

Dense understory patches in a  
tropical moist forest in La Chonta:  
***occurrence and effects on seed removal***



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Photo on cover: Part of block 2 showing all three understory groups in one area.

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## **Preface**

While working on this thesis report I learned a lot about myself, the tropical rainforest and working independently. To start with the tropical rainforest, I loved to work there (even with all the mosquitoes) and I experienced some very exciting and scaring moments while working alone. Although reading literature about the tropics also added to my understanding of the tropical rainforest, I still believe being there in Bolivia, in the rainforest, using all my senses, was the way to learn the most about this beautiful forest. Besides the rainforest, it was a pleasure to stay in Bolivia and Santa Cruz in general. What I learned about myself and working independently is somewhat less positive. However, to not go into detail and to keep this preface positive, I can now say what my weaknesses and strengths are, what pitfalls I ought to be avoiding, which skills I should be developing and which future career direction I should (not) take. For all these learning processes (about the thesis, the rainforest and myself) I would like to thank the Forest Ecology and Management chair group and the Bolivian Forest Research Institute (IBIF), who made this thesis possible. I furthermore thank the Alberta Mennega Stichting for their financial support.

From the Forest Ecology and Management chair group I would like to thank Prof. Dr. Frans Bongers who helped me with the proposal as well as the end result and pushed me towards my colloquium. Furthermore I would like to thank Dr. Ir. Lourens Poorter (WUR) and Dr. Marielos Peña-Claros (IBIF) for the wonderful time and support they gave me in Bolivia, and of course for the “finishing touch”, which I so very much needed.

I also want to thank Ir. Arnold van Gelder for the help he gave me in the field, but mainly for his persistence to keep asking me about my thesis. The other students, who were, like me, doing research in La Chonta and entering data in Santa Cruz, also deserve gratitude for the fun we had in the forest. I would especially like to thank Bram Houben whose company made it so easy for me to go to a foreign country in the tropics.

All this work could not have been possible without the support of many materos (guides), drivers and of course our grate cook. Particularly Don Wicho deserves many thanks because he helped me gathering most of my data and knows the forest so well that he surprised me every time with finding good plots, the best seeds, delicious fruits, large monkey groups and spotting wasp-nests from a safe distance.



## Abstract

Tropical understory herbs and shrubs are an important part of the forest, because they contribute significantly to tropical forest diversity and structure. Nowadays, many understory species are found to form denser and more monospecific patches, characterized by conditions that are, among others, unfavourable to seeds and seedlings. Dense understories can therefore interfere with canopy replacement and canopy dominance. Since Bolivia is nowadays more focusing on certified sustainable timber harvesting, it is consequently important that interference of dense understories is minimal. In the forests of La Chonta three understory groups, fern species, *Heliconia spp.*, and *Erythrochiton fallax*, have been observed to form dense patches. A long-term silvicultural project (LTSRP) in these forests offered an ideal setting to study these groups with respect to selective logging. In the present study I investigated the effects of logging and environmental variables, such as light availability, topography and soil, on the distribution of the three groups (research questions 1 and 2). Furthermore I investigated their effects on seed removal (research question 3).

To investigate the effects of logging and environmental variables, the design of the LTSRP was used: 12 experimental plots representing three different management systems and a control, with 3 replicas each. Within these plots two transects with nine 2 x 2m plots were investigated. For the third research question plots were installed at places with a dense cover (appr. 80%) of ferns, *Heliconia spp.* or *Erythrochiton*. A fourth type served as control and contained less than 20% cover of each of the understory groups. In total 233 plots were installed, in which seed depots were investigated. In each seed depot 10 seeds were laid of one, out of six, seed species.

The silvicultural treatments played a role in determining the distribution of two of the three understory groups (ferns and *Heliconia spp.*). Ferns were more common in the control treatment compared to the other treatments. For *Heliconia spp.* this relation was more complicated; they were more common in the intensive treatment compared to other treatments for block 1, but this was not the case for block 2 and 3.

Light availability was an important factor explaining *Heliconia spp.* (positively) and *Erythrochiton* distribution (negatively). Fern cover was moderately affected by soil type and topography, while *Heliconia spp.* were profoundly affected by topography. They occurred more on the lower parts. This could explain the high presence in the control treatment of block 3 where the elevation is quite low. *Erythrochiton* is clearly more abundant on sandy soils, but this group also shows a highly patchy distribution.

Seed removal proved to be higher in dense vegetations, the group-specific characteristics however also seemed to influence seed removal. The main difference was the generally lower seed removal in the *Erythrochiton* plots (30%) compared to the fern and *Heliconia* plots (>50%). An explanation can be the low ground cover in *Erythrochiton* plots, due to an absence of an herb and litter layer. In addition to the differences between the understory groups, seed species also differed in their removal rates among groups.

