Aspidosperma*), while others had the same HGR in all successional stages (*Cedrela* and *Buchenavia*, Fig. 3). Combining the RGR data over successional stages, *Aspidosperma* had the lowest RGR, while *Bellucia* had the highest one. All other species were intermediate. The interaction found between age and species is probably due to *Cedrela* and *Buchenavia* (Table 3). The RGR of *Cedrela* was equal in both the 1 and 10 year old secondary forest, and the RGR of *Buchenavia* was similar in all successional stages (Fig. 3).

The RGR of the species in the 1 year old regrowth was not correlated with the RGR in the 10 and 20 year old secondary forest (Spearman's correlation; 1 vs. 10: $r = 0.37$, $p = 0.47$, $n = 6$; 1 vs. 20: $r = 0.54$, $p = 0.27$, $n = 6$).

The LPR was higher in the wet than in the dry season (Repeated measurement ANOVA, for season: $F_{1,52} = 36.2$, $p < 0.001$). The interaction between season and species was significant (Repeated measurement ANOVA, $F_{6,08} = 5.41$, $p < 0.001$), probably mainly due to the relatively constant LPR of *Aspidosperma* (Table 4). The LPR decreased as the age of the site increased (Repeated measurement ANOVA, for age: $F_{2, 53} = 12.54$, $p < 0.001$), and it varied among species (Repeated measurement ANOVA, for species: $F_{4, 53} = 16.7$, $p < 0.001$). Over seasons and successional stages, *Tachigali* had the lowest LPR (0.24 leaves month⁻¹), while *Buchenavia* had the highest one (0.81 leaves

A. MORTALITY IN THE 20 YEAR OLD SECONDARY FOREST



B. GROWTH IN THE 1 YEAR OLD REGROWTH

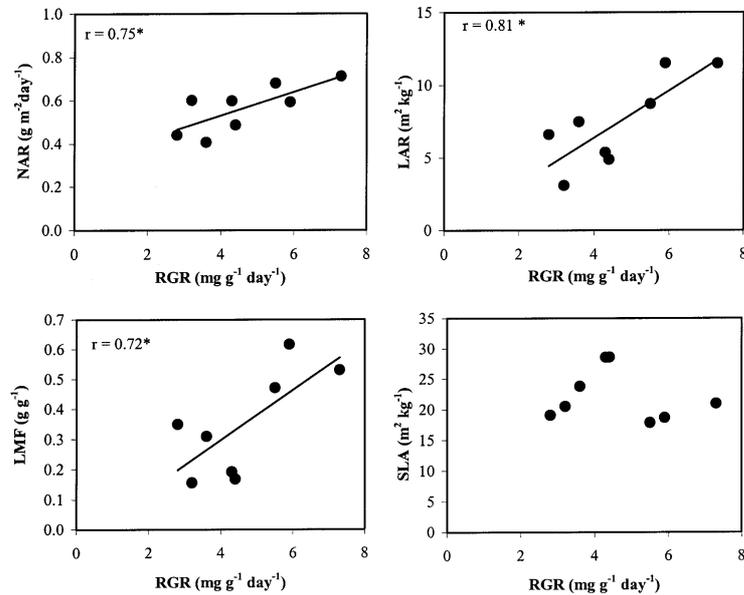


Fig. 6. LMF and SMF related to mortality rate in the 20 year old secondary forests (A), and NAR, LAR, LMF, SLA related to RGR in the 1 year old regrowth (B). Values shown are species mean at a given successional stage. Correlation coefficients and significance levels are also shown. * $P < 0.05$.

month⁻¹). The interaction between successional stage and species was not significant (Repeated measurement ANOVA: $F_{8, 53} = 1.3$, $p = 0.26$).

Survival rate versus growth

Survival rate and RGR of species at a given successional stage were not correlated with each other (for all possible correlations, $n = 6$). Species survival rate in the 20 year old secondary forest and species RGR in the 1 year old regrowth tended to be positively correlated (Spearman's correlation; $r = 0.63$, $p = 0.07$, $n = 9$).

Allocation, morphology and assimilation

All parameters but SMF varied with successional stage (Table 3). Combining all species, plants growing in the 1 year old regrowth had a lower LMF, SLA and LAR, and a higher RMF than plants growing in the 10 and 20 year old secondary forests. Species differed significantly from each other in all variables measured (Table 3, and Fig. 4 and 5). The interaction between species and age was significant for SMF, SLA and LAR (Table 3), probably due to *Cedrela* and *Buchenavia*. Both of them had a significantly higher SMF, lower SLA, and lower LAR in the 1 year old regrowth than in the 10 and 20 year old secondary forest, while all other species did not show significant differences among successional stages (Fig. 4, Fig. 5). *Inga* showed the same response as *Cedrela* and *Buchenavia* for SLA.

NAR was affected only by successional stage (Table 3). It was high in the 1 year old regrowth and much lower both in the 10 and the 20 year old secondary forests. NAR tended to decrease from pioneer to shade tolerant species but differences among species were not significant (Table 3).

What plant traits are related to mortality and growth?

Mortality rate in the 20 years old secondary forests was only significantly correlated to LMF and SMF (Table 5, Fig. 6). RGR in the 1 year old regrowth was correlated to NAR and LAR. The effect of LAR on RGR was mostly due to LMF, which correlated positively to RGR (Table 5, Fig. 6).

Discussion

Light

Irradiance has been reported to decrease during secondary succession (Saldarriaga 1994, Ellsworth & Reich 1996, Chapter 4). Regrowth of the vegetation is very fast, and after 1 year the canopy openness has declined to a value of 8.9 % at 0.7 m aboveground. There was a decline in canopy openness with succession, although differences among successional stages were not significant. This is probably due to the large variation in canopy openness found in the 1 year old regrowth (Fig. 1), and the method used to assess the light availability. The patchiness of the vegetation early in succession causes that light is not evenly and equally distributed throughout the area. At individual plots, the canopy openness at a given spot could be two to five times higher than in another one (data not shown). This high variation in light in the young areas was also reflected into a higher variation in plant parameters of seedlings growing in those areas. For example, the total height of individual

plants ranged from 3 to 203 cm in the 1 year old regrowth, while it ranged from 4 to 86 cm, and 5 - 32 cm in the 10 and 20 year secondary forests, respectively. Furthermore, hemispherical photographs provide only a first approximation of the actual light availability, as in the analysis leaves are presumed not to transmit any light. Moreover, differences in irradiance due to differences in number of overlapping leaves are not picked up by the method.

The decrease in growth and changes in allocation and morphology found with an increase in stand age parallels the plant responses found in controlled studies with a decrease in irradiance. Therefore, although I did not find significant differences in canopy openness among successional stages, I do believe that the sites differed in the amount of irradiance, and that irradiance explains the plant responses observed in this experiment.

Survival

In general, species had a higher survival rate in the 1 year old regrowth than in the 10 and 20 year old secondary forest (Fig 2). The similar survival rate in the 10 and 20 year old secondary forests is probably related to the fact that these forests have a more similar forest structure, and therefore, similar light levels. A positive effect of higher light levels on survival has also been reported for other tree species (Osunkoya et al. 1992, Augspurger 1984a, Augspurger 1984b, Kobe 1999, Walters & Reich 2000, Rose 2000). This positive effect may be due to an enhanced growth in high light. Taller seedlings are able to intercept more light, which in turn may help them to store more carbohydrates to overcome stressful events (such as drought, damage, herbivory). This result implies that most species have a higher chance of surviving when they establish early in succession than later on.

Species differed in their survival rate (Fig. 2), light demanding species (*Cecropia*, *Schizolobium* and *Jacaranda*) having a lower survival rate than more shade tolerant species (*Tachigali*, *Buchenavia* and *Inga*). As a consequence, there is a positive correlation between the survival percentages of species in the younger and older successional stages. The higher mortality of light demanding seedlings is also observed in other studies (Augspurger 1984a, Boot 1993, Walters & Reich 2000), and has been related to herbivory and drought (Coley 1988, Reich et al. 1991) Another possible cause is that the light level of the 1 year old regrowth was already sub-optimal for the survival of *Cecropia*, *Schizolobium* and *Jacaranda*. All of them are known to survive better in high light levels than under low light levels (Poorter & Hayashida 2000, Chapter 4). *Bellucia* had a fairly high survival in the shade (Fig. 2), although it is a

typical pioneer species that is found as seedling and sapling only in younger successional stages (van Uft 1998). No naturally occurring seedlings have been found in secondary forests of 20 years, although adults of this species dominated the canopy and had a constant fruit production. Consequently, its distribution is more likely to be restricted by its germination requirements than by its survival requirements. These results suggest that pioneer species and certain long-lived pioneer species have a restricted time-window of opportunity in which they can establish in succession, and that their light requirement for survival limits their regeneration in older successional stages.

It has been proposed that long-lived pioneer species establish at the same time during succession as pioneer species because they require high light levels for survival (Finegan 1996, Guariguata 2000). My results suggest, however, that within the group of long-lived pioneer species there is a large variation in light requirement for survival. This range seems to vary from high light demanding species, whose successful establishment is restricted to early successional stages (such as *Jacaranda*, Fig. 2) to more shade tolerant species (such as *Inga* and *Tachigali*) that survive in a broad range of successional stages. The latter species are likely to be able to form a seedling bank below the canopy of pioneer species. These seedlings would benefit from canopy gaps created in the course of succession due to the death of dominant tree species like *Cecropia* or *Bellucia*. Seedlings and saplings growing in the understory of secondary forests have been found to respond with increased growth to canopy openings (Mesquita 2000).

Growth

The growth of seedlings decreased with age of successional stage (Fig. 3). Similar responses have been found in studies that have assessed seedling growth under high and low light levels (Veneklaas & Poorter 1998, and references therein). These results suggest that regardless of the shade tolerance of the species, it would be advantageous to arrive early in succession when light levels are still high (at many spots). Assuming that all species have an equal probability to arrive at an area undergoing succession, then species which have the highest RGR would be the ones most likely to dominate the canopy of early successional stages. In a study performed in gaps of different sizes in Guyana, the fastest growing species (which had the smallest seed size) indeed became dominant in gaps larger than 200 m² after 5 months (Rose 2000). Fast-growing species such as *Trema*, *Cecropia*, and *Ochroma* have been found to dominate the early successional stages elsewhere in the Neotropics (Budowski 1965, Finegan 1996). These results suggest that under high light conditions differences in species growth rates play an important role in

determining the species composition of the canopy of early successional stages (cf. Glitzenstein et al. 1986, Finegan 1996).

In general, pioneer and long-lived pioneer species tended to have higher RGR than shade tolerant species in young and old successional stages (Fig. 3) (cf. Veneklaas & Poorter 1998 and reference therein, Agyeman et al. 1999, George & Bazzaz 1999, Walters & Reich 2000). Pioneer species perform better than shade tolerant species because of their higher photosynthetic capacities and high leaf turnover rates in high light (Kitajima 1994, Ellsworth & Reich 1996, Strauss-Debenedetti & Bazzaz 1996), and higher LAR in low light (Osunkoya et al. 1993, Kitajima 1994, Veneklaas & Poorter 1998).

The RGR of species in high and low light are positively correlated (Popma & Bongers 1988, Boot 1993, Kitajima 1994, Poorter 1999). This correlation was, however, not significant in this study. That may be related to the fact that few species are included in the analysis (only six species). It could also be due to the fact that *Inga* and *Tachigali* had much lower RGR in the 10 and 20 year old secondary forests than expected, based on their RGR in the 1 year old regrowth (Fig. 3). These species survived equally well in all successional stages (Fig. 2). It is possible that under lower light conditions they traded growth potential for survival by allocating more biomass to defense than to growth (Kitajima 1996, Coley 1988).

Is there a trade-off between growth and survival?

In this study, the RGR in 1 year old regrowth tended to be positively correlated with the survival rates in the 20 year old secondary forest. Other studies found a trade-off between high-light growth and low-light survival. These studies included a broad range of light levels (e. g. Kobe et al. 1995, Kobe 1999, Rose 2000) or the low extreme of the light range (0.6 % to 7.3 %; Walters & Reich 2000). My values of daylight are intermediate (range from 11 - 19 %), suggesting that the trade-off among growth and survival is only observed when extreme light values are present.

Allocation and morphology

Successional stage had also an effect on biomass allocation and seedling morphology (Table 3). Seedlings growing in the 1 year old regrowth invested more biomass in their roots (Fig. 4) to increase water uptake. At the same time they had lower SLA, LAR (Fig. 5) and leaf area to root mass ratios (data not shown) to reduce transpiration (Poorter & Nagel 2000). Additionally, the low SLA and higher irradiance allowed for high photosynthetic rates, and consequently, the NAR was highest in the 1 year old regrowth. At older

successional stages, light is a limiting resource, and seedlings enhance their light interception by allocating more biomass to their leaves (Fig. 4), and by producing leaves with a high SLA, which results in a high LAR (Fig. 5). Similar patterns of biomass allocation, morphology, and assimilation have been reported for other studies comparing seedlings growing under low and high light conditions (Pompa & Bongers 1988, Osunkoya et al. 1993, Veenendaal et al. 1996, Poorter 1999).

What plant traits are related to mortality and growth?

Mortality of species in the 20 years old secondary forest was positively related to LMF and negatively related to SMF (Table 5). Species with high LMF had high survival rates (i.e., low mortality rates) (Fig. 6). High biomass allocation to the leaves may enhance light interception in a light-limited environment, allowing plants to maintain a positive carbon balance, and therefore, to have a higher survival. Controlled experiments have shown that in low light, species with a high SLA have also a high RGR (e.g. Poorter & van der Werf 1998, Poorter 1999). Leaves with a high SLA, however, are probably more sensitive to mechanical damage and herbivory (Reich et al. 1991, Kitajima 1996). Under field conditions species with a high SLA may therefore have a high mortality rate. In my data I found such a negative relation between SLA and survival rate, although it was not significant (Table 5). A high biomass allocation to the stem resulted in low survival rates (i.e., high mortality rates) (Fig 6). That may be due to the fact that a high SMF may represent a burden to the plant because of respiration costs (Givnish 1988 but see Veneklaas & Poorter 1998).

In the 1 year old site, the RGR of species was positively correlated with NAR and LAR. The effect of NAR and LAR on RGR was of similar magnitude, as indicated by their correlation coefficients (Fig. 6). Other studies have found similar results for seedlings growing in large gaps (39 - 53 % daylight, Popma & Bongers 1988), or at intermediate light levels (25 % daylight, Poorter 1999). Variation in LAR among species was related to LMF and not SLA, as reported in other studies (Kitajima 1996, Poorter 1999).

Conclusions

Pioneer tree species have a small time-window of opportunity during succession to establish due to their high light requirements for establishment. Long-lived pioneer species show a large variation of responses, implying that their recruitment is not restricted to early successional stages as has been proposed before (Finegan 1996, Guariguata 2000). Additionally, my study supports the idea that different plant traits are important for determining high

survival rates in low light than high growth rates in high light, as has been proposed before (Kitajima 1994, Kitajima 1996). My data also indicate that there is not a trade-off between growth and survival when intermediate light levels are considered. Consequently, differences in survival and growth rates among species at different successional stages should play an important role in determining the set of species that will be present in a given successional stage.

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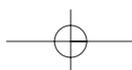
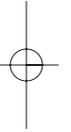
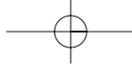
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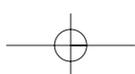
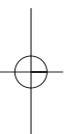
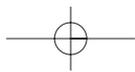
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Appendix 1. Total height, leaf area, and leaf, stem and root biomass of seedlings at the initial and final harvest in the different successional stages. Data shown are raw data and are mean values per successional stage. Plots = number of plots in which seedlings of a given species were found; n = total number of seedlings at a given successional stage.