Dense understories can establish after human interference through logging. In the case of ferns however, they can also diminish (temporally). The responses of understory groups to environmental variables are group-specific, and probably even species-specific. Other factors, like vegetative spread, may also play a role. Dense understories create conditions that are favourable to seed removal. Due to the total variability in seed removal among groups and seed species, but generally higher removal rate than the control group, the understories could potentially negatively influence the future tree community composition.



## 1. Introduction

Recently some attention has been directed towards inventorying the understory composition of tropical forests (Costa, 2004). The overstory, in contrast, has already been well studied and much information can be drawn from its structure, its composition and the manifestation of its major disturbances (Costa, 2004; Royo and Carson, 2006). Understory plants contribute significantly to tropical forest diversity (21-47% reported by Costa and Magnusson, 2003), are important food sources to forest fauna and serve several functions in human culture (Costa and Magnusson, 2002). Ground herbs are often found to have a patchy distribution and large areas of the forest floor are often lacking herbaceous cover (Poulsen and Balslev, 1991).

Understory species have received more attention because their distribution is reported to expand extremely in some cases (Royo and Carson (2006) list 38 species throughout the world). These cases have been called 'native invasive', 'low canopy' and 'recalcitrant understory layer' (Royo and Carson, 2006), but I will refer to these patches as 'dense understory'. The increasing focus on these understories is not surprising, since their extent has increased. According to Royo and Carson (2006) these understories are nowadays more dense and monospecific than was common in the past. Different causes have been identified, under which overstory thinning and browsing of competing understory plants (De la Cretaz and Kelty, 1999). Dense understory patches create conditions near ground level that are unfavourable for seeds and seedlings of many species, which makes these species resistant to displacement by other species (Royo and Carson, 2006).

An increasing focus in the last decade has been on sustainable timber harvesting (Fimbel *et al.*, 2001). Important factors highlighting the need for a change in the forestry sector in Bolivia have been high costs of production, a lack of investment, inadequate internal transport, poor regulation and shrinking forest cover. The rate of decline in Bolivia's forests of as much as 200,000 ha per year is recognized as the nation's most urgent environmental concern (Guzman and Cordero, 1998). Solutions to this devastation were promptly available; a new forestry law was created in 1996, the role of communities in managing the land was recognized and large parts of the forested area became certified by the Forestry Stewardship Council (The Nature Conservancy, 2004; BOLFOR, 2000; Quevedo, 2004).

Natural regeneration systems rely on natural regeneration to produce the next crop of timber. It is therefore vital to minimize damage to residual trees and to conserve the natural regeneration potential (Fimbel *et al.*, 2001). Mostacedo and Fredericksen (1999) already showed that for 60%, of 68 species reviewed in Bolivia, regeneration was inadequate. The most frequently cited mechanisms for regeneration problems included high rates of seed predation or otherwise low germination rates, and the small size of clearings created by selective logging. Regeneration will largely take place in logging and tree-fall gaps (Park *et al.*, 2005). Tropical tree species, however, face competition from understory species in gaps, where growth is high and flowering and fruiting of these understory species is more abundant (Costa *et al.*, 2002; Ellison *et al.*, 1993; Smith, 1987). Understory species may therefore suppress woody seedlings and in this way contribute to forest composition, structure and dynamics (Costa *et al.*, 2002; Ellison *et al.*, 1993; Harms *et al.*, 2004; Lawes and Chapman, 2006). Logging may not remain economically viable if understory species, dense or not, interferes with canopy replacement or shifts future canopy dominance to species with low timber values (Fagan and Peart, 2004).

Knowledge gaps about tropical understory species in general, and dense understories specifically, emphasize the need to study understory species in the tropics. The changed forestry

situation in Bolivia combined with the potential impact on tree regeneration shows the need to know how understory species 'act' in selective logging systems. In this study I therefore investigated three understory groups in a tropical moist forest in Bolivia. These understory groups, fern spp., *Heliconia spp.*, and *Erythrochiton fallax*, have been observed to form dense patches in the forest concession of La Chonta, in the lowlands of Bolivia. The Long-Term Silvicultural Research Program (LTSRP) plots established in this forest site offer an ideal setting to study these groups with respect to selective logging. The LTSRP in La Chonta is a design of 12 experimental plots, representing three different management systems and a control, with 3 replicas each (IBIF, 2007 - *webpage*). Within this experiment a variety of aspects (logging, environmental variables and effects on seed removal) will be studied in relation to the above mentioned understory groups. Never before has a study been performed for more than one understory group, in one area and taking into account several logging intensities (Costa *et al.*, 2002; Royo and Carson, 2006).

### **1.1 Scientific objectives**

The objectives of this study are to determine the distributions of dense understories of ferns, *Heliconia spp.* and *Erythrochiton fallax* in relation to four silvicultural treatments and environmental variables. Another objective is to reveal the effects of dense understories on seed removal. A more general objective is to contribute to the knowledge about the impact of these understory groups on the regeneration of commercial tropical timber species.

### **1.2 Research questions and hypotheses**

Several research questions are formulated to achieve the scientific objectives. The first part of this study will focus on the distribution of dense understories of ferns, *Heliconia spp.* and *Erythrochiton fallax* and specifically on the circumstances under which they occur. Many environmental factors (e.g. light, topography) can influence their distribution. Moreover, management treatments can play a major overall role because numerous characteristics of the forest are altered through logging. Research questions 1 and 2 will deal with this first part of this study. Research question 3 copes with the second part of this study; the effects of the three understory groups on seed removal. After each research question a hypothesis is formulated.

**RQ1** *Can silvicultural treatments influence the occurrence of dense understories composed of ferns, Heliconia spp. or Erythrochiton fallax?*

The research area of La Chonta consists of several experimental plots covering four different management systems. These systems differ in the degree and diversity of silvicultural treatments. Roughly spoken, silvicultural treatments intensify from treatment 1, the control treatment, towards treatment 4, the intensive treatment (see appendix I for a more precise description of the LTSRP-treatments in La Chonta). Because different management systems alter the ecosystems in many ways, light regime, vegetation and soil characteristics will also be affected to a certain extend. Therefore I hypothesize that the four management treatments will (differently) influence the distributions of ferns, *Heliconia spp.* and *Erythrochiton fallax*. And more precisely:

- Ferns will be more abundant in the control (1) and normal (2) treatment because they need moist environments to counter high rates of water loss and they have a low light-saturation efficiency and can therefore occur in highly shaded places where angiosperms can not (Page, 2002).
- *Heliconia spp.* will be more abundant in the improved (3) and intensive (4) treatment because numerous *Heliconia spp.* are highly adapted to high light conditions and consequently are rapid colonizers and can form dense stands (Rundel *et al.*, 1998).

**RQ2** *Is the presence of ferns, Heliconia spp. or Erythrochiton fallax related to environmental factors like light regime, topography or soil type?*

Light is the most important factor influencing vegetation. Forest structure and canopy composition can influence light regime, but also nutrient cycling in the soil, while topography and soil type can constraint the growth of species, for example, by water availability or nutrient availability. The general hypothesis for this question will therefore be that the presence of ferns, *Heliconia spp.* and *Erythrochiton fallax* are, in a group-specific way, related to environmental factors. More specifically:

- Ferns will occur under low light circumstances because they have a low light-saturation efficiency and can therefore occur in highly shaded places where angiosperms can not (Page, 2002).
- *Heliconia spp.* will occur under high light condition (gaps) because numerous species are adapted to high light conditions, under which they can rapidly form dense stands (Berry and Kress, 1991).

**RQ3** *Is seed removal influenced by dense understories of ferns, Heliconia spp. or Erythrochiton fallax?*

Different understory patches can influence seed establishment by providing shelter to mammal and bird species. A logical consequence is that rodent density and as a result seed removal will be higher. The spectrum of predator species (rodents, birds and larger mammals) include species which can act as seed disperser and consequently have a positive effect on seed establishment. In this research I take seed removal as a proxy for seed predation, therefore not taking into account the 'dispersal factor'. I therefore hypothesize that seed removal is influenced by dense understories of ferns, *Heliconia spp.* and *Erythrochiton fallax*. And more specifically:

- Seed removal will be higher in areas with dense vegetation because dense vegetation can provide shelter to rodents and other animals (Den Ouden, 2000).

### 1.3 Conceptual diagram

The conceptual diagram (Figure 1) illustrates the presumed important processes and concepts. How these concepts will act in the case of these three understory groups will be the focus of this research. Only the grey sections will be discussed in this report. Dense understories are known to interfere with tree regeneration through resource competition and environmental competition (Denslow, 1990; George and Bazzaz, 1999). The general question in this diagram therefore is 'How can these dense understory groups influence the regeneration of tree species?'. This research is only partly able to answer this question, which will be in the case of seed dispersal. Other aspects relating to this general question are answered by Houben (2006).