Species	Height (cm)	plots	n	Leaf area (cm ²)	Leaf mass (g)	Stem mass (g)	Root mass (g)
Initial harvest							
<i>Bellucia</i>	7.3		30	16.7	0.038	0.014	0.010
<i>Cecropia</i>	2.6		29	11.1	0.056	0.011	0.017
<i>Schizolobium</i>	22.7		30	133.0	0.446	0.443	0.147
<i>Cedrela</i>	7.1		18	6.20	0.009	0.015	0.007
<i>Inga</i>	7.2		30	15.9	0.090	0.034	0.017
<i>Jacaranda</i>	6.8		30	13.1	0.047	0.019	0.014
<i>Tachigali</i>	7.9		30	21.1	0.130	0.052	0.039
<i>Aspidosperma</i>	8.9		30	13.1	0.098	0.047	0.028
<i>Buchenavia</i>	10.8		30	24.8	0.106	0.051	0.029
Final harvest							
2 year old							
<i>Bellucia</i>	52.9	4	31	1515.3	9.442	7.281	2.080
<i>Cecropia</i>	29.0	1	1	47.8	0.120	0.307	0.072
<i>Schizolobium</i>	64.8	3	18	295.8	2.686	6.097	1.322
<i>Cedrela</i>	17.3	4	12	41.9	0.151	0.332	0.199
<i>Inga</i>	51.0	4	33	1869.9	13.782	9.068	5.323
<i>Jacaranda</i>	19.3	4	28	331.8	1.378	1.133	3.585
<i>Tachigali</i>	44.4	4	33	2469.4	15.791	7.633	1.943
<i>Aspidosperma</i>	18.4	4	29	89.4	0.540	0.471	0.487
<i>Buchenavia</i>	31.7	4	46	388.6	1.739	1.989	1.021
10 year old							
<i>Bellucia</i>	18.5	6	23	231.9	0.855	0.356	0.218
<i>Cecropia</i>		0	0				
<i>Schizolobium</i>	65.1	1	1	828.5	0.268	1.350	0.298
<i>Cedrela</i>	17.3	5	20	138.0	0.184	0.597	0.402
<i>Inga</i>	10.1	6	55	77.3	0.329	0.121	0.211
<i>Jacaranda</i>	25.7	2	2	127.4	0.416	0.720	0.547
<i>Tachigali</i>	18.0	6	37	203.6	0.982	0.434	0.188
<i>Aspidosperma</i>	15.3	5	15	29.9	0.130	0.160	0.143
<i>Buchenavia</i>	19.4	6	48	174.1	0.667	0.565	0.286
20 year old							
<i>Bellucia</i>	13.7	6	28	81.5	0.294	0.164	0.110
<i>Cecropia</i>		0	0				
<i>Schizolobium</i>		0	0				
<i>Cedrela</i>	11.3	4	6	34.6	0.052	0.052	0.046
<i>Inga</i>	7.8	6	61	32.4	0.123	0.062	0.085
<i>Jacaranda</i>	13.0	1	1	2.8	0.004	0.049	0.018
<i>Tachigali</i>	11.6	6	40	72.9	0.303	0.136	0.080
<i>Aspidosperma</i>	13.8	4	5	15.0	0.058	0.101	0.051





Chapter 6

Enrichment planting of *Bertholletia excelsa* in secondary forest in the Bolivian amazon: effect of cutting line width on survival, growth and crown traits

with Rene G. A. Boot & Jhovania Dorado - Lora

Abstract

Enrichment planting is commonly used for enhancing the density of desired tree species in secondary forests. *Bertholletia excelsa* is one of the most important economic species of northern Bolivia, and there is interest in increasing its density in secondary forests. The aim of this study was to evaluate the effect of line planting on the survival, height growth and crown traits of *Bertholletia* plants growing in a secondary forest. Seedlings were planted randomly to five different treatments: cutting lines of 2 m, 4 m, and 6 m wide, total clearing of the vegetation, and untouched vegetation; each with four replications. Light levels were estimated twice during the experiment using hemispherical photographs. Survival and height growth were measured for a period of 4 years, while crown traits were measured once.

Cutting lines with different widths resulted in significantly different canopy openness (range from 16 to 55 %). The reduction in canopy openness above the plant crown through the study period ranged from 32 to 54 % depending on the treatment. Survival rate of *Bertholletia* plants was lower in the untouched vegetation (86.5 % year⁻¹) than in the other treatments (97 % year⁻¹). After 4 years mean plant height ranged from 0.7 to 3.9 m. Height growth rate was higher during the period 1995 - 1996 than during 1998 - 1999, and it was higher in the more open treatments. The crown traits of the *Bertholletia* plants varied with plant size, and were not affected by treatment.

There was no effect of line width on survival of *Bertholletia* plants, but plants performed better in terms of height growth rate in the 6-m line width and the total clearing of the vegetation. These results indicate that for enrichment planting of secondary forests with *Bertholletia*, it is necessary to open and to maintain line widths that allow for a canopy openness in the range of 25 - 40 % to guarantee high rates of height growth.

Introduction

Secondary forests have been traditionally used as a source of forest products, and there is nowadays an increasing interest in their management (Finegan, 1992; Sips et al., 1997). The management of secondary forests is thought to be easier than the management of primary forest because their structure is simpler, there are fewer species present, and some economically important species may occur in high densities (Lamprecht, 1990; Finegan, 1992; Sips et al., 1997). When desirable species are absent or are present at low densities, then enrichment planting can be undertaken. Enrichment planting has commonly been used for restoration of previously logged forests and for increasing the timber volume and the economic value of secondary forests (Lamprecht, 1990; Ådjers et al., 1995; Montagnini et al., 1997).

Several methods of enrichment planting are used in secondary forests. One commonly used method is line planting, which basically consists in cutting lines or transects of a given width through the existing vegetation. The light level created by the line depends on the direction and width of the lines, and on the height of the surrounding vegetation (Lamprecht, 1990; Montagnini et al., 1997). Several line planting systems have been developed for different forests in different regions (Lamprecht, 1990). These systems recommend different line widths and stand management rules, trying to create light levels that allow for the maximum growth rate of the desired species (Catinot, 1965, cited in Lamprecht, 1990). The line width, however, needed to be opened (and the maintenance frequency) to create the appropriate light level for a species is apparently highly species specific (Ådjers et al., 1995; Montagnini et al., 1997). In this paper we investigate the influence of line width on the performance of seedlings of the Brazil nut tree (*Betholletia excelsa*) during a four year period.

Although line planting has been successfully applied in different places, it is not widely practiced due to the high costs associated with regular maintenance of the lines. Due to the regrowth of the vegetation in the lines and growth of the neighboring vegetation, the line closes up gradually and light levels decline. Information is needed on the rate of this closure process to be able to fine-tune weeding and maintenance activities. In this paper we study the changes in light climate that result from gradual closure of lines differing in width over a 4 year period, and relate that to the adequate light conditions for the growth of *Betholletia excelsa* seedlings.

Brazil nuts are collected from *Bertholletia excelsa* trees growing naturally in primary forests. The Brazil nut industry, which includes the collection and the processing of the fruits, is one of the main economic activities in the Bolivian Amazon. It has generated about 30 million US\$ per year during the last three years, and it has provided work to about 15 % of the total population of the region (Stoian 2000). Because of the economic importance of *Bertholletia* and its low density in primary forests, there is interest in carrying on enrichment activities with the species in secondary forest to increase its density near human settlements. In this way, the production of Brazil nut per unit area and the productivity of the Brazil nut collector per unit time would be increased (Broekhoven, 1996; Kainer et al., 1998).

The aim of this study is to determine if line planting of *Bertholletia* in secondary forests is an appropriate way of increasing its density. The specific objectives were: (1) to define the light availability of lines differing in width through time, (2) to determine the plant responses to the different line widths in terms of seedling survival, height growth rate, and tree crown traits, and (3) to define the most appropriate light availability for obtaining high height growth rates.

Methodology

Study area

The experiment was carried out in the 870 ha forest reserve El Tigre (11°59'S, 65°43'W), located in the northern Bolivian Amazon. El Tigre is the research and training area of the Programa de Manejo de Bosques de la Amazonía Boliviana (PROMAB), and is located 45 km to the east of the town of Riberalta. It receives an annual rainfall of 1780 mm with a dry season from May to September (Beekma et al., 1996). The vegetation of El Tigre consists mainly of lowland tropical moist forest and patches of secondary forests (< 25 ha) differing in successional stage. One of the secondary forest patches was used for this research. According to the local inhabitants, the area had been used for agriculture in the beginning of the 70s, and apparently also in the mid 80s. The vegetation height was 14 to 18 m at the beginning of the experiment, and it was dominated by secondary tree species such as *Cecropia sciadophylla*, *Ochroma pyramidalis*, *Bellucia pentamera*, and *Jacaranda copaia*.

Study species

Bertholletia excelsa H. B. K. (Lecythidaceae) is an emergent tree species that can reach 30 to 40 m of height. It occurs in unflooded forests (terra firme) in the Amazon basin and in the Guianas (Mori & Prance 1990). It occurs in areas with rainfall ranging from 1400 and 2800 mm/year and a dry season ranging from 2 to 7 months (< 60 mm/ month rainfall) (Diniz and Bastos 1974, cited in Kainer et al., 1998). The density of reproductive *Bertholletia* trees can vary widely throughout the Amazon (Mori & Prance, 1990; Salhuna Sanchez, 1973 cited in Broekhoven, 1996; Kainer et al., 1998). For northern Bolivia densities varying from 1 to 5 trees per ha have been reported (DHV, 1993).

Bertholletia is a light demanding species that regenerates more successfully in gaps and secondary forests than in the primary forest understory (Salomão 1991, Rijsoort et al., 1993; Myers et al., 2000;). In northern Bolivia, trees in the forest have 50 % probability of being reproductive when they reach a diameter at breast height (DBH) of 40 cm. Based on matrix modeling, trees that reach that size are estimated to be 100 - 110 years old (Zuidema, 2000). Trees in plantation begin to produce fruits after 6 to 12 years (Figueroa, 1972; Prance & Mori 1979; Mori & Prance, 1990), or 25 cm DBH in a small 15-years old plantation in northern Bolivia (Zuidema, unpublished data). There is no data on minimum age or diameter of reproduction of *Bertholletia* trees growing in secondary forests or agroforestry systems.

Experimental design

In March 1995 twenty 20 x 40 m plots were established in a secondary forest of 1.8 ha. Plots were separated from each other by a buffer zone of 5 m of natural vegetation. Plots were randomly assigned to the different treatments, so that there were 4 replicate plots per treatment. The treatments consisted of: cutting lines of 2 m, 4 m, and 6 m width, total clearing of the vegetation, and untouched vegetation. Each of the line treatments consisted of four lines per plot which were created in east - west direction by cutting all existing vegetation. An east - west direction was used to increase the time period in which the plants would receive sunlight (Lamprecht, 1990). In the total clearing of the vegetation treatment (hereafter, referred as total clearing), all the vegetation was removed. In the untouched vegetation plots the vegetation of the secondary forest was left undisturbed.

In April 1995 *Bertholletia* plants growing in a nursery in the city of Riberalta with a mean height of 25 cm (SD 12.5 cm) were planted to the

plots. A total of 160 plants were used: 8 plants per plot, and 32 plants per treatment. Plants were spaced 10 m apart from each other. Plant height was measured at the beginning of the experiment and after 1, 3, 6, 9, 12, 27 and 39 months. Plant survival was monitored during the same evaluations as plant height. Height to the first leaf and crown diameter (measured in the north - south and east - west directions) were measured only during the last evaluation to calculate crown traits.

During the first year of the study, the lines were maintained by cutting the regrowing vegetation every three months. During 1996 to 1998 the maintenance of the treatments was done three times in total, and it consisted of removing the vegetation in a 1-m diameter circle around the *Bertholletia* plants, and cutting branches that had grown over the crown of the *Bertholletia* plants. No maintenance was done during the last year of the experiment (1998 - 1999).

To characterize the light environment in each treatment and its change in time, canopy openness was estimated using 3 different sets of hemispherical photographs. All photographs were taken under overcast sky conditions using a Canon AE-1 camera with a 7.5-mm fish-eye lens and ILFORD FP 4 plus (125 ISO) black and white films. In June 1995 hemispherical photos were made in half of the plots at 1 m height aboveground, exactly above the *Bertholletia* plants (80 plants in total). In August - September 1998, hemispherical photos were made at the same height and position as in 1995 bending the plants to the side. Only half of the plants were included (i.e., 40 plants chosen in a systematic way). In this way it could be evaluated how much the lines had closed over time. Other photographs were also made above the crown of individual plants. These photographs gave an estimation of the canopy openness above the plants in 1998. Only those plants were included for which photographs were made in 1995, and that were still alive in 1998 and were > 0.70 m high. To increase sample size, 24 additional, randomly chosen plants were also incorporated, so that 89 photographs were made. The height at which this set of photographs was made varied with plant height and ranged from 0.7 m to 5.2 m. To take photographs at a height > 2 m, the camera was attached to a leveling device to maintain it horizontally, and then it was mounted on an extension pole. Negatives of 1995 were scanned using a Sony XC-77CE black and white CCD camera attached to a VIDAS image analysis system (Kontron/ Zeiss, Eching, Germany), while photographs of 1998 were scanned using a HP ScanJet 4C (1200 dpi). Afterwards the images were analyzed with Winphot 5 (ter Steege 1997) to determine canopy openness.

Hemispherical photographs provide an accurate measure of canopy openness but are labor intensive and require relatively sophisticated equipment. For the daily practice of forest management, it would be useful to have an easier way to assess light conditions. Therefore, the light conditions of 1998 were evaluated using two other techniques. First, the forest overstory density (in %) was measured at three spots in each strip using a spherical crown densiometer (Forestry Suppliers Inc., Jackson, MS, USA). The forest overstory density is a measurement of how much open space there is in the forest canopy. Four measurements were taken at each spot in the four compass directions; these were averaged per spot (Lemon, 1957), and subsequently per line. The other technique estimated the angle of canopy opening above each plant (hereafter referred to as angle of canopy opening). This angle depends on the height of the vegetation bordering the line and on the line width. If the height of the target plant remains constant, the angle of canopy opening will decrease with increasing vegetation height and/or with decreasing line width (Fig. 1). To calculate the angle of canopy opening, the height of the tallest tree found perpendicular to the line at each side of each *Bertholletia* plant was measured. Then the angle of canopy opening was estimated as $180 - (\alpha^1 + \alpha^2)$, where α^1 and α^2 are the angles, calculated as the cotangent of the height difference between the *Bertholletia* plant (x) and the tallest tree next to it (y^1 and y^2 , respectively) divided by half of the line width (Fig. 1).