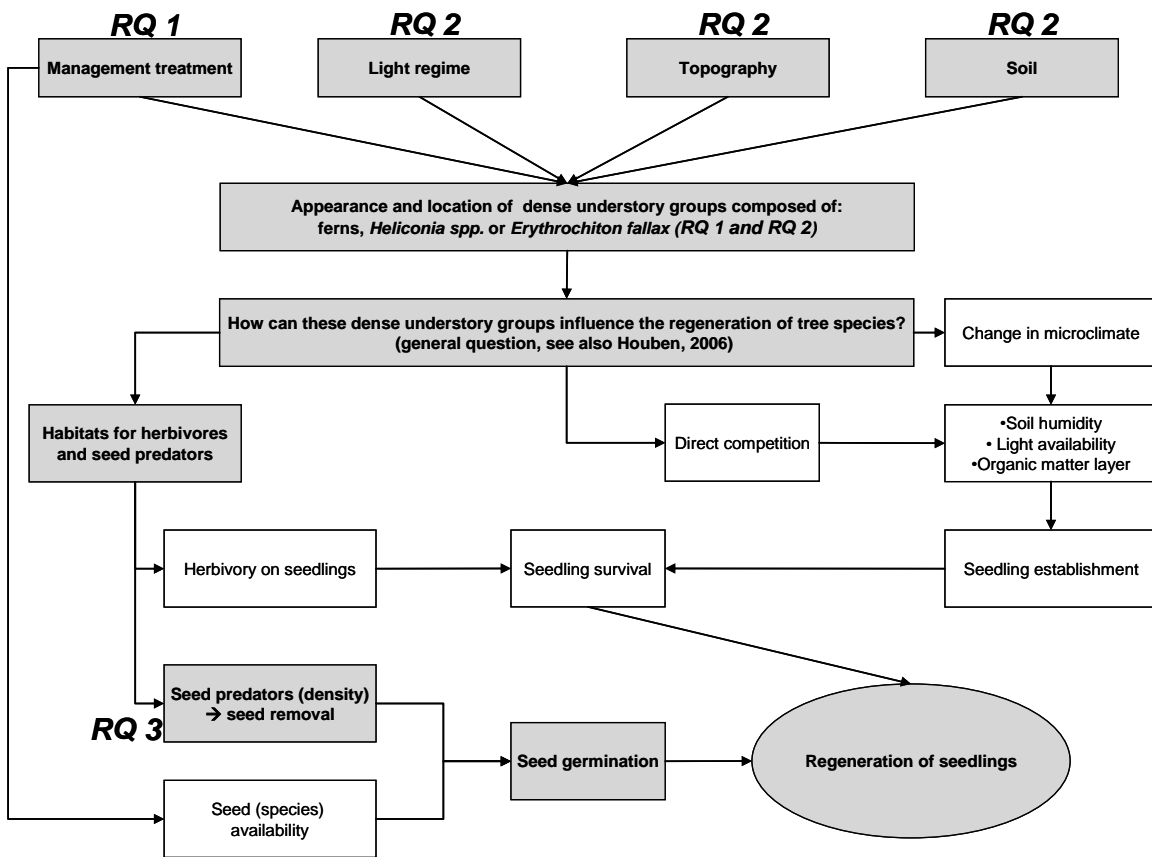


Figure 1. Conceptual diagram of research problem. Grey areas indicate the parts that are treated in this thesis report. For some parts a reference has been added to the related research questions (RQ). White areas indicate parts that have been treated in another thesis report (Houben, 2006) or concepts that are important to this research, but have not been dealt with (seed availability).

As the diagram shows, a couple of factors are assumed to influence the distributions of patches of ferns, *Heliconia spp.* and *Erythrochiton fallax*. Management treatments are believed to affect the vegetation composition through, among others, direct changes of vegetation composition (harvesting of certain tree species) or soil (scarification), and indirect changes of the light regime and soil characteristics. Understory species tend to have specific microhabitat requirements (Costa *et al.*, 2005). Therefore some abiotic factors will be investigated for their role in determining suitable growth sites for these understory groups. These factors will be light regime, topography



and soil. Costa *et al.* (2005) already indicated that floristic differences may be linked to more subtle environmental gradients instead of the large landscape-level differences, which have mainly been investigated in the past. Small-scale environmental gradients are indeed present in La Chonta (Vroomans, 2003) and therefore these factors are thought to play a role.

Ferns, *Heliconia spp.* and *Erythrochiton fallax* can have an affect on regeneration of tropical tree species through several mechanisms. Seed germination and seedling survival are controlled by a couple of processes, acted upon by the dense understories. Seed germination is influenced by the availability of seeds from the upper canopies and by seed removal. Removal is dependent on predators/dispersers, which can be affected by the vegetation through creation of suitable habitats (Jansen, 2003; George and Bazzaz, 1999). Seedling establishment and survival may be influenced by direct competition for light, nutrients and water. Changes of microclimate by ferns, *Heliconia spp.* or *Erythrochiton fallax* will result in differences in light availability, soil humidity and the organic matter layer, indirectly affecting seedling establishment and survival (George and Bazzaz, 1999; see for a discussion of these points the thesis report of Bram Houben). Sork (1987) also showed that mammalian predator-dispersers, light condition, and site conditions all influence patterns of seedling abundance.

## 2. Theoretical framework

### 2.1 The three understory groups

The three understory groups (ferns, *Heliconia* spp. and *Erythrochiton fallax*) have not been thoroughly studied in the past. Scientific knowledge about ferns in temperate regions is quite abundant, but for the tropics it is still lacking. Nevertheless, ferns and fern allies are known for the fact that they can form dense vegetation patches (Kricher, 1997; Poulsen and Nielsen, 1995; Poulsen and Balslev, 1991). Other studies in the tropics have focused on fern diversity. In the Neotropics fern



Figure 2. The most abundant fern species in La Chonta.

species richness has been estimated to encompass 3500 species and the diversity within 0.01 ha range from 20 to 60 species in different studies (Poulsen and Nielsen, 1995). Effects of dense fern patches (Figure 2) on seed removal/dispersal and regeneration have been studied in temperate areas, but scarcely in the tropics (George and Bazzaz, 1999; De la Cretaz and Kelty, 1999; Den Ouden, 2000).

Heliconias (*Heliconia* spp., family Heliconiaceae, order Zingiberales) are recognized by their huge, elongate, paddle-shaped leaves (bananas are closely related to heliconias) and their distinctive, colourful red, orange, or yellow bracts (Figure 3) surrounding the inconspicuous flowers (Kricher, 1997). These bracts vary greatly in arrangement and orientation within the family of Heliconiaceae (Bronstein; 1986). The fruits of *Heliconia* spp. are often blue-coloured and are dispersed by birds and mammals (Berry and Kress, 1991; Maas and Westra, 1993). Some heliconias grow well in shade, but most grow best where light is abundant, in open fields, along roadsides, forest edges, and stream banks. They grow quickly, clumps spreading by underground rhizomes (Berry and Kress, 1991; Kricher, 1997; Maas and Westra, 1993; Rundel *et al.*, 1998; Stiles, 1975). Rundel *et al.* (1998) also indicates that heliconias can form dense stands of 50 shoots or more. These shoots are actually leaf sheaths that form pseudo-stems (Berry and Kress, 1991; Maas and Westra, 1993). All *Heliconia* spp. are Neotropical in origin, with approximately 200 species distributed throughout Central and South America (Kricher, 1997; Rundel *et al.* 1998). Most heliconias are 1-2 meter long, but a few species can be 5 meter or even longer (Gentry, 1993; Maas and Westra, 1993).



Figure 3. One of the *Heliconia* species in La Chonta.

*Erythrochiton* is best described as a genus belonging to the family Rutaceae and its subtribe Cuspariinae Engl. The genus is little-known and can be distinguished by its red or white large, valvate calyx (Figure 4). All seven species are understory shrubs or treelets, the latter applies to *Erythrochiton fallax* Kallunki (hereafter referred to as *Erythrochiton*) (Kallunki, 1992). *Erythrochiton* can attain a height of maximal 4.5-5.0 meter, a dbh (diameter at 1.3 m) of 5 cm and is few-branched with dark-green leaves (Kallunki, 1992; personal observation). It occurs in the lowlands and on the lower slopes east of the Andes in Peru and Bolivia, as well as in the Sierra de la Macarena in Colombia. Flower and fruits are produced throughout the year (Kallunki, 1992). In Bolivia the species is called 'Chocolatillo'. *Erythrochiton* is thought to be a clonal tree (personal communication M. Peña-Claros).

Vegetative spread is important in ground herb reproduction resulting in regenerative capabilities and mobility not found in trees (Poulsen, 1996; Poulsen and Balslev, 1991). Many understory herbs and shrubs possess a clonal nature and ability to resprout after disturbance. They commonly form dense, monospecific patches that are relatively temporally stable. Clonal plants can be extremely long-lived, with life spans exceeding those of individual trees (George and Bazzaz 1999).



Figure 4. Inflorescence of *Erythrochiton fallax*.

## 2.2 Logging and understory species

The most obvious impact of logging is enlarging light availability through the opening of gaps (Costa and Magnusson, 2002). Most tropical primary forest species need gaps or increased light for germination, growth, or reproduction (Costa *et al.*, 2002). For the temperate region, *Pteridium aquilinum* (bracken) is an excellent example. This species is often released from its subdominant position in the forest floor vegetation through deforestation (Den Ouden, 2000). On the contrary, light-levels may increase above the tolerated level of some species, causing photo-inhibition (Costa *et al.*, 2002). Effects of logging on tropical understory herbs are for this, and other reasons, not uniform for all species. Various effects can also be obtained for species-specific life stages and time after logging (Costa *et al.*, 2002).

In the tropics, the formation of dense understories has not yet been proven to be dependent on logging intensity, although Costa *et al.* (2002) suggest that plant populations will be increasingly affected as the intensity of logging rises. Regionalism, nevertheless, seems to be important; formation of a dense layer of aggressive herb species has been documented for "heavily" logged areas (21 m<sup>3</sup>/ha, Africa), but could not be determined for "selective" logging (45.3 m<sup>3</sup>/ha, Brazil) (Costa and Magnusson, 2002). In the latter study, even locality within 4 ha plots was important; alterations in composition were mainly restricted to the most disturbed patches.

Logging also changes other variables; level of soil compaction and consequently soil porosity and water runoff (Costa and Magnusson, 2002). Fragmentation through access roads and clearings is another effect of logging, while interior forest environments may become scarce (Fimbel *et al.*, 2001).