Data analysis

We tested for the effects of the different treatments on light environment, survival, height growth, and crown traits. To evaluate whether the treatments resulted in initial differences in canopy openness, the canopy openness data of 1995 was analyzed with a one-way ANOVA with treatment as a factor. Differences among treatments were evaluated with a post-hoc test (Student-

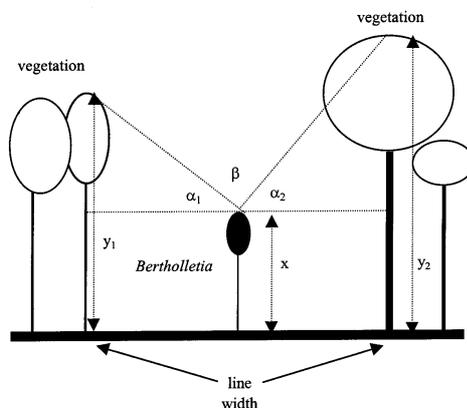


Fig. 1. Schematic diagram representing the way in which the angle of canopy opening (β) was obtained. x = total height of *Bertholletia* plant, y_1 or y_2 = total height of tallest tree next to the *Bertholletia* plant, $\alpha_1 + \alpha_2$ = the angles formed by the difference in height between y and x and half of the line width.

Newman-Keuls). Changes in the canopy openness at 1 m height aboveground through time were assessed with a repeated measurement ANOVA, with time (1995 - 1998) as within subject factor and treatment as between subject factor. Similarly, the changes in canopy openness above the *Bertholletia* plants through time were analyzed as well with a repeated measurement ANOVA. All data were arcsine transformed prior to analysis. The forest overstory density and the angle of canopy opening were related to the canopy openness above each plant in 1998 with a Spearman rank correlation.

Survival was averaged per plot, and then the fourth root was taken to account for the length of the evaluation period (4 years, sensu Sheil and May 1996). Survival rate was arcsine transformed and analyzed with a one-way ANOVA with treatment as a factor. The Student-Newman-Keuls test was used as post-hoc test.

Because the height was not measured at regular time intervals throughout the experiment, height growth rate was estimated for two different periods (1995 - 1996 and 1998 - 1999). Height growth rates were analyzed with a repeated measurement ANOVA with treatment as the between subject factor, followed by a post-hoc test (Student - Newman - Keuls test). Data were ln-transformed prior to the analysis to increase homoscedasticity. All plants that were broken by falling stems or had their apical meristem removed by animals were excluded from the data analysis (14 plants in total). Regression analyses were used to determine the relation between height growth rate and canopy openness for each evaluation period (1995 - 1996 and 1998 - 1999). Height growth rate was ln - transformed prior to analysis.

Three crown traits were calculated: the crown area ($\pi \times 0.25 \times \text{average crown diameter}^2$, in m^2), the relative crown depth ($100 \times (\text{total height} - \text{height to the first leaf})/\text{total height}$, in %) and the crown depth/crown diameter ratio. As several tree form features are size-dependent, differences in crown traits among treatments were analyzed with ANCOVA, using total height as the covariate. Differences among treatments were evaluated with a post-hoc test (Simple contrast, 10 possible contrasts, so the p value was accordingly corrected). If necessary the variable and/or covariate were ln-transformed. Only non-damaged plants were included in the analysis.

Results

The application of different treatments resulted in different levels of canopy openness in 1995 (ANOVA, $F_{4, 74} = 63.16$, $p < 0.001$). The canopy openness gradually increased with line width although there was no significant difference between the 2 m and 4 m line widths. The untouched vegetation had the lowest canopy openness while the total clearing had the highest canopy openness (Table 1). From 1995 to 1998 there was a significant reduction in canopy openness at 1 m height aboveground (Repeated measurement ANOVA, for year: $F_{1, 34} = 351.9$, $p < 0.001$). The reduction in canopy openness varied depending on the treatment (Repeated measurement ANOVA, for treatment: $F_{4, 34} = 19.6$, $p < 0.001$; Table 1). In 1998 the 6 m line width had the highest canopy openness, and all the other treatments were not significantly different from each other (Table 1). At the crown level, there was also a reduction in canopy openness but the reduction was smaller than at 1 m height aboveground (Table 1, Table 2). The 6 m line width and the total clearing had still the highest values in canopy openness at crown level three years after the treatments were applied. The forest overstory density and the angle of canopy opening were positively correlated with canopy openness above the plant in 1998 (Fig. 2).

Table 1. Mean canopy openness (\pm SD, in %) of the different treatments in 1995 and in 1998 at 1 m height aboveground and at crown level, and the corresponding reduction (%) in canopy openness from 1995 to 1998. Values in the same column followed by different letters are significantly different at $p = 0.05$ (Student - Newman - Keuls post-hoc test).

Treatment	Canopy openness at 1 m height 1995	Canopy openness at 1 m height 1998	Canopy openness at crown level 1998	Reduction at 1 m level ¹	Reduction at crown level ¹
untouched	15.8 \pm 4.7 ^a	8.0 \pm 1.9 ^a	7.7 \pm 1.9 ^a	49.4	51.3
2 m line width	29.5 \pm 9.4 ^b	11.0 \pm 3.8 ^a	16.2 \pm 7.6 ^b	62.7	45.1
4 m line width	27.4 \pm 6.9 ^b	10.9 \pm 2.5 ^a	12.7 \pm 4.5 ^{ab}	60.2	53.6
6 m line width	38.0 \pm 6.4 ^c	16.7 \pm 5.9 ^b	26 \pm 9.5 ^c	56.0	31.6
total clearing	54.7 \pm 6.8 ^d	10.7 \pm 2.2 ^a	31.8 \pm 13 ^c	80.4	41.9

¹ The reduction was calculated by taking the canopy openness of 1995 as a reference.

Table 2. Results of the repeated measurement ANOVA testing for differences between years (1995 and 1998) and among treatments in canopy openness above *Bertholletia* plants.

	SS	df	MS	F	P
Within factors					
year	2225.3	1	2225.3	143.3	< 0.001
year x treatment	174.6	4	43.7	2.8	0.035
error	792.1	51	15.5		
Between factors					
treatment	2557.9	4	639.5	40.9	< 0.001
error	798	51	15.6		

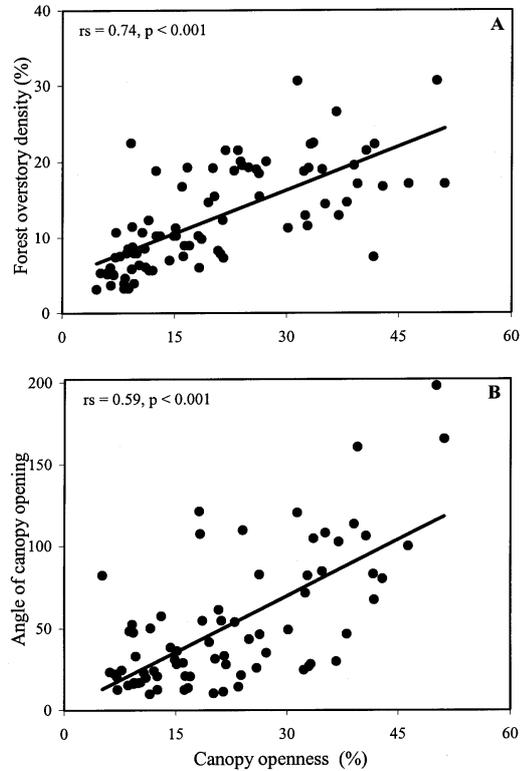


Fig. 2. The relationship between the forest overstory density (A) and the angle of canopy opening (B) and the canopy openness above *Bertholletia* plants in 1998. r_s = correlation coefficient.

In four years, 26 *Bertholletia* plants died (16.3 % of the total amount of plants). The survival rate varied with treatment (ANOVA, $F_{4, 15} = 3.76$, $p = 0.026$). The significant difference found among treatments is due to the significantly lower survival rate in the untouched vegetation than in all the other treatments (Table 3).

Table 3. Survival rate and mean height of *Bertholletia* plants growing in different treatments. Survival rate values followed by different letters are significantly different at $p = 0.05$. Survival data are mean of four plots per treatment \pm SE. Mean height data are mean of plants per treatment (at the end of the experiment) \pm SD.

Treatment	Survival rate (% y^{-1})	Mean height (m)
untouched vegetation	86.5 \pm 2.8 a	0.68 \pm 0.56
2 m line width	97.0 \pm 6.0 b	2.29 \pm 1.13
4 m line width	98.4 \pm 1.9 b	2.48 \pm 1.81
6 m line width	96.4 \pm 5.2 b	3.76 \pm 2.00
total clearing	98.4 \pm 1.9 b	3.86 \pm 1.75

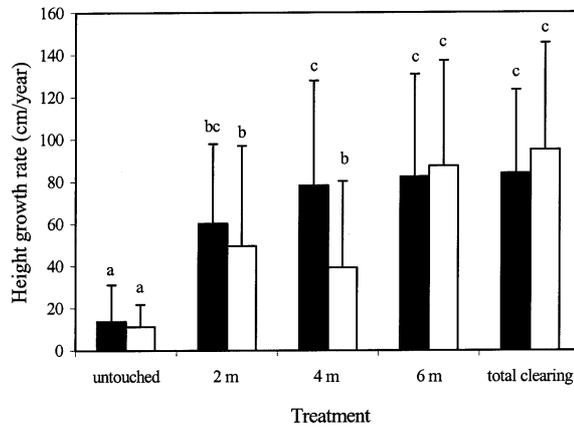


Fig. 3. Mean height growth rate (\pm SD) of *Bertholletia* plants in the different treatments during 1995 - 1996 (shaded bars) and 1998 - 1999 (open bars). Different letters represent significant differences at $p = 0.05$.

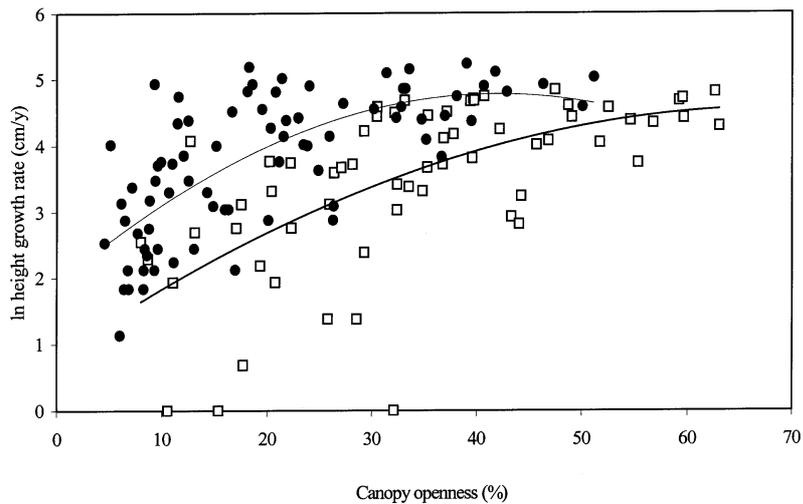


Fig. 4. Relationship between \ln height growth rate and canopy openness above *Bertholletia* plants in 1995 - 1996 (open square) and 1998 - 1999 (closed circles). The equation for 1995 - 1996 is: \ln height growth rate = $0.8104 + 0.1098$ canopy openness - 0.0008 (canopy openness)², and for 1998 - 1999: \ln height growth rate = $1.8991 + 0.1371$ canopy openness - 0.0016 (canopy openness)².

Mean plant height 39 months after transplantation ranged from 0.7 to 3.9 m, being highest in the total clearing (Table 3). In general, the height growth rate was higher in the period 1995 - 1996 than in the period 1998 - 1999 (Repeated measurement ANOVA, for year: $F_{1, 100} = 8.53$, $p = 0.004$) and higher in the more open treatments than in the untouched vegetation and the 2 m line width (Repeated measurement ANOVA, for treatment: $F_{4, 110} = 17.34$, $p < 0.001$; Fig. 3). The interaction between period and treatment was also

Table 4. Results of ANCOVA on various crown traits of *Bertholletia* plants with treatment as factor and total plant height as covariate.

Variable	Covariate	Slope covariate	Treatment		Covariate		TTT * Cov	
			F	p	F	p	F	p
Crown area ¹	total height ¹	1.414	1.31	0.272	234.85	< 0.001	2.86	0.027
Relative crown depth	total height	2.614	1.72	0.151	30.99	< 0.001	2.45	0.051
Crown depth/ crown diameter	total height	0.101	1.60	0.18	43.38	< 0.001	3.21	0.016

¹ data are ln transformed (x + 1)

significant (Repeated measurement ANOVA, $F_{4, 110} = 3.55$, $p = 0.009$) due to differences in height growth rate in the 4 m line width (Fig. 3). The height growth rates of plants in the untouched vegetation and the 2 m line width tended to decrease in time while height growth rates of plants in the 6 m line width and the total clearing tended to increase with time but differences were not significant (Fig. 3).

Height growth rate in 1995 - 1996 and 1998 - 1999 had a positive quadratic relationship with the canopy openness in 1995 ($p < 0.001$, $r^2 = 0.41$) and 1998 ($p < 0.001$, $r^2 = 0.50$), respectively (Fig. 4). At similar canopy openness, the height growth rate is higher in 1998 - 1999 than in 1995 - 1996, probably due to the fact that larger plants grow more in cm per year than smaller plants.

The crown area, the relative crown depth and the crown depth/crown width ratio increased with plant size, and were not affected by the different treatments (Table 4).

Discussion

As expected the application of the different treatments led to a higher canopy openness in the lines of different width and in the total clearing than in the untouched vegetation of the secondary forest. The 2 m and 4 m line widths did not differ in canopy openness (Table 1), although they were carefully established. This was probably due to the large local variation in forest structure. After three years the canopy openness at 1 m height aboveground had been reduced more dramatically (49 to 80 %) than the canopy openness above the crown of the plants (32 to 54 %) (Table 1). The change in canopy openness above the crown of the plants was smaller because plants maintained access to light by growing in height.

The forest overstory density and the angle of canopy opening were correlated with the canopy openness above the plants (Fig. 2). Consequently, both methods may be used to assess the light environment as alternatives to hemispherical photographs. From the two methods, the angle of canopy opening is more easily implemented than the forest overstory density because it requires very simple field measurements (plant height and line width). The use of the above mentioned methods would allow a rapid assessment of the light environment, so that the decision of cleaning the lines could be made based on actual canopy cover instead of time-fixed management prescriptions (Lamprecht, 1990). Time-based management prescriptions for maintaining enrichment lines are difficult to formulate, as the actual light levels depend on the height of the surrounding vegetation, and the closure rate of the lines.

After 4 years, the survival of *Bertholletia* plants in the different treatments ranged from 59 to 94 %. The lower survival rate found in the untouched vegetation (Table 3) might be caused by seed predation and/or low light levels (Table 1). In *Bertholletia* the cotyledons remain attached to the stem until they are gradually surrounded by lignified tissue as the plant gets taller (Kainer et al., 1998). Plants in the untouched vegetation had lower growth rates and needed more time until their cotyledons were lignified. Consequently, they had a higher mortality rate, as seedlings with unlignified cotyledons have a higher chance of getting predated by agoutis than seedlings with lignified cotyledons (Oliveira 2000, Dorado - Lora, personal observation).

It has been reported that seeds of *Bertholletia* are able to germinate in the forest understory but that the plants need higher light levels for survival and further development (Myers et al., 2000). Survival rates of seedlings (< 35 cm height) in the primary forest understory are much lower than the survival rate found in the secondary forest understory of this study (ranged from 0.49 to 0.61; Zuidema, 2000). This is probably due to lower light levels in the primary forest understory than in the secondary forest understory. Once the minimum light level is reached, however, a further increase in light levels does not affect survival since there were no significant differences in survival among the different line widths and the total clearing (Table 3). A similar finding has been reported also for different *Shorea* species planted in lines of different width (Ådjers et al., 1995).