## **2.3 Environmental variables and understory species**

### **Light regime**

Light availability is the most important factor affecting regeneration; emergence, growth and survival (Denslow *et al.*, 1990; 2002; Kabakoff and Chazdon, 1996; Valladares *et al.*, 2002). Montgomery and Chazdon (2001) show light to be a very variable resource. On a small scale, light availability depends on tree architecture, species composition, and vertical distribution of foliage. They measured that mean light availability decrease from over 10% at 9 m above ground to less than 2% at 0.75 m above ground. Other studies also indicate that closed canopy micro-sites in tropical rain forests often receive only 0.1- 2% of the photosynthetically active radiation (PAR) reaching the canopy above (Svenning, 2002; Valladares *et al.*, 2002). This photosynthetically active radiation consists of very low background diffuse radiation interspersed with randomly short duration sunflecks (Valladares *et al.*, 2002).

Light levels in gaps are related to size: 200 m<sup>2</sup> gaps receive 9% of full sunlight, while 400 m<sup>2</sup> gaps receive between 20-35% of full sunlight (Denslow *et al.*, 1990). Regeneration controlling factors such as light, air and soil temperature and relative air and soil humidity are influenced by gap size (Martins and Rodrigues, 2002). Different adjustments to light regimes have divided the trees of the world in broad categories of light-demanding and shade-tolerant species. Light-demanding species ("pioneers") or gap-dependent species have small seeds with extended dormancy and rapid germination and growth in response to increasing light levels, while shade-tolerant species ("climax" species) tend to have larger seeds with little dormancy, and rapid germination following dispersal (Ellison *et al.*, 1993, following Swaine and Whitmore 1988). This division is, of course, quite coarse and many tree species fall between these limits (Ellison *et al.*, 1993).

In tropical shrubs we find a similar coarse division. At one extreme are small-seeded species, characteristics of large clearings, which depend on high light levels, high ratios of red to far-red light and high temperatures for seed germination and growth. At the other extreme are slower growing, shade-tolerant, large-seeded species that are able to survive in the forest understory but that may grow and reproduce in small gaps where light resources are improved (Denslow *et al.*, 1990). Denslow *et al.* (1998) points out that in large gaps, growth of existing and newly established shrubs, lianas and large herbs rapidly reduces light availability at seedling levels. In smaller gaps, initial light levels are not sufficient to promote high growth rates or the establishment of high-light demanding liana and herbaceous species. Thus, the size of the gap defines its occupation by pioneer species or by shade-tolerant species (Denslow *et al.* 1998; Martins and Rodrigues, 2002).

### **Topography & soil type**

Habitat diversity is provided by many environmental gradients. Topography is an important one, but also a very complex one; it is inclusive of many factors (Takyu *et al.*, 2002). The topography itself can vary in slope angle, aspect or elevation (Robert and Moravie, 2003). A couple of studies indicated that topography can influence the distribution of understory species, in the temperate and tropical forests (Gibbons and Newbery, 2002; Kimura and Simbolon, 2002; Takyu *et al.*, 2002). Species diversity generally increases from ridge to valley, while species with smaller and thicker leaves decrease in dominance (Takyu *et al.*, 2002).

The complexity of a topographic gradient is exemplified by a study of Kimura and Simbolon (2002), investigating a palm species. The distribution of this palm species was restricted by soil or water and/or nutrients. Availability of water and nutrients were related to the topography of the

site. Other studies also mention changes can occur in soil composition, soil drainage and light availability (Robert and Moravie, 2003). The number of species able to grow and survive is thus affected by environmental variation along the topographic position, leading to differences in species richness, productivity and stand structure (Kubota *et al.*, 2004; Robert and Moravie, 2004). The first study found that understory species were more abundant on slopes and ridges than in the valley, suggesting that species distribution is controlled by light conditions in combination with topography. Gibbons and Newbery (2002), in contrast, found species distribution to be determined by an interaction of water availability and topography. Poulsen and Tuomisto (1996) listed distribution of terrestrial ferns, in several studies, to reflect topographic differences, soil differences or soil-water availability.

Nutrient content of the soil, however, is not solely determined by topography. Soils also have their own inherent characteristics, and these strongly affect plant species distributions and total species richness for herbs, tropical rain forest trees, lianas and ferns (Poulsen and Balslev, 1991; Tuomisto *et al.*, 2002). Sharma *et al.*, (2004) clearly demonstrates how nutrient content can change with soil particle composition. They concluded from their research that total content of micronutrients increased with an increase in silt and clay, while it would decrease with an increase in sand. However, organic carbon content showed to be influencing available micronutrient content.

La Chonta is situated on a continuation of the Crystalline Shield Chiquitano and generally consists of oxisols, inceptisols and ultisols (Park *et al.*, 2005). However, Rivera (2003) recognizes three slightly different soil types at the research site of La Chonta. Besides inceptisols, about 10-15 % of the research site exists of *tierra negra* and *tierra morena*. Both soils have, among other characteristics, a higher nutrient content compared to inceptisols, with *tierra negra* having the highest content. *Tierra negra* and *tierra morena* soils both contain residues of a former culture (anthropogenic soils), like charcoal and pottery, and are darker compared to inceptisols. *Tierra negra* soils are mostly found on flat terraces nearby streams that flow at least during the rainy season.

## **2.4 Seed predation and dense understories**

A lot of plant-animal interactions exist in every forest type. Some of these interactions are antagonistic, some are mutualistic, and many unite elements of both (Andresen and Levey, 2004). The following diagram (Figure 5), copied from Wang and Smith (2002), shows the most important stages in population dynamics of plants or trees and the corresponding processes. A lot of processes in this so-called "seed dispersal cycle" comprise plant-animal interactions. Examples are pollination by birds, bats or insects, frugivory by monkeys, dispersal by rodents, dungbeetles etc. (Andresen *et al.*, 2005; Bongers *et al.*, 2001). Seedling survival can be influenced by mammalian herbivory and seed predation or mammalian herbivory are known to influence the amount and spatial character or recruitment in animal-dispersed species (Howe, 1990).

Seed dispersal dynamics in all probability affect plant processes ranging from colonization of new habitats to maintenance of diversity, with consequences for succession, regeneration and conservation (Wang and Smith, 2002).

### **Seed predation versus dispersal in relation to tropical tree species**

The seed to seedling transition is generally considered to be one of the most vulnerable stages (Sork, 1987). The establishment of trees in successional habitats is limited by seed predation (Meiners and Stiles, 1997). This is a selective process; seed predators often show selective predation on a subset of available species within a community. Small seeds are an adaptation to

increasing the likelihood of encountering a favourable site for establishment, while the internal energy reserves of large seeds decrease the risk of mortality after arrival at particular sites (Van Ulft, 2004). The Janzen-Connell hypothesis postulates that a main benefit of seed dispersal is that it enables seeds and seedlings to escape the high density-dependent mortality that results from pathogens, seed predators, and/or herbivores directly under the parent plant (Wang and Smith, 2002). Seed dispersal furthermore enhances a plant's chance to place seeds in suitable establishment sites and improve germination when it involves passage through the gut of animals (Jansen, 2003). Zoochory (dispersal of seeds by active transport of animals) is the most common means of dispersal in many tropical rain forests (Bongers *et al.*, 2001; Jansen, 2003). Frugivorous species (species that only digest the pulp of fruit and discard most of the seeds) are important, mostly primary, seed dispersers which perform the coarse dispersal away from the parent tree. A couple of frugivorous species in the Neotropics are toucans, guans, cotingas, fruit bats, howler monkey and spider monkeys (Jansen, 2003).

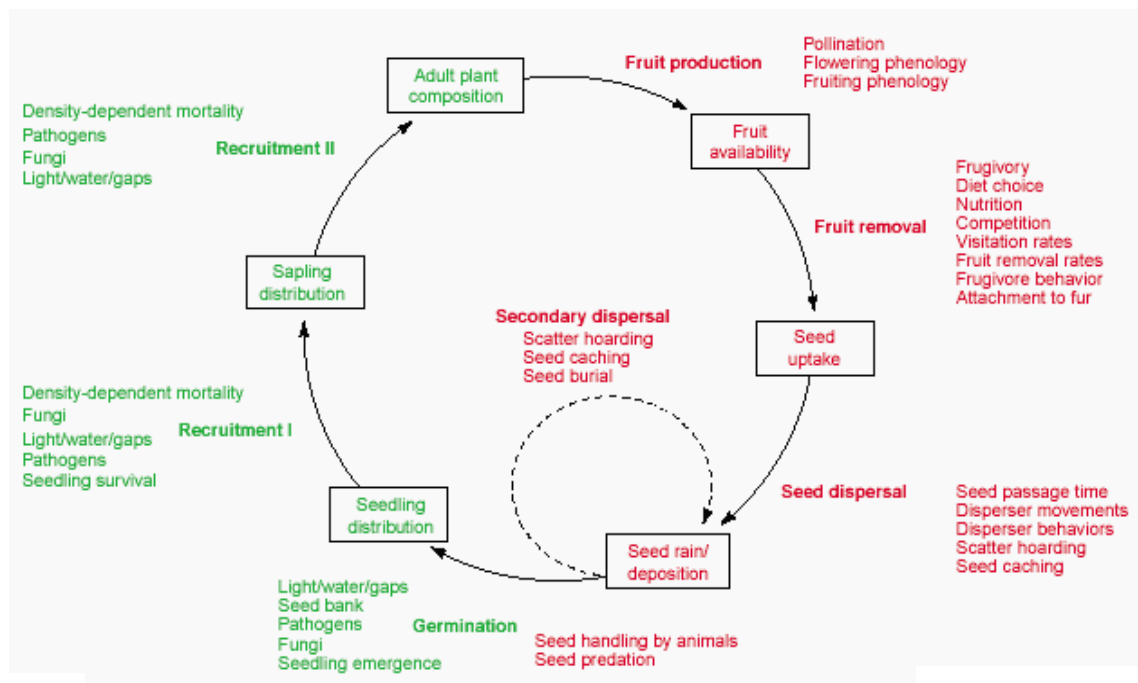


Figure 5. Seed dispersal cycle, following Wang and Smith (2002). The main stages and processes are shown.