The overall survival found in this study is higher than that found in a similar study carried out in Acre, Brazil (about 40 % after two years; Kainer et al., 1998). The difference in survival is probably due to differences in plant size at the beginning of the experiments (25 cm height in this study and 6.7

cm in the Acre study). The survival of *Bertholletia* plants in our study was also higher than the survival rate obtained for several other tree species in different enrichment planting studies (Caycedo, 1988; Ramos & del Amo, 1992; Ådjers et al., 1995; Montagnini et al., 1997). This suggests that, with regard to survival, *Bertholletia* seems a suitable species for enrichment planting activities.

The height growth rate of *Bertholletia* varied with treatment and between years (Fig. 3). In 1995 - 1996 plants growing in the untouched vegetation had the lowest height growth, whereas plants growing in the other treatments had similar height growth rates (Fig. 3). In 1998 - 1999 plants in the 2 m and 4 m line widths had lower height growth rates than in 1995 - 1996 (Fig. 3), probably related to the reduction in canopy openness from 1995 to 1998 (Tables 1 and 2). The highest reduction in height growth rate was observed in the 4 m line width, which had also the highest reduction in canopy openness (Table 1). A similar reduction in height growth rate through time has been observed in *Bertholletia* plants planted in exploitation gaps and skidding trails in Acre (Brazil). This reduction was also related to a decrease in canopy openness due to the regrowing vegetation (Oliveira 2000). Plants growing in the 6 m line width and in the total clearing maintained their height growth rates through time (Fig. 3), probably because in 1998 both treatments had still a canopy openness larger than 26 % (Table 1). High height growth rates allowed these plants to maintain their crowns at higher canopy openness levels, avoiding in this way to be completely overtopped by the vegetation growing from the sides of the lines. Differences in height increment due to differences in line widths were also found for three *Shorea* species (Ådjers et al., 1995).

The height growth rate of *Bertholletia* increased steadily with canopy openness until 25 - 40 % canopy openness was achieved, remaining at a constant high level afterwards (Fig. 4). In controlled experiments, *Bertholletia* plants growing under different light levels were found to have the higher biomass in the range between 10 to 100 % light (Poorter, 1999; Zuidema et al., 1999). *Bertholletia* plants, however, growing in very open environments such as in pastures have shown reduced height growth in comparison to plants growing in shifting cultivation plots and gaps (Kainer et al., 1998, Zuidema et al., 1999). The height growth rates obtained with a canopy openness in the range of 25 - 40 % are similar to the ones observed in pure and mixed plantations in Brazil (1.2 to 1.3 m year⁻¹; Fernandes & Alencar, 1993; Vieira et al., 1998). These results suggest that the opening and maintenance of lines that allow for a canopy openness in the range of 25 - 40 % (which correspond to an angle of canopy opening of 58 - 92°) are sufficient to obtain high height

growth rates. Above that range of canopy openness, the benefit of an increased in canopy openness is very low because the height growth rate remains relatively constant (Fig. 4).

As fruit production of *Bertholletia* is better related to crown area than to diameter at breast height (Leigue - Gomez & Boot, submitted), there is a long-term interest in creating conditions that would allow the development of large crowns. The crown area, the relative crown depth and the ratio crown depth/crown width were not affected by treatment, and they were mainly size dependent (Table 4). In order to get large crowns in a shorter time period, *Bertholletia* plants should be grown under high light conditions to allow higher height growth rates, and consequently, larger crowns.

The results of this study indicate that *Bertholletia* is a suitable species for enrichment planting activities in secondary forests. *Bertholletia* had high survival rates in lines of different width but it had a high height growth rate only in the 6 m line width and in the total clearing. These results indicate that enrichment planting with *Bertholletia* should not be performed in the untouched understory of secondary forests. They also indicate that lines that create a canopy openness in the range of 25 - 40 % (or an angle of canopy opening of 58 - 92°) should be opened for enrichment of secondary forests with *Bertholletia* plants. The line width that would create that canopy openness range depends on the height of the surrounding forest (Lamprecht, 1990, Ådjers et al., 1995). Another advantage of opening wide lines is that less maintenance is required because of several reasons. First, *Bertholletia* plants with high height growth rates are able to maintain their crowns at high canopy openness levels. Second, the canopy closure rate of wider lines is slower than the closure rate of narrow lines (Table 1). Third, three years after the opening of the lines, the canopy openness created by wide lines was still well above the height growth light saturation point of the plants.

Another option for enrichment planting with *Bertholletia* is to introduce the plants to agricultural fields still in use. Results from the total clearing treatment of this study and from a study carried out in abandoned agricultural fields (Kainer et al., 1998) show that plants respond well to high light levels in terms of survival and height growth rates (Table 3 and Fig. 3). An advantage of this method is that planting in agricultural fields requires very little additional labor (Kainer et al., 1998) and hence costs. Furthermore, the association of a tree with annual crops seem not to affect the tree growth rate, as has been shown for other tree species (Agbede, 1985; Chingaibe, 1985). Drawbacks of such a system is that plants may get stressed by the high light

intensity (Kainer et al., 1998; Zuidema et al., 1999), and that it may require regular maintenance after cessation of agricultural activities if the regenerating vegetation grows faster than the *Bertholletia* plants do. In conclusion, enrichment planting of *Bertholletia* in secondary forests or agricultural fields that are still in use seem to be sound management practices to increase the density of this species.

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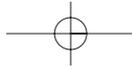
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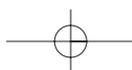
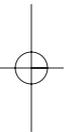
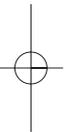
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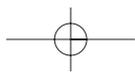
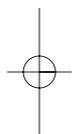
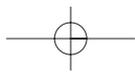
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Chapter 7

General discussion and summary

Processes in secondary succession

This study was carried out in secondary forests of the Bolivian Amazon, that were the result of slash-and-burn agriculture. One of the objectives of this thesis was to study some of the processes that determine the presence and abundance of tree species in secondary forests. Differences in the life cycle and in the life history among species are thought to play a key role in determining the course of succession (Finegan 1984, Glitzenstein et al. 1986, Pickett et al. 1987, Bazzaz 1991). Pickett et al. (1987) have recognized three conditions for the occurrence of succession: 1) availability of open sites, 2) differential availability of species to colonize a site, and 3) differential performance of species at the site (Pickett et al. 1987). The focus of this study is on processes and factors that affect the last two conditions. In the field experiments carried out I studied seed removal, germination, survival and growth rates of tree species differing in shade tolerance. All these experiments were carried out in different successional stages. The main results are summarized in the following paragraphs.

Seed removal

Seeds of nine rain forest tree species dispersed into secondary and mature forests were removed at high rates (Chapter 3). Seven weeks after dispersal, the seed removal rates varied from 50 to 100 % depending on the species, and from 74 to 90 % depending on the successional stage. The seed removal rates were not related to seed size. This suggests that both ants and rodents were present in the different successional stages. Ants are known to remove small seeded species, while rodents remove larger seeded species, so that within a particular successional stage all the studied species had a similar probability of being removed. The probability of being removed varied with successional stage. Removal rate was higher in the 2 year old regrowth and 10 year old secondary forest than in the 20 year old secondary forest and mature forest. This suggests that the density of removal agents varied with successional stage. Ants are known to be present in higher densities in younger successional stages than in older ones (Kaspari 1995, Vasconcelos & Cherret 1995), while small mammals are likely to prefer the dense vegetation of young secondary forests to hide from large predators (e.g., Manson & Stiles 1998). Although the final fate of the removed seeds was not assessed, other studies have showed that a small percentage of the removed seeds are able to germinate.

The results of this study support the idea that post-dispersal seed removal plays a role in the establishment of trees in abandoned agricultural areas. Seed removal rates decreased with an increased in forest age, so that seeds dispersed to younger stages of succession had lower chances of surviving than seeds dispersed to older ones. This has different implications for tree species differing in shade tolerance. Shade tolerant species are known to establish themselves slowly in areas undergoing succession. This may be due to the fact that they have other establishment requirements than pioneer species (Finegan 1984, Uhl 1987) or that their seeds arrive to the area in smaller quantities than the seeds of pioneer species (Uhl et al. 1981, Uhl 1987). The latter case combined with a higher seed removal rate in younger stages of succession may explain better the low density of forest tree seedlings found in young successional stages (Uhl et al. 1981). Pioneer tree species, on the other hand, get established in higher densities in younger successional stages. Apparently they are able to overcome the high seed removal rates typical of younger stages of succession. A massive seed production, a seed production throughout the year, and a high seed dispersal rate are probably important characteristics that compensate for the high seed removal values found in early stages of succession.

Germination rate

Germination success varied largely among tree species, ranging from 0.6 to 59 % after 3 - 7 months (depending on the species). For most of the six study species germination success varied with successional stage (Chapter 4). All species had little or no germination in the agricultural fields, probably due to dessication. This indicates that even pioneer tree species need some shade for germination. Contrary to the belief that pioneer species and long-lived pioneer tree species require high light levels for germination (e.g., Swaine & Withmore 1988, Finegan 1996), all six species included in the experiment except for *Jacaranda copaia* were able to germinate in secondary forests ≥ 10 years old and in mature forests. A pioneer (*Cecropia sciadophylla*) and two long-lived pioneer species (*Cedrela odorata* and *Inga thibuadiana*) had even higher germination rates in the older successional stages than in the younger ones. These results suggest that germination requirements are not necessarily the limiting factor for the establishment of pioneer and long-lived pioneer species in older successional stages.

Leaf litter may represent a physical barrier to reach the light for seedlings emerging from the seed bank, or to reach the soil for seedlings emerging from seeds recently dispersed to the site on the litter layer. In this study, the presence of litter delayed or reduced the germination success of three of the six studied species: the two small seeded ones (*Bellucia pentamera* and *Cecropia sciadophylla*) and of *Inga thibuadiana*. The leaf litter thickness increases with stand age, and it is higher in the dry than in the wet season. Therefore, the effect of leaf litter on the germination success will depend on the species considered, the successional stage in which the seeds are dispersed and on the period of the year.

Survival

Seedling survival was studied in two different experiments. In the first one, the survival of recently germinated seedlings was followed for approximately 11 to 14 months depending on the species (Chapter 4). In the other study, relatively older seedlings were planted in different successional stages, and their survival was followed for two years (Chapter 5). In that way, it was possible to look at survival rates after germination and survival rates after seedling establishment.

In the first study, survival of recently germinated seedlings varied among species. Of some species not one individual survived until the end of the

experiment, while others had relatively high survival (79%) over a period of approximately 11 to 14 months. Different species showed again different responses to the successional stage (Chapter 4). As expected, pioneer species had higher survival rates in the younger successional stages than in the older ones. At the end of the experiment, the only surviving individuals of these species were growing at the agricultural fields, which had the highest light levels from all successional stages. Combining these results with that of the germination study, it becomes clear that pioneer seedling survival is a more crucial factor in determining the abundance of pioneers in different successional stages than germination. Consequently, pioneer tree species are restricted to younger stages of succession because of their light requirements for survival and not necessarily because of their requirements for germination (cf. Kyereh et al. 1999). Long-lived pioneer species showed a variety of responses, ranging from species showing high survival rates in younger (*Cedrela odorata*, *Jacaranda copaia*) or in older successional stages (*Inga thibuadiana*) to species surviving equally well in all successional stages (*Tachigali* cf. *vasquezii*). Thus, these species do not necessarily require a high light level for seedling survival. As a consequence, the establishment of long-lived pioneer species seems not to be restricted to early successional stages as previously stated (cf. Finegan 1996).

In the second study, older seedlings planted in secondary forests of 1, 10 and 20 years showed in general a decrease in survival with increasing age of the stand (48, 29 and 25 % survival in the 1, 10 and 20 year old secondary forests) (Chapter 5). Apparently, for most of the species, regardless of their shade tolerance, it is more advantageous to establish early in succession than later on. A positive effect of higher light levels on survival has also been reported for other tree species (e.g. Augspurger 1984a, 1984b, Osunkoya et al. 1992, Rose 2000). Species differed in their survival rates: a pioneer species (*Cecropia sciadophylla*) had the lowest survival (0.5 %), while some long-lived pioneer and a shade tolerant species had the highest one (range 51 - 70 %). Other studies also demonstrated that pioneer species have low survival rates (Augspurger 1984a, Boot 1993, Walters & Reich 2000). This phenomena has been related to their sensitivity to herbivory and poor resistance to drought (Coley 1988, Reich et al. 1991). As in the previous study, some long-lived pioneer species seem to require higher light levels than others for surviving.

Growth

Seedling growth decreased with age of the secondary forests, both when measured as height growth or as relative growth in biomass (RGR; Chapter 4

and 5). This decrease in growth is probably due to a decrease in light availability, as canopy openness decreases with stand age (Saldarriaga 1994, Chapter 4 and 5). These results also suggest that species, regardless of their shade tolerance, would benefit from arriving early in succession.

In general, pioneer and long-lived pioneer tree species had higher RGR than shade tolerant species in young and old successional stages. Pioneer tree species are reported to have high growth rates (e.g., Swaine & Hall 1983), and to be able to out-compete other species relatively rapidly (e.g. Uhl 1987, Poorter 1998, Rose 2000). As a consequence, in young successional stages pioneer species can dominate and form a closed canopy after a few years (< 5 years), although non-pioneer species also become established at the same time (Uhl 1987, Swaine & Hall 1983, Chapter 2). These results support the idea that under high light conditions differences in species growth rates can play an important role in determining the species composition of the canopy of early successional stages (cf. Glitzenstein et al. 1986, Finegan 1996).

Allocation and morphology

Tree seedlings adjust their allocation of biomass and morphology to the successional stage where they grow (Chapter 5). Very young successional stages are characterized by a higher light level and a lower air humidity (Bazzaz & Pickett 1980). Consequently, seedlings tended to invest more in roots to obtain more water and have lower specific leaf areas (SLA) and lower leaf area ratios (LAR) to reduce transpiration. At the same time they attained higher net assimilation rates than seedling growing in older successional stages. In secondary forests of 10 or 20 years, light was probably the limiting resource, and seedlings enhanced their light interception by allocating more biomass to leaves and by producing leaves with high SLA, which results in high LAR. Similar responses have been reported in other studies comparing seedlings growing in low and high light conditions (Popma & Bongers 1988, Osunkoya et al. 1993, Veenendaal et al. 1996, Poorter 1999).

Relating the different experiments

The processes studied in this research influence the course of succession by determining the performance of species that arrived in an area undergoing succession. The optimal conditions for the various processes are not necessarily met in one single successional stage (Fig. 1). For example, a species may undergo a lower removal rate in the 2 year old regrowth, it may germinate better in the 10 year old secondary forests, it may equally survive in all successional stages, and it may grow at a higher rate in the 2 years old regrowth

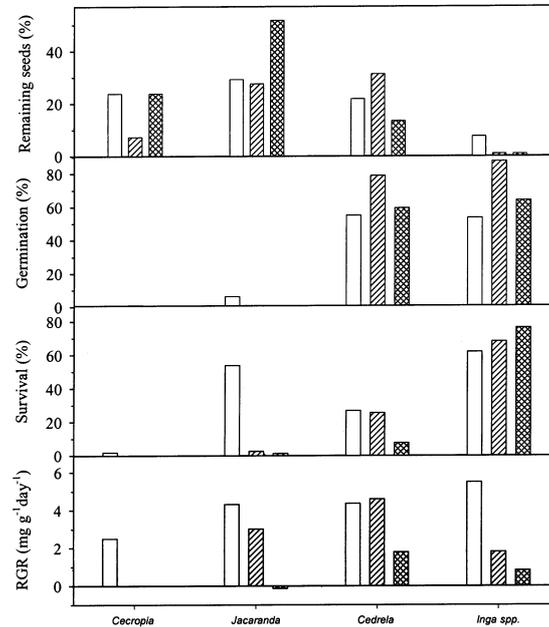


Fig. 1. The effect of different processes on early stages of the life cycle of a tree species. The species has arrived as a seed in an area undergoing succession. Data of remaining seeds correspond to day 21 of the removal experiment (Chapter 3), germination data are from chapter 4, and survival and relative growth rates (RGR) are from chapter 5. Data of remaining seeds of *Inga* correspond to *Inga* sp., the rest of the data is from *Inga thibuadiana*. *Cecropia* = *C. sciadophylla*, *Jacaranda* = *J. copaia*, *Cedrela* = *C. odorata*. The first species is a pioneer tree species, the other three are long-lived pioneer tree species. Open bars = 1 year old regrowth, cross-hatched = 10 years old secondary forest, double cross-hatched = 20 years old secondary forest.

(as it is the case of long-lived pioneer species *Inga thibuadiana*). Therefore, the probability that a species will finally be present as a seedling in a given successional stage depends on the outcome of all these processes acting in the different stages of the life cycle, and on the species requirements for establishment.

The abundance of species in a given successional stage is shaped by different processes, which filter the number of individuals that can move from one stage of the life cycle to the other. If it is assumed that 1000 seeds of each species were dispersed in the different successional stages, and the results found in the different experiments are used, it is possible to calculate how many seedlings would survive two years after seed arrival to the area. For all species, the final number of established seedlings in the different successional stages would be very much determined by seed removal. Twenty-one days after dispersal, the number of seeds available for germination would be reduced drastically in all successional stages (Fig. 2). Additionally, germination would

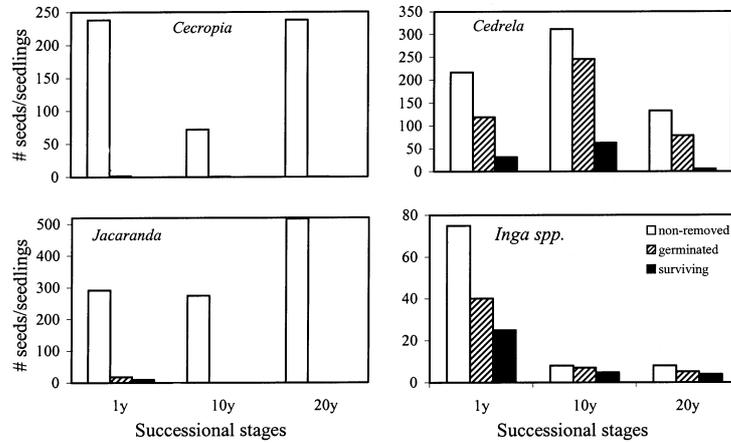


Fig. 2. Number of surviving seeds and seedlings two years after dispersal. It is assumed that 1000 seeds of the different species are dispersed in the various successional stages. The number of seeds/seedlings moving from one stage to the other is determined by using the data of Fig. 1. For complete species name see legend of Fig. 1.

limit the presence of *Jacaranda* and *Cecropia* to the 1 year old regrowth or the agricultural field (not showed), respectively. For *Cedrela* and *Inga* spp., germination and survival would reduce the final number of established individuals but would not restrict them to a given successional stage.

In the course of succession, the environmental conditions of the area change, and these changes have consequences for the performance of the species. Under high light levels (i.e., in the agricultural fields), germination was a limiting factor for all species; even the pioneer species did poorly under those conditions. This suggests that species require some facilitation (i.e., shade) for germination. Probably, herbs, shrubs, and dead stems play an important role in seed germination at the onset of succession, as many pioneer tree species are only found to germinate in their shade (M. Peña-Claros, personal observation). In early successional stages (< 2 years) not only pioneer species establish but also long-lived pioneer and shade tolerant species (Chapter 2). These areas are, however, rapidly dominated by pioneer species mainly due to a high growth rate, and not because of a higher germination or survival rate. All species seem to benefit from entering early in succession because chances of surviving and growth rates are higher.

At later successional stages, seeds of all species were subjected to a lower removal rate, and species had also a higher germination rate. The limiting factor in this successional stage was apparently the species requirements for survival. Individuals of pioneer and some long-lived pioneer tree species could

survive only for some weeks. On the other hand, shade tolerant and other long-lived pioneer species were able to survive in high percentage. These species are likely to benefit from an increase in light levels once the pioneer tree species forming the canopy begin to die off (cf. Mesquita 1999).

Long-lived pioneer tree species

The group of long-lived pioneer species has been recognized long ago (Budowski 1965). These species are reported to dominate the last phase of the secondary succession in tropical rain forest areas (e.g. Budowski 1965, Finegan 1996, Richards 1996). Additionally, there is nowadays a large interest in this species group because of economic reasons. Long-lived pioneer tree species are present in secondary forests at high densities (e.g. Müller & Solis 1997), and they attain high growth rates. Furthermore, this group includes several economically important species, e.g. *Swietenia macrophylla* (mahogany), *Cedrela odorata* (tropical cedar), *Simarouba amara*, *Jacaranda copaia* and *Bertholletia excelsa* (Brazil nut). In spite of their importance, information regarding its requirements for establishment and early growth are scarce (but see Guariguata 2000). In this research, this group was represented by several species in order to generate information on establishment requirements and growth characteristics. The classification of the species as long-lived pioneer species was based on previous studies and field observations.

The long-lived pioneer species included in this study showed a variety of responses in terms of germination, survival and growth rates (Chapter 4 and 5). Some of the species behaved more like pioneers while others resembled more shade tolerant species. These results support the idea that regeneration strategies of long-lived pioneer species are more diverse than those of pioneer species (cf. Finegan 1996). Long-lived pioneer tree species that were more pioneer-like needed higher light levels for survival (Chapter 4 and 5), and therefore, their establishment was restricted to early successional stages. Species that were more shade tolerant did not have specific light requirements for germination and survival (Chapter 4 and 5), and they established in a wide range of successional stages. These species seem to be able to form a seedling bank in the understory of secondary forests, and they respond with high growth rates to an increase in light availability (Chapter 5).

Variation among long-lived pioneer species is also observed when the relative abundance of these species is plotted against stand age (Chapter 2). Two groups of species could be distinguished. There was one group of species

that became established in early successional stages, together with pioneer species. Their relative abundance increased with time, showing an optimum in secondary forests 20 - 40 years old, and then decreasing. Another group did not show any relation to stand age, which suggest that their establishment was possible in the whole range of stand ages. These results contradict the idea that long-lived pioneer species are obligatory early colonizers of areas undergoing succession (Finegan 1996).

Implications for management

The interest on managing secondary forest for production of timber and non-timber forest products has increased over the last years. This interest is caused by the fact that in some tropical regions small areas of primary forests are left (e. g. Costa Rica, Finegan 1992). Secondary forests are generally closer to human settlements than primary forests (Brown & Lugo 1990), and they have a high abundance of economically interesting species, many of which have been classified as long-lived pioneer species (e.g., Müller & Solís 1997). Although the density of long-lived pioneer species in a given stand may be high, there is also a great variation in species presence and abundance among different secondary forests. In the following paragraphs, I discuss some of the management implications of this study from an ecological point of view. The appropriate management option for the management of secondary forests will need to take also into account economic and social aspects, such as social actors involved, distance to the markets, accessibility to land, and market availability for the products.

To guarantee the regeneration of economically interesting species in areas undergoing succession, several management options are available. One is seeding of the species during the agriculture phase of the agricultural cycle. The cultivated crop would provide sufficient shade for the seeds to germinate, which is a limiting factor in agricultural fields without vegetation cover (Chapter 4). The emerged seedlings would benefit from the relatively high light levels in the agricultural fields, and would have consequently high growth rates. Once the area is abandoned, and secondary succession begins, these seedlings would have a size-advantage over the recently established and fast-growing pioneers. The larger the size-advantage is, the more likely it would be that these individuals would be the dominant ones in the regrowing vegetation (cf. Zagt & Werger 1998, George & Bazzaz 1999, Rose 2000). Direct seeding in early successional stages is not recommended because seeds will undergo high removal rates and low germination rates (Chapter 3).

Seeding or transplantation of seedlings in later stages will be advantageous only if it is followed by an opening of the canopy to increase light levels, and consequently, growth rates (Guariguata 2000, Chapter 4 and 5).

Another option for increasing the density of desired species is to carry out enrichment planting during the early successional stages (i.e., the fallow period of the agricultural cycle). There are several methods of enrichment planting in secondary forests: line planting is a common practice. This method was also used in this study to increase the density of a highly economically important species of the Bolivian Amazon, *Bertholletia excelsa* (the Brazil nut tree, Chapter 6). Seedlings of this species, which has been classified as light demanding (Myers et al. 2000, Zuidema 2000), were planted in lines of different widths cut in a secondary forest. Seedling survival was not affected by line width, but height growth rate was higher in wider lines. Wide lines allowed plants to have high height growth rates and to maintain their crowns at high canopy openness levels. Another advantage of opening wider lines was that their canopy closure rate was slower than the closure rate of narrow lines. Both advantages also imply a reduction in the costs made for maintaining the appropriate line width for the growth of the species.

The selection of species to be used in enrichment planting should be carefully done. All species studied showed an increase in growth rate with an increase in light level (Chapter 5). The change in growth rate was, however, not equal for all species (Chapter 5, Fig 3 and 4). For example, long-lived pioneer species responded stronger to an increase in light than shade tolerant species. Consequently, for enrichment planting it would be better to use species that show a strong response to a high light level. In that way, it would be possible to reduce the time span needed for the species to become mature (in the case of fruit harvesting) or to reach a certain diameter (in the case of timber). Consequently, the time that has to elapse to obtain some economic benefit from the management of the stand will be shortened. Similarly, the response of species to an increase in light levels should also be considered when there is interest in applying a silvicultural treatment (such as the opening of the canopy) to the whole stand (Guariguata 1999, Mesquita 2000).

As mentioned previously, certain long-lived pioneer species are likely to form a seedling/sapling bank in secondary forests of different ages. This ability is an important characteristic for timber species harvested from secondary forests. Once the larger individuals have been harvested, the seedlings and saplings present in the understory will have a size-advantage over the fast-growing species that are likely to enter in the area if the harvesting of the

timber species has resulted in large canopy openings. Several forest regeneration studies have found that the seedlings and saplings established before disturbance make an important contribution to the future stand composition (e.g., Rose 2000). To take advantage of this advanced regeneration, it is important to minimize the damage to the remaining forest stand during logging operations.

Secondary forests provide a variety of forest products, and their management should allow for higher production levels. Although the knowledge on secondary forests has increased over the last decades, information is still lacking on their dynamics, and on the characteristics of the long-lived pioneer species. The long-lived pioneer species are the most economically important species group growing in these forests. More information about them is necessary given the fact that they show a large variety of responses to light.

Acknowledgements

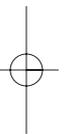
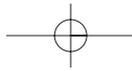
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Resumen ejecutivo

Bosques secundarios

Los bosques húmedos tropicales están sujetos a diferentes tipos de disturbios naturales. Estos disturbios pueden ser muy locales y de pequeño impacto, o muy extensos y de gran impacto. El primer tipo de disturbio incluye la creación de pequeños claros en el dosel del bosque, causados por la caída de una rama; mientras que el segundo tipo incluye disturbios a grandes superficies de bosque causados por huracanes, inundaciones o fuegos. En términos de superficie, la mayor parte de los disturbios son causados en la actualidad por actividades humanas. Las actividades humanas pueden causar un aumento en la cantidad de luz en el sotobosque, debido a la extracción de hojas de palmeras; la creación de claros debido a la extracción maderera; la destrucción total de la vegetación para la creación de áreas agrícolas y pastizales. En el último caso, las áreas creadas son usadas por un tiempo hasta que su productividad disminuye (Theile, 1993; citado en Smith et al., en prensa), y después son abandonadas. Al mismo tiempo, nuevas plantas recolonizan estas áreas, de tal manera que un bosque se desarrolla paulatinamente. Estos bosques reciben el nombre de bosques secundarios (Brown & Lugo, 1990) y son el objeto de este estudio. Bosques residuales o bosques de extracción maderera no son incluidos en esta definición, porque mantienen la estructura y la composición florística de los bosques primarios.

En Latinoamérica el área cubierta por bosques secundarios ha aumentado en las últimas décadas. En 1990 se estimó que 165 millones de ha. estaban cubiertas por bosques secundarios, mientras que 871 millones de ha. estaban cubiertas por bosque húmedo tropical (FAO, 1996). Sin embargo, no existe al momento una estimación exacta de la superficie que ocupan los bosques secundarios. Esta incertidumbre se debe a que existen diferentes definiciones de bosques secundarios, y que las actuales técnicas de asesoramiento remoto no permiten distinguir entre bosque primario y bosque secundario (Sips et al., 1997).

Importancia de los bosques secundarios

Los bosques secundarios juegan un papel muy importante, tanto en términos ecológicos como económicos (Brown & Lugo, 1990; Smith et al., 1997). Los bosques secundarios ayudan a restaurar la productividad del área y reducen las poblaciones de malezas después de que el sitio ha sido usado para la agricultura. Estos bosques son también fuente de una serie de productos, que varían desde frutos comestibles a madera, y desde plantas medicinales a plantas artesanales. Asimismo pueden servir como áreas de cacería porque tienen una mayor productividad que los bosques primarios (Brown & Lugo 1990, Smith et al. 1997). Los bosques secundarios están generalmente localizados cerca de asentamientos humanos, y por lo tanto, la extracción de productos forestales es más factible. Por consiguiente, se cree que un apropiado manejo de los bosques secundarios podría reducir la presión que existe sobre los bosques primarios (Brown & Lugo, 1990; Sips et al., 1997; Sips, 1997).

Varias de las características de los bosques secundarios hacen que su manejo sea probablemente más factible que el manejo de bosques primarios. Los bosques secundarios se caracterizan por tener una alta tasa de producción de biomasa, alta densidad de especies arbóreas económicamente importantes, las cuales tienen una alta tasa de crecimiento y forman poblaciones coetáneas (Finegan, 1992). En Costa Rica se encontró que 50% de las especies presentes en bosques secundarios tenían uso comercial, y que la mayoría de estas especies pertenecían al grupo de las heliófitas durables (Müller & Solís, 1997). Es posible aumentar la tasa de crecimiento de las especies de interés mediante la aplicación de tratamientos silviculturales, como ser la liberación de individuos (Guariguata, 1999) y la apertura del dosel (Finegan, 1992; Mesquita, 2000). En el caso de que las especies de interés estén presentes en densidades bajas o ausentes, se tiene varias opciones de manejo para aumentar la densidad de estas especies. Entre ellas están la siembra de semillas o el transplante de plantines.

El interés en el manejo de bosques secundarios varía de país a país y de región a región (Smith et al., en prensa). En países como Costa Rica, donde extensas áreas han sido deforestadas, los bosques secundarios son más importantes como fuente de recursos forestales que en países con niveles bajos de deforestación (Finegan, 1992). Además varios factores socioeconómicos afectan la decisión de los campesinos para hacer un manejo de sus bosques secundarios. Entre estos factores están la existencia de un mercado para especies maderables poco conocidas o para productos no maderables, la accesibilidad al mercado y a la tierra, la tenencia de la tierra, el nivel de desarrollo de la frontera agrícola, y las políticas gubernamentales (Smith et al., en prensa). En las fronteras agrícolas de Nicaragua, Brasil y Perú se encontró que el manejo de los bosques secundarios para la obtención de productos no maderables era más factible que el manejo para la producción de madera. Esto debido a que la producción de productos no maderables necesita menos tiempo, y por ello combina mejor con el ciclo agrícola de la agricultura de tala y quema (Smith et al., en prensa).