The most important post-dispersal (after the seeds have fallen or dispersed to the ground by primary dispersers) mammalian seed predators are rodents (Van Ulft, 2004). However, many species also suffer heavy predation by insects (Fimbel *et al.*, 2001). Rodents benefit from denser undergrowth following habitat disturbance (Jansen, 2003). Some seed predators (rodents, but also dung-beetles) bury seed surplus in order to build up reserves and are called scatterhoarders. Seeds can escape predation if the cached seeds are not retrieved by the scatterhoarder (Bongers *et al.*, 2001; Den Ouden *et al.*, 2005). Furthermore, scatterhoarding may enhance seed survival and seedling establishment because it secures seeds from predators such as insects and wild pigs (Jansen and Den Ouden, 2005). Andresen and Levey (2004) showed that burial of seeds increased the probability of seedling establishment. Scatterhoarding and other forms of secondary dispersal are potentially highly influential on vegetation structure (Wang and Smith, 2002). Overall

composition of the rodent community is influenced by the productivity and composition of the vegetation, while the spatial patterning in densities and species composition of rodent populations is dependent on the structural characteristics of the habitat (Den Ouden, 2000). Vegetation cover, presence of dead wood or litter depth greatly determine local habitat suitability for most rodent species, but there may be large differences among rodent species in local habitat utilisation.

### **3. Methods**

#### **3.1 Research site**

Research was carried out at La Chonta, a 100,000-ha timber concession located in the Guarayos Forest Reserve in the province of Guarayos of the department Santa Cruz of Bolivia, (15°45'S, 62° 55'W, Krueger, 2003). The area receives an annual mean precipitation of 1,562 mm and an annual mean temperature of 25.3°C, with a dry season from May-September. The forest has been classified as tropical moist semi-deciduous and represents a transition between dry forests and Amazonian forests. La Chonta is one of the study sites of IBIF where LTSRP plots have been established, there are three blocks with 4 treatments each. Treatments are control, normal, improved and intensive treatment and these are applied to approximately 600 x 450 m plots each, resulting in large rectangular plots of 27 ha.

Blocks were located in different logging compartments, leading to variation; block 2 is located near block 1, but more to the east and includes quite a large stream. Block 2 also shows the highest variability in altitude, with steeper hills, while block 3 has the smallest variation in altitude (Vroomans, 2003). Block 3 is about 15 kilometres from the research station, and is located more to the northwest. Moreover, blocks are established in different years, block 1 in the beginning of 2001, block 2 in 2000 and block 3 in 2002, and were thus harvested between 2001 and 2002.

#### **3.2 Experimental design 1 – presence of understory groups**

The main focus of this research are three dense understory groups; ferns, *Heliconia spp.* and *Erythrochiton fallax*. Research question 1 focuses on the general presence of these three groups in the understory. More specifically this research concentrated on differences in presence of these understory groups among the management treatments. Research question 2 discusses the relation for each of the understory groups with environmental variables. Therefore, a general analysis of the forest understory in every block and for every treatment was performed.

##### **3.2.1 Transect design**

Distribution of ferns, *Heliconia spp.* and *Erythrochiton fallax* were measured in the second/third week of November and the first half of December 2004. Trails, created by IBIF, were used as transects, two for every treatment in every block (except for the control treatment in block 2 which burned down in October that year). Transects were 200 m apart (trails 100 and 300 for block 1, and trails 200 and 400 for block 2 and 3), and approximately 450 m long. Every 50 m a measurement was done in a 2x2 m plot. The 2x2 m plot was established 1 m distant from the trail and skidder trail, but sometimes intermediate intervals of 25 m or 75 m were used, for several reasons. In some cases it was impossible to enter the forest, due to lianas and the stinging pioneer species *Urera baccifera L.*, and establish a 2x2 m plot. In other cases the coordinates coincided with skid-trails or very recently originated natural gaps. In these cases, a plot was established 25 m further from the original place, at the next coordinate. In total, 198 plots were investigated, 54 in each of the treatments, except the control treatment (only 36).



### 3.2.2 Environmental variables data

Variables measured in these plots were cover and height of ferns, *Heliconia spp.* and *Erythrochiton fallax*. Several morphospecies of fern and *Heliconia* could be distinguished in the field and for these species cover and height per species were also recorded. Furthermore, for each of the 198 plots, seedling cover and number (until a height of 2 m), liana and herb cover, canopy openness, litter cover and depth, topography class (Table 1) and soil type (Table 2) were measured. Cover is visually estimated and defined as the vertical projection of the shoot area to the ground surface. The maximum height, defined as the height of the largest tree with a crown above the 2x2 m plot, was recorded for each plot as well as all diameters of trees with a dbh > 10 cm and within a range of 5 m (Figure 6) from the middle of the plot. Canopy openness was measured with a densiometer at the centre of every plot. Litter depth, also including woody debris, was measured with a ruler in 4 different places. These places were the centres of the four 1x1 m quadrants of the 2x2 m plot