Sucesión

Los bosques secundarios son el resultado de la sucesión de la vegetación. La sucesión ha sido definida como “una alteración progresiva en la estructura y composición de especies de la vegetación” (Grime, 1979), y puede ser clasificada como sucesión primaria y secundaria. La sucesión primaria se refiere al establecimiento y desarrollo de una comunidad de plantas en un área que nunca antes había sido ocupada por plantas, como ser dunas de arena nuevas, arena depositada al margen de los ríos, corrientes de lava. La sucesión secundaria se refiere a la sucesión que se lleva a cabo en áreas donde la vegetación ha sido (total o parcialmente) removida por un disturbio mayor (Ricklefs, 1993), pero donde todavía existe un suelo bien estructurado y un banco de semillas. Estos factores favorecen el restablecimiento de la vegetación.

Clasificación de las especies

Con base en sus requerimientos para la germinación y establecimiento, las especies arbóreas pueden ser clasificadas en especies heliófitas (con subgrupos según tamaño máximo y longevidad) y especies esciófitas. Las especies heliófitas requieren de altos niveles de luz para su germinación y establecimiento, de tal manera que su reclutamiento está restringido a etapas

sucesionales muy jóvenes o a claros de bosque grandes (Uhl, 1987; Richards, 1996; Kyereh et al., 1999). Las especies esciófitas, por otro lado, se pueden establecer y crecer con bajos niveles de luz (e.g., Popma & Bongers, 1988). Por lo consiguiente, se cree que las especies esciófitas se regeneran en etapas sucesionales dominadas por especies heliófitas. Entre estos dos grupos de especies, existe un tercer grupo con características intermedias (Budowski, 1965; Denslow, 1980). En el presente estudio, este grupo es denominado como especies heliófitas durables. Se piensa que estas especies también se deben establecer en etapas sucesionales jóvenes, pero tienen una longevidad considerablemente mayor que las especies heliófitas (Budowski, 1965; Finegan, 1996). Se cree que este grupo de especies tiene para su regeneración un rango de requerimientos más amplio que las especies heliófitas (Finegan, 1996). En este estudio, se incluyeron especies pertenecientes a los diferentes grupos, enfatizando en las heliófitas durables, para generar información sobre este grupo de especies.

Etapas de la sucesión secundaria

Después de que un área agrícola o ganadera es abandonada, ésta es rápidamente ocupada por plantas a través de la sucesión secundaria. A medida que la sucesión progresa hay un aumento en la altura de la vegetación, en el índice de área foliar y en el área basal (Brown & Lugo, 1990; y referencias), de tal manera que con el tiempo la estructura del bosque se parece cada vez más a la estructura de un bosque maduro. Estos cambios durante la sucesión modifican asimismo las condiciones ambientales del lugar.

En el neotrópico, los primeros 100 años de la sucesión secundaria han sido descritos en tres fases (Finegan, 1996). En áreas que no han sido degradadas y que tienen fuentes de semillas cercanas, la primera fase de la sucesión es corta (< 3 años), y está dominada por hierbas, arbustos y lianas, que se establecen rápidamente después del disturbio y desaparecen bajo la sombra de las especies heliófitas arbóreas. Estas especies heliófitas arbóreas forman rápidamente un dosel y dominan la segunda fase de la sucesión, la cual dura entre 10 y 20 años, dependiendo de la longevidad de las especies. A medida que las especies heliófitas mueren, son remplazadas en el dosel por especies heliófitas durables. Las especies heliófitas durables dominan durante la tercera fase de la sucesión, que dura entre 75 y 100 años, dependiendo también de la longevidad de las especies. Se piensa que las especies esciófitas colonizan el área continuamente durante las últimas dos fases de la sucesión (Budowski, 1965; Gomez-Pompa & Vázquez-Yanes, 1981; Finegan, 1996).

Mecanismos y procesos

En la actualidad se considera que la sucesión es el resultado de una combinación de procesos y factores, los cuales fueron incorporados en un esquema jerárquico (Pickett et al., 1987). En este esquema, se enfatiza las diferencias que existen entre las especies en términos de sus ciclos de vida y estrategias de vida. Se distinguen tres condiciones para que la sucesión pueda ocurrir: 1) disponibilidad de sitios desocupados, 2) variación en la disponibilidad de especies para colonizar un sitio, y 3) desempeño diferencial de las especies en el sitio. Los sitios desocupados pueden ser colonizados por cualquier especie. Las especies difieren en sus tasas de dispersión, y en su habilidad de establecerse en una determinada área. Por lo tanto, el grupo de especies que estará finalmente presente en un sitio depende de la disponibilidad de semillas y/o rebrotes, de la capacidad de los individuos de establecerse y crecer bajo las condiciones ambientales del sitio, y de su habilidad para superar en altura a sus vecinos.

Varios procesos y factores influyen en las diferentes etapas del ciclo de vida de un árbol, así como en las transiciones de una etapa a la próxima. En este estudio se ha enfatizado en los procesos y factores que afectan la disponibilidad de especies para colonizar un sitio y el desempeño diferencial de las especies en el sitio. En los experimentos de campo se estudió la predación de semillas, las tasas de germinación, supervivencia y crecimiento de especies arbóreas que difieren en su tolerancia a la sombra. Estos procesos fueron relacionados con características ambientales que cambian durante la sucesión (como ser apertura del dosel, hojarasca, densidad de lianas). Los experimentos se llevaron a cabo en diferentes etapas sucesionales, con lo que se pudo evaluar si el éxito de una especie está limitado por el mismo proceso en diferentes etapas sucesionales.

Contexto regional e institucional

Este estudio se llevó a cabo en la Amazonía boliviana (norte del país), que comprende el departamento de Pando y las provincias Vaca Diez (departamento del Beni) e Iturrealde (norte del departamento La Paz). La región se caracteriza por una temperatura media anual de 26 °C, y una precipitación media anual de 1830 mm (Pando) y 1780 mm (Riberalta), con una marcada estación seca de mayo a septiembre (Beekma et al., 1996).

La mayor parte del trabajo de campo se llevó a cabo en la Reserva Forestal El Tigre y alrededores. El Tigre es el área de investigación y extensión del Programa de Manejo de Bosques de la Amazonía Boliviana (PROMAB), y se encuentra ubicado a 45 km al este de la ciudad de Riberalta, y a unos 5 km al norte de la carretera Riberalta - Guayaramerín. Tiene una extensión de 830 ha, cubierta mayormente por bosque húmedo tropical. Existen también algunas áreas de bosque dominado por lianas ("chaparral"), bosque secundario (3 a 20 años de edad) y un pastizal dominado por *Imperata* spp. (Poorter et al., 2000).

Este estudio forma parte del Programa de Manejo de Bosques de la Amazonía Boliviana (PROMAB), el cual es un proyecto de investigación, extensión y educación del Instituto para el Hombre, Agricultura y Ecología (IPHAE, Riberalta, Bolivia), la Carrera de Ingeniería Forestal de la Universidad Técnica del Beni (CIF/UTB, Riberalta, Bolivia) y la Universidad de Utrecht (Holanda). El objetivo del programa es contribuir al mejoramiento de la calidad de vida de los habitantes de la región a través del uso sostenible y conservación de los bosques y sus recursos.

Objetivos del estudio

Los objetivos del estudio son:

1. estudiar algunos de los procesos que determinan la presencia y abundancia de las especies en bosques secundarios y cómo estos procesos varían con la etapa sucesional,
2. proveer información sobre los requerimientos para la supervivencia y crecimiento de especies heliófitas durables,
3. evaluar opciones de manejo para bosques secundarios.

Procesos durante la sucesión secundaria

Como se mencionó anteriormente, en este estudio se realizaron varios experimentos en bosques secundarios de diferentes edades. Los principales resultados son resumidos a continuación.

Remoción de semillas

Las semillas de nueve especies arbóreas tropicales dispersas en bosques secundarios y bosque maduro sufrieron una alta tasa de remoción (Capítulo 3). Siete semanas después de que las semillas fueron dispersadas, la tasa de

remoción varió entre 50 a 100 %, dependiendo de la especie; y entre 74 a 90 % dependiendo de la etapa sucesional. La tasa de remoción no estuvo relacionada al tamaño de la semilla. Este resultado sugiere que tanto hormigas como roedores estaban presentes en las diferentes etapas sucesionales. Hormigas remueven semillas pequeñas, mientras que los roedores remueven semillas de mayor tamaño, de tal manera que en una determinada etapa sucesional todas las especies incluídas en el estudio tuvieron la misma probabilidad de ser removidas.

La probabilidad de ser removida varió con la etapa sucesional. Las tasas de remoción son más altas en el bosque secundario de 2 años que en los bosques secundarios de 10 y 20 años de edad. Esto sugiere que la densidad de los agentes de remoción varía con la etapa sucesional. Las hormigas están presentes en mayor densidad en etapas sucesionales jóvenes que en las tardías (Kaspari, 1995; Vasconcelos & Cherret, 1995), mientras que mamíferos pequeños prefieren la vegetación densa de bosques secundarios jóvenes para esconderse de predadores grandes (e.g., Manson & Stiles, 1998). A pesar que no se estudió el destino final de las semillas removidas (predación o dispersión secundaria), otros estudios han demostrado que el porcentaje de semillas removidas que finalmente germina es muy bajo.

Los resultados de este estudio apoyan la idea de que la remoción de semillas post-dispersión es importante en el establecimiento de árboles en áreas agrícolas abandonadas. La tasa de remoción de semillas disminuyó al aumentar la edad del bosque secundario, de tal manera que las semillas dispersadas en áreas jóvenes tuvieron una menor probabilidad de sobrevivir que las semillas dispersadas en áreas más viejas. Esto tiene diferentes implicaciones para especies arbóreas que difieren en su tolerancia a la sombra. Las especies esciófitas se establecen paulatinamente en áreas sujetas a sucesión. Esto se puede deber a que estas especies tienen otros requerimientos para el establecimiento que las especies heliófitas (Finegan, 1984; Uhl, 1987) o a que sus semillas son dispersadas al área en menores cantidades que las semillas de especies heliófitas (Uhl et al., 1981; Uhl, 1987). Esta última opción, en combinación a una alta tasa de remoción en bosques secundarios jóvenes, puede explicar la baja densidad de plantines de las especies referidas que se encuentra en estos bosques (Uhl et al., 1981). Por otro lado, las especies heliófitas se establecen en altas densidades en etapas sucesionales jóvenes. Aparentemente estas especies pueden escapar a la alta remoción típica de estas etapas sucesionales. Una alta y continua producción de semillas y una alta tasa de dispersión son probablemente características importantes para compensar la alta tasa de remoción típica de etapas sucesionales jóvenes.

Tasa de germinación

La tasa de germinación varió entre las especies, de 0.6 a 59 % después de 3 - 7 meses (dependiendo de las especies). Para la mayoría de las seis especies estudiadas, el éxito de la germinación varió con la etapa sucesional (Capítulo 4). Para todas las especies la tasa de germinación fue baja o nula en las áreas agrícolas, probablemente debido a disecación de las semillas. Esto indica que las especies heliófitas necesitan de sombra para germinar, contrariamente a la creencia de que las especies heliófitas y heliófitas durables requieren de altos niveles de luz para germinar (e.g., Swaine & Withmore, 1988; Finegan, 1996). Las seis especies estudiadas en este experimento, con la excepción de *Jacaranda copaia*, germinaron en los bosques secundarios (10 años de edad y en el bosque maduro. La especie heliófita (*Cecropia sciadophylla*) y dos de las heliófitas durables (*Cedrela odorata* y *Inga thibuadiana*) tuvieron inclusive una tasa de germinación mayor en las etapas sucesionales tardías que en las jóvenes. Estos resultados sugieren que los requerimientos para la germinación no son necesariamente el factor limitante para el establecimiento de especies heliófitas y heliófitas durables en etapas sucesionales tardías.

La hojarasca puede representar una barrera física para tener acceso a la luz en el caso de los plantines que emergen del banco de semillas, o para tener acceso al suelo, en el caso de los plantines que germinan de semillas dispersadas recientemente sobre la hojarasca. En este estudio, la presencia de hojarasca retrasó o disminuyó el éxito de la germinación de tres de las especies estudiadas: de las especies con semillas pequeñas (*Bellucia pentamera* y *Cecropia sciadophylla*) y de *Inga thibuadiana*. El grosor de la hojarasca aumenta con la edad del rodal, y es mayor en la época seca que en la época de lluvias. Consecuentemente, el efecto de la hojarasca en el éxito de la germinación dependerá de la especie considerada, de la etapa sucesional en que la semilla ha sido dispersada, y de la época del año.

Supervivencia

La supervivencia de los plantines fue estudiada en dos diferentes experimentos. En el primero, se evaluó durante 11 a 14 meses la supervivencia de plantines recién germinados, dependiendo de las especies (Capítulo 4). En el segundo estudio, se transplantó plantines un poco mayores a las diferentes etapas sucesionales, y su supervivencia fue monitoreada por dos años (Capítulo 5). De esta manera fue posible estudiar las tasas de supervivencia después de la germinación y después del establecimiento.

En el primer estudio, la tasa de supervivencia de los plantines recién germinados varió entre las especies. En el caso de algunas de las especies,

ningun plantín sobrevivió hasta el final del experimento, mientras que otras especies tuvieron una alta tasa de supervivencia (79%) durante el periodo de evaluación (11 - 14 meses). Las especies tuvieron respuestas diferentes a las etapas sucesionales (Capítulo 4). Como se esperaba, las especies heliófitas tuvieron una tasa de supervivencia más alta en las etapas sucesionales jóvenes que en las viejas. Al final del experimento, los únicos individuos sobrevivientes de estas especies se encontraban en las áreas agrícolas, las cuales tenían los mayores niveles de luz. Combinando estos resultados con los del estudio de germinación, se puede concluir que la supervivencia de plantines de especies heliófitas es más importante que la germinación en la determinación de la abundancia de las especies heliófitas en diferentes etapas sucesionales. Por lo tanto, las especies heliófitas están restringidas a etapas sucesionales más jóvenes, por sus requerimientos de luz para sobrevivir, y no necesariamente por sus requerimientos para germinar (cf. Kyereh et al., 1999). Las respuestas de las especies heliófitas durables fue más diversa, variando desde especies que muestran la mayor tasa de supervivencia en las etapas sucesionales más jóvenes (*Cedrela odorata*) o en las más viejas (*Inga thibuadiana*), a especies que sobrevivieron igualmente bien en todas las etapas sucesionales (*Tachigali* cf. *vasquezii*). Estos resultados indican que las especies durables no requieren necesariamente de altos niveles de luz para sobrevivir, y que por lo tanto, el establecimiento de especies heliófitas durables no está aparentemente restringido a etapas sucesionales jóvenes, como ha sido sugerido anteriormente (cf. Finegan, 1996).

En el segundo estudio, los plantines transplantados en bosques secundarios de 1, 10 y 20 años mostraron en general reducción en la supervivencia a medida que la edad del bosque secundario aumentó (48 % de supervivencia en bosques secundarios de 1 año, 29 % en el bosque secundario de 10 años, y 25 % en los bosques secundarios de 20 años (Capítulo 5). Aparentemente, para la mayoría de las especies, y sin tomar en cuenta su tolerancia a la sombra, es más ventajoso establecerse temprano durante la sucesión que en etapas más viejas. El efecto positivo de altos niveles de luz en la supervivencia de plantines ha sido reportado anteriormente para otras especies arbóreas (e.g. Augspurger 1984a, 1984b; Osunkoya et al., 1992; Rose, 2000). Las especies difieren en sus tasas de supervivencia: la especie pionera (*Cecropia sciadophylla*) tiene la tasa de supervivencia más baja (0.5 %), mientras que algunas de las especies heliófitas durables y esciófitas tienen las mayores tasas de supervivencia (rango 51 - 70 %). Otros estudios han demostrado que las especies heliófitas tienen tasas de supervivencia bajas (Augspurger 1984a; Boot, 1993; Walters & Reich, 2000), debido a una alta sensibilidad a la herbivoría y una baja resistencia a la sequía (Coley, 1988; Reich et al., 1991). Algunas de las especies heliófitas durables

requieren niveles de luz más altos que otras especies para sobrevivir, como fue encontrado en el anterior estudio de supervivencia.

Crecimiento

El crecimiento de plantines disminuyó a medida que la edad del bosque secundario aumentó, tanto cuando el crecimiento fue evaluado como crecimiento en altura, como cuando fue evaluado como crecimiento en biomasa (TCR; Capítulo 4 y Capítulo 5). Esta disminución en el crecimiento se debe probablemente a una declinación en la disponibilidad de luz, ya que la apertura del dosel disminuye a medida que la edad del rodal aumenta (Saldarriaga, 1994; Capítulo 4 y Capítulo 5). Estos resultados también sugieren que es beneficioso para las especies, sin tomar en cuenta su tolerancia a la sombra, ingresar temprano durante la sucesión.

En general, las especies heliófitas y las especies heliófitas durables tuvieron una mayor TCR que las especies esciófitas, tanto en las etapas sucesionales jóvenes como viejas. Se ha reportado que las especies heliófitas tienen una alta tasa de crecimiento (e.g., Swaine & Hall, 1983) y que consiguen rápidamente sobrepasar en altura a otras especies (p.e., Uhl, 1987; Poorter, 1998; Rose, 2000). Debido a estas características, las especies heliófitas pueden dominar en etapas sucesionales jóvenes, formando un dosel cerrado después de unos pocos años (< 5 años), a pesar de que otras especies no heliófitas se establecen al mismo tiempo (Uhl, 1987; Swaine & Hall, 1983; Capítulo 2). Estos resultados apoyan la idea de que en condiciones de alta luminosidad las diferencias entre las especies en términos de tasas de crecimiento pueden jugar un papel importante en la determinación de la composición de especies del dosel de etapas sucesionales jóvenes (cf. Glitzenstein et al., 1986; Finegan, 1996).

Alocación y morfología

Los plantines de especies arbóreas ajustan su alocación de biomasa y su morfología a la etapa sucesional en la que crecen (Capítulo 5). Etapa sucesionales muy jóvenes se caracterizan por tener un alto nivel de luz y una baja humedad del aire (Bazzaz & Pickett, 1980). Por lo consiguiente, los plantines tendieron a invertir más en raíces para obtener más agua, y a tener hojas con un área foliar específica (AFE) y un área foliar relativa (AFR) pequeño para reducir la transpiración. Al mismo tiempo, tuvieron una tasa de asimilación neta mayor que la de los plantines creciendo en etapas sucesionales tardías. En bosques secundarios de 10 ó 20 años, el factor limitante es probablemente luz, y por lo tanto, los plantines mejoraron su intercepción de luz asignando más biomasa a las hojas y produciendo hojas con un alto AFE,

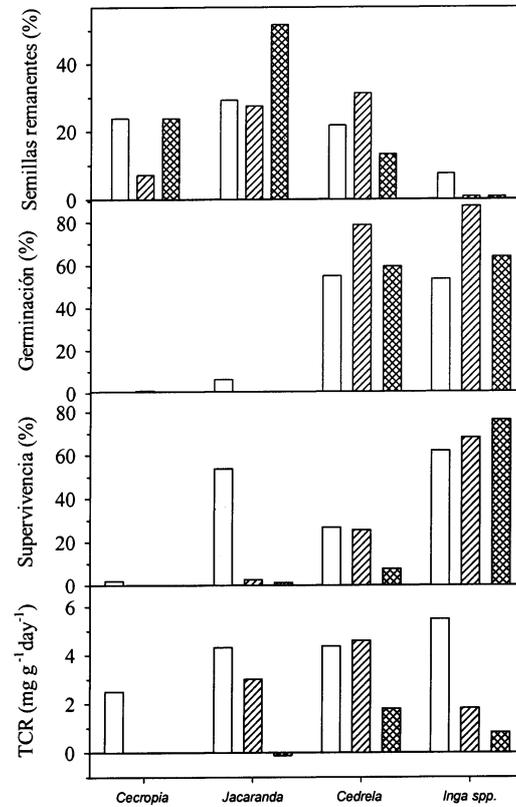


Fig. 1. El efecto de los diferentes procesos en las primeras etapas del ciclo de vida de una especie arbórea. La especie fue dispersada a un área en sucesión. Los datos de las semillas remanentes corresponden al día 21 del experimento de remoción (Capítulo 3), los datos de germinación son del capítulo 4, y la supervivencia y la tasa de crecimiento relativo (TCR) son del capítulo 5. Los datos de las semillas remanentes de *Inga* son de *Inga* sp., el resto son de *Inga thibudiana*. *Cecropia* = *C. sciadophylla*, *Jacaranda* = *J. copaia*, *Cedrela* = *C. odorata*. La primera especie es una heliófita, las otras tres son heliófitas durables. Columnas abiertas = bosque secundario de 1 año, rayadas = bosque secundario de 10 años, rayado doble = bosques secundarios de 20 años.

que resultó en un alto AFR. Se han encontrado similares respuestas en estudios que han comparado plantines creciendo en condiciones bajas y altas de luz (Popma & Bongers, 1988; Osunkoya et al., 1993; Veenendaal et al., 1996; Poorter, 1999).

Relacionando los diferentes experimentos

Los procesos estudiados en esta investigación influyen en el rumbo de la sucesión, determinando el desempeño de las especies que llegan a un área en sucesión. Las condiciones óptimas para los diferentes procesos no se encuentran en una sola etapa sucesional (Fig. 1). Por ejemplo, una especie puede sufrir una baja tasa de remoción de semillas en el bosque secundario

de 2 años de edad, puede germinar mejor en los bosques secundarios de 10 años, puede tener una tasa de supervivencia alta en todas las etapas sucesionales y puede tener una mayor tasa de crecimiento en el bosque secundario de 2 años (como es el caso de la especie heliófita durable *Inga thibudiana*). Por lo tanto, la probabilidad de que una especie esté finalmente presente como un plantín en una etapa sucesional dada, depende del resultado de todos estos procesos actuando en las diferentes etapas del ciclo de vida de un árbol, y de los requerimientos específicos de las especies para su establecimiento.

La abundancia de las especies en una dada etapa sucesional es el resultado de diferentes procesos que filtran el número de individuos que pueden pasar de una etapa del ciclo de vida a otra. Si asumimos que llegan 1000 semillas de cada especie a diferentes etapas sucesionales, y si aplicamos los resultados encontrados en los diferentes experimentos, es posible calcular cuántos plantines pueden sobrevivir por dos años después de la dispersión de semillas. La cantidad de plantines que lograrían establecerse en las diferentes etapas sucesionales es mayormente determinada por la remoción de semillas. Veintiun días después de la dispersión de semillas, el número de semillas disponibles para la germinación había sido reducido fuertemente en las diferentes etapas sucesionales (Fig. 2). Además, la germinación limitaría la presencia de *Jacaranda* y *Cecropia* al bosque secundario de 1 año o a las áreas agrícolas (datos no presentados), respectivamente. Para *Cedrela* e *Inga* spp., la germinación y supervivencia reduciría el número final de individuos establecidos, pero no los restringiría a una etapa sucesional específica.

Especies heliófitas durables

El grupo de especies heliófitas durables dominan la última fase de la sucesión secundaria (e.g. Budowski, 1965; Finegan, 1996; Richards, 1996), y actualmente existe un gran interés en este grupo debido a razones económicas. Las especies heliófitas durables están presentes en bosques secundarios en altas densidades (e.g. Müller & Solis, 1997) y pueden tener altas tasas de crecimiento. Asimismo, este grupo incluye varias especies de importancia económica, e.g. *Swietenia macrophylla* (mara), *Cedrela odorata* (cedro), *Simarouba amara*, *Jacaranda copaia* y *Bertholletia excelsa* (castaña). A pesar de la importancia de este grupo de especies, existe poca información sobre sus requerimientos para su establecimiento y crecimiento (sin embargo, ver Guariguata, 2000). En este estudio, este grupo de especies fue representado por varias especies para generar de esta manera información sobre sus requerimientos de establecimiento y para caracterizar su crecimiento.

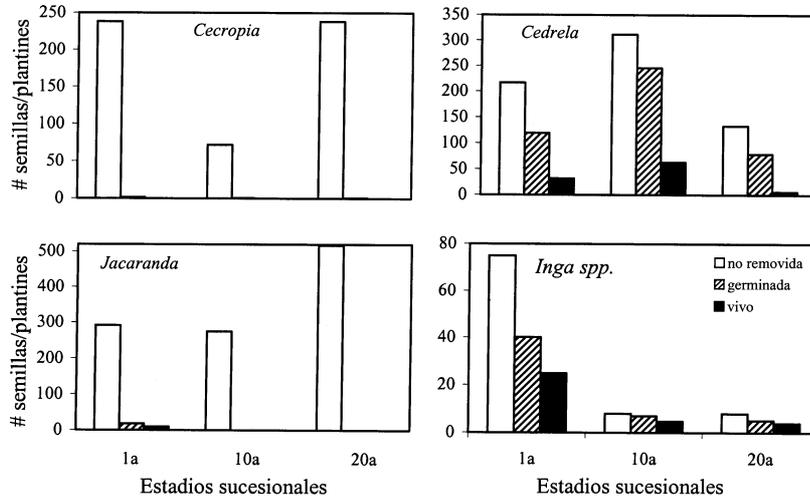


Fig. 2. Número de semillas y plantines sobrevivientes dos años después de la dispersión. Se asume que 1000 semillas de cada especie son dispersadas a varias etapas sucesionales. El número de semillas/plantines que pasan de una etapa a la otra es determinado por las tasas correspondientes presentadas en la Fig. 1. Para conocer el nombre completo de las especies ver Fig. 1.

Las especies heliófitas durables incluidas en este estudio mostraron variedad de respuestas en términos de las tasas de germinación, supervivencia y crecimiento (Capítulos 4 y 5). Algunas de las especies se comportaron más como especies heliófitas, mientras otras más como especies esciófitas. Estos resultados concuerdan con la idea de que las estrategias de regeneración de este grupo de especies son mucho más diversas que las de las especies heliófitas (cf. Finegan, 1996). Las especies heliófitas durables con comportamiento similar a las heliófitas necesitaron niveles de luz altos para sobrevivir (Capítulo 4 y 5), y por lo tanto, su establecimiento estuvo restringido a etapas sucesionales jóvenes. Las especies con comportamiento similar a las especies esciófitas no mostraron requerimientos de luz específicos para germinación y supervivencia (Capítulos 4 y 5), y se establecieron en un rango más amplio de etapas sucesionales. Estas especies parecen ser capaces de formar un banco de plantines en el sotobosque de bosques secundarios, y de responder con un incremento en la tasa de crecimiento a un aumento en la cantidad de luz (Capítulo 5).

Se observa también variación entre las especies heliófitas durables cuando se relaciona la abundancia relativa de estas especies con la edad del rodal (Capítulo 2), pudiéndose distinguir dos grupos de especies. Uno de los grupos se establece en etapas sucesionales jóvenes, al mismo tiempo que las especies heliófitas. Su abundancia relativa aumenta con el tiempo, mostrando un óptimo en bosques secundarios de 20 - 40 años, y disminuyendo después. El

otro grupo no muestra ninguna relación con la edad del rodal, sugiriendo que su establecimiento es posible en rodales de diferentes edades. Estos resultados contradicen la idea de que las especies heliófitas durables tienen que colonizar un área al inicio de la sucesión (Finegan, 1996).

Implicaciones para el manejo

Como el interés en el manejo de bosques secundarios para la producción de productos maderables y no maderables ha aumentado en los últimos años, se presenta en los próximos párrafos algunas de las implicaciones que tiene este estudio para el manejo de bosques secundarios desde el punto de vista ecológico.

Para garantizar la regeneración de especies con valor económico en áreas en sucesión, existen varias opciones de manejo. Una de ellas es la de sembrar semillas de especies arbóreas durante la fase agrícola del ciclo agrícola. El cultivo proveería suficiente sombra para que las semillas germinaran y los plantines emergentes se beneficiarían de la relativamente alta disponibilidad de luz en las áreas agrícolas, y por consiguiente, tendrían altas tasas de crecimiento. Una vez el área es abandonada, y la sucesión secundaria sigue su curso, estos plantines tendrían una ventaja de tamaño sobre las heliófitas que se establezcan después. Mientras más grande sea la ventaja de tamaño, mayor será la probabilidad de que estos individuos sean los individuos dominantes en la vegetación que se desarrolla (cf. Zagt & Werger, 1998; George & Bazzaz, 1999; Ros, 2000). La siembra de semillas al voleo en etapas sucesionales jóvenes no es una opción de manejo recomendada debido a la alta tasa de remoción de semillas observada (Capítulo 3). La siembra de semillas o el trasplante de plantines en etapas sucesionales viejas es solamente aconsejable si esta acción es seguida de una apertura del dosel para aumentar los niveles de luz, y por consiguiente, las tasas de crecimiento (Guariguata, 2000; Capítulos 4 y 5).

Otra opción de manejo para aumentar la densidad de especies deseables en bosques secundarios es la de realizar actividades de enriquecimiento en etapas sucesionales jóvenes. Existen varios métodos de enriquecimiento de bosques secundarios: plantación en fajas es una práctica común. Este método fue también usado en este estudio para aumentar la densidad de una especie de alto valor económico en la región amazónica de Bolivia: *Bertholletia excelsa* (castaña, Capítulo 6). Plantines de esta especie, clasificada como una especie heliófita durable (Myers et al., 2000; Zuidema, 2000), fueron plantados en fajas

de diferente ancho, abiertas en un bosque secundario. La supervivencia de los plantines no fue afectada por el ancho de la faja. El crecimiento en altura, por otro lado, fue mayor en las fajas más anchas (6 m de ancho). Como las plantas crecieron más en estas fajas, pudieron mantener sus copas en niveles altos de luz y no mostraron una disminución en su tasa de crecimiento a través del tiempo. Las plantas que crecían en las fajas más angostas (2 y 4 m de ancho) fueron sobrepasadas por la vegetación circundante y su crecimiento se redujo. La apertura de fajas anchas tiene también como ventaja que se cierran más lentamente que las fajas angostas. Por lo tanto, el costo de su mantenimiento es menor que el costo de mantenimiento de fajas angostas, las cuales deben ser abiertas periódicamente para mantener el nivel de luz apropiado para el crecimiento óptimo de la especie.

La selección de las especies a usar en actividades de enriquecimiento debe ser hecha cuidadosamente. Todas las especies mostraron un aumento en la tasa de crecimiento con un aumento en el nivel de luz (Capítulo 5). Este aumento, sin embargo, no fue igual para todas las especies (Capítulo 5, Fig. 3 y 4). Por ejemplo, las especies heliófitas durables tuvieron un mayor aumento en la tasa de crecimiento que las especies esciófitas. Por lo consiguiente, es más apropiado para actividades de enriquecimiento utilizar especies que responden fuertemente a un aumento en el nivel de luz. De esta manera, se podría probablemente reducir el tiempo que se necesita para que una especie alcance su madurez reproductiva (en el caso de que el interés sea en la producción de frutos) o alcance un determinado diámetro (en el caso de que el interés sea maderero). De esta manera, se podría reducir el tiempo necesario para obtener un beneficio económico del rodal. Similarmente, se debe tomar en cuenta la respuesta de las especies a un incremento en el nivel de luz cuando existe interés en realizar un tratamiento silvicultural (como ser la apertura del dosel) en todo el rodal (Guariguata, 1999; Mesquita, 2000).

Algunas de las especies heliófitas durables son probablemente capaces de formar un banco de plantines y brinzales en el sotobosque de bosques secundarios de diferentes edades. Esta habilidad representa una importante característica para especies maderables que son extraídas de bosques secundarios. Una vez los individuos de mayor diámetro son cosechados, los plantines o brinzales presentes en el sotobosque tendrían una ventaja de tamaño sobre las especies de rápido crecimiento, las cuales probablemente ingresen al sistema si la extracción de madera ha resultado en claros grandes. Varios estudios sobre la regeneración de bosques han encontrado que los individuos presentes antes del disturbio contribuyen grandemente a la composición futura del rodal (por ejemplo, Rose, 2000). Para poder aprovechar esta regeneración

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existente es importante que el daño causado al bosque remanente durante las actividades de extracción sea minimizado.

Los bosques secundarios ofrecen una diversidad de productos forestales, y un manejo apropiado de los mismos deberá aumentar los niveles de producción de estos bosques. A pesar de que el conocimiento sobre los bosques secundarios ha aumentado en los últimas décadas, todavía falta información sobre su dinámica y sobre las características de las especies heliófitas durables. Este grupo de especies representa el grupo con mayor valor económico de estos bosques, y muestra una gran variedad de respuestas hacia la luz, lo que hace que más información sea necesaria para un manejo adecuado de los bosques secundarios.

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Referencias

Ver lista de referencias del capítulo 1 y 7.

Samenvatting

Gedurende de cyclus van zwerflandbouw wordt het regenbos gekapt, de grond gecultiveerd, en na enige jaren verlaten. Deze gebieden worden gedurende secundaire successie opnieuw gekoloniseerd door planten en na enige jaren zijn ze bedekt met secundair bos. De afgelopen tientallen jaren is de interesse in secundair bos sterk toegenomen; deze bossen zijn een belangrijke bron van bosproducten en enkele economisch belangrijke boomsoorten komen er in hoge dichtheden voor. Dit proefschrift richt zich op de processen die de loop van successie bepalen en op het beheer van secundaire bossen.

In hoofdstuk 2 worden in twee studiegebieden in de Boliviaanse Amazone de veranderingen in bosstructuur en soortensamenstelling geanalyseerd. Secundaire bossen, variërend in leeftijd van 2 tot 40 jaar, worden met elkaar en met ongestoord, volgroeid bos vergeleken. De hoogte van het kronendak en het grondvlak (de som van de oppervlakten die de stammen op grondniveau innemen) nemen toe met de leeftijd van het bos. De structuur van secundair bos lijkt daardoor vrij snel op dat van een ongestoord bos. In totaal zijn er 250 soorten in de inventarisatie gevonden. De helft van deze soorten beslaat 87% van de gevonden individuen. Het soortenaantal neemt toe met de leeftijd van het bos, terwijl de dominantie van de soorten varieert per boslaag. Het kronendak is de boslaag met de hoogste dominantie van soorten. Een

multivariate analyse geeft aan dat de soortensamenstelling varieert met de leeftijd van de opstand, de boslaag en het studiegebied. De soortensamenstelling van het bos herstelt zich voor verschillende boslagen met verschillende snelheden. De soortensamenstelling van het kronendak herstelt zich het minst snel. Over de leeftijd van het bos gemeten laten de soorten verschillende patronen in abundantie met de tijd zien. Kortlevende pioniersoorten komen alleen in de eerste successie stadia voor, terwijl langlevende pioniersoorten en schaduwtolerante soorten zich gedurende verschillende successie stadia kunnen vestigen.

Processen

Verschiedende processen beïnvloeden de loop van successie. In dit proefschrift worden processen zoals zaadverwijdering, kieming, de overleving van kiemplanten en groei in detail bestudeerd. Zodoende kan bepaald worden welke processen beperkend zijn voor de aanwezigheid en abundantie van boomsoorten gedurende verschillende stadia van successie. Het is mogelijk, dat verschillende processen van belang zijn voor verschillende stadia. Diverse veldexperimenten werden uitgevoerd in de verschillende successiestadia. De onderzochte successiestadia zijn landbouwvelden, secundair bos van 1 (2), 10 en 20 jaar oud, en volgroeid bos. Zes tot negen soorten, die verschillen in hun schaduwtolerantie, werden in de experimenten meegenomen. Deze soorten zijn voorheen geclassificeerd als kortlevende pioniersoorten, langlevende pioniersoorten, en schaduwtolerante soorten. In de experimenten werden relatief veel langlevende pionier soorten bestudeerd, om zodoende meer informatie over de overlevings- en groei behoeften van deze groep te genereren.

Hoofdstuk 3 behandelt het belang van zaadverwijdering voor de regeneratie van boomsoorten in verschillende successiestadia. Zaden van 9 soorten werden in secundaire bossen van 2, 10 en 20 jaar, en in volgroeid bos uitgezaaid. Gedurende een periode van zeven weken is er gevolgd hoeveel van deze zaden verwijderd werden. De snelheid van zaadverwijdering werd vervolgens gerelateerd aan verschillende opstandkarakteristieken. In jonge successiestadia werden er meer zaden verwijderd dan in oude. Verschillen in de gemeten opstandkarakteristieken konden de verschillen in zaadverwijdering niet verklaren. De hogere verwijdering van zaden in jonge secundaire bossen lijkt gerelateerd te zijn aan de dichtheid van mieren en knaagdieren, die de zaden verwijderen. Zowel de dichtheid van mieren als van knaagdieren neemt met de leeftijd van het bos af. Deze resultaten ondersteunen de hypothese, die

stelt dat als zaden eenmaal verspreid zijn, zaadverwijdering een belangrijke rol speelt bij de vestiging van bomen in braakliggende landbouwgebieden.

De kieming, groei en overleving van zes lichtminnende boomsoorten wordt in hoofdstuk 4 bestudeerd. Het uitgevoerde experiment heeft als doel om te bepalen of de vestiging van lichtminnende soorten tot de eerste stadia van successie beperkt is. Zaden werden in landbouwvelden, secundaire bossen van 2, 10 en 20 jaar, en in volgroeid bos uitgezaaid. Kieming, groei en overleving werden gedurende een periode van 13-19 maanden gevolgd, en aan de openheid van het kronendak en de dikte van de strooisellaag gerelateerd. De soorten kiemden niet goed in de landbouwvelden. Over het algemeen was de kieming beter in de oudere successiestadia dan in de jongere. Bladstrooisel had een negatief effect op de kieming van een aantal van de soorten. Kortlevende pioniersoorten overleefden beter in jonge successiestadia, terwijl langlevende pioniersoorten hun hoogste overleving en groei in verschillende successie stadia realiseerden. De resultaten geven aan dat niet kieming, maar groei en overleving beperkend zijn voor de regeneratie van langlevende pioniers. Voor langlevende pioniersoorten is het niet noodzakelijk om zich vroeg in de successie te vestigen. Ook vestiging in een later stadium van successie kan hun aanwezigheid in latere stadia garanderen.

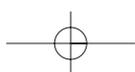
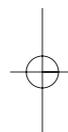
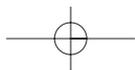
Hoofdstuk 5 behandelt de groei, overleving en biomassa-allocatie van zaailingen van negen boomsoorten, die verschillen in schaduwtolerantie. De onderzoeksvraag was a) of de overleving van zaailingen beperkt is tot een bepaald successiestadium, en b) of de groei van zaailingen varieert met het successiestadium. Zaailingen werden in secundaire bossen van 1, 10 en 20 jaar uitgeplant. Hun overleving werd gedurende twee jaar gevolgd, waarna hun toename in biomassa werd gemeten. De overleving, hoogtegroei en relatieve biomassa toename namen af met de leeftijd van het successiestadium. De soorten verschilden in hun overlevingskansen: een kortlevende pioniersoort had de laagste overlevingskans (0.5 %), terwijl sommige langlevende pioniersoorten en schaduwtolerante soorten de grootste overlevingskansen hadden (51- 70 %). Langlevende pioniersoorten verschilden in de hoeveelheid licht die ze nodig hadden om te overleven: sommigen hadden veel licht nodig, terwijl anderen evengoed onder allerlei lichtomstandigheden overleefden. Wat betreft de groei lieten de kortlevende pioniersoorten en de langlevende pioniersoorten een sterkere toename in biomassa zien dan de schaduwtolerante soorten, zowel in de vroege als in de latere successiestadia. Zaailingen pasten hun morfologie en biomassa-allocatie aan, aan het milieu waarin ze groeiden. In de jongste successiestadia is er het meeste licht beschikbaar en is de luchtvochtigheid het laagst. Als gevolg daarvan investeerden de zaailingen

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meer biomassa in hun wortelsystemen, zodat ze meer water konden bemachtigen, en ze hadden er dikkere bladeren, zodat ze minder verdampten. Ook bereikten ze er hogere netto-assimilatiesnelheden dan de zaailingen in de oudere successiestadia. In de secundaire bossen van 10 en 20 jaar oud was licht hoogstwaarschijnlijk beperkend voor de groei en zaailingen verbeterden daar hun lichtinvangst door meer biomassa naar hun bladeren te alloceren en door dunne bladeren aan te maken.

Beheer van secundaire bossen

Secundaire bossen kunnen door aanplant verrijkt worden, als de gewenste boomsoorten slechts in lage dichtheden voorkomen, of zelfs geheel afwezig zijn. Een veel gebruikte methode hiervoor is lijnbepanting. Hierbij worden lijnen, of transecten van een bepaalde breedte, in de bestaande vegetatie uitgekapt. *Bertholletia excelsa* (de paranotenboom) is een van de belangrijkste economische boomsoorten van het Boliviaanse Amazonegebied. Lokaal is er interesse om de abundantie van deze soort in secundaire bossen te verhogen. Zaailingen van *Bertholletia* werden in lijnen van verschillende breedte aangeplant, en hun overleving en groei werd gedurende vier jaar gevolgd (hoofdstuk 6). Er was geen effect van lijnbreedte op de overleving van de planten. Planten realiseerden wel een hogere groei in brede lijnen dan in smalle. Brede lijnen zorgden ervoor dat de planten een hoge groeisnelheid konden realiseren en dat hun kronen een hoge lichtintensiteit bleven ontvangen. Een additioneel voordeel van brede lijnen is dat ze slechts langzaam weer dichtgroeien, en dat er daarom minder onderhoud nodig is om de lijnen open te houden.





*Caminante,
son tus huellas el camino,
y nada más.
(Antonio Machado)*

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My path during these last four and half years has never been the same. Sometimes it was dusty (during the dry period), sometimes it was muddy (in the wet season), and sometimes even frozen (in the Netherlands)! Fortunately, there were always people around me willing to help and to laugh.

Riberalta... a small point in the map, in the middle of the Amazon forest, where the rio Beni and Madre de Dios join each other, and where everything else is far away. Riberalta ... where you can feel yourself as being in between the lines of a book of Gabriel Garcia Marquez because stories are incredible, events have the tendency to seem unreal, and daily life is a bit magic. The sun, the rain, the skies, the forest, the sunsets, and most importantly the friends have made the three years that I lived there a unique experience!!!

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y hace mucho calor. Sin la ayuda de los “barbecheros de corazón”, este trabajo hubiera sido demasiado tedioso, demasiado ambicioso e imposible de ser hecho. Gracias don Nico por identificar tantas plantas, gracias Rene por medir tan rápido tantos plantines, gracias Miguel por estar dispuesto a socorrernos cuando necesitabamos una mano sabia midiendo plantas, y gracias Luis por estar siempre presente cuando teniamos que trabajar en los barbechos más feos! Quiero agradecerles principalmente por toda la amistad, por los chistes y las risas, por el apoyo y la confianza. Compartir con Uds. el trabajo de campo, las cenas en la RET, las lluvias y los calores, los almuerzos en los caminos, los viajes, las plantadas (a lo mero macho!) fue realmente muy especial!!!

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Utrecht...also a small point in the map, in the corner of Europe, where the A27 meets the A28, where everything is flat and green, and full of water. The Netherlands... where old buildings are abundant, where houses could tell amazing stories if they could talk, where there is more beauty than the tulips in flower and the windmills in movement, and where the motorcycles have been replaced by bicycles.

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Life is made of moments, and I thank all my friends and relatives that have allowed me to share some moments of their lives. Muchas gracias de corazón!!

Marcelos

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- Peña-Claros, M. Changes in forest structure and species composition during secondary forest succession in the Bolivian Amazon. Submitted.

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Curriculum vitae

Marielos Peña-Claros was born in Santa Cruz, Bolivia on June 21st 1969. She completed high school in 1986 at the German School in Santa Cruz, Bolivia. In 1987 she began to study biology at the Biological Science Institute, University of Sao Paulo (USP), Sao Paulo, Brazil. During her studies she carried out two research projects, one at the Plant Taxonomy department and another one at the Ecology department. She obtained her BSc. degree in 1990.

Back in Santa Cruz she worked for 2.5 years at the Fundación Amigos de la Naturaleza, an NGO working on conservation issues. She assisted in the implementation of two projects carried out in two national parks of Santa Cruz department, first as the project assistant, and afterwards as the project coordinator. In the meanwhile she also gave general biology classes at the local university, participated in several expeditions done by members of the Rapid Assessment Program of Conservation International, and worked in 1992 with Dr. Robin Foster in Barro Colorado Island, Panama.

In August 1993 she began the Masters Program of the University of Florida, Gainesville, USA supported by a Fulbright scholarship. She worked at the Department of Botany under the supervision of Dr. Francis E. Putz. In eastern Bolivia she carried out field work on the ecological and socioeconomic aspects of palm heart extraction from natural stands of *Euterpe precatoria*. The field work was financially supported by a grant of the Tropical Conservation and Development program (University of Florida) and the Bolivian Forestry Project (BOLFOR, an USAID project). She graduated in May 1996.

In June 1996 she joined the Programa de Manejo de Bosques de la Amazonía Boliviana (PROMAB), as one of the Bolivian senior researchers. From June 1996 to August 1999 she worked in Riberalta where she carried out research on secondary forests. During that period she supervised Bolivian and Dutch BSc. and MSc. students, collaborated with other researchers of the team, participated in the formulation and implementation of a forest ecology course given to students of the local university, and wrote with other members of the project a technical report and governmental regulations for the extraction of palm heart from *Euterpe precatória*. She also assisted in the (logistic) management of the project. She was member of the board directory of the Bolivian Council for Forest Certification (CFV), and in this position she contributed to the development of indicators for the certification of Brazil nut harvesting activities. In September 1999 she moved to Utrecht, the Netherlands, where she worked at the Department of Plant Ecology, University of Utrecht to finish her Ph.D. thesis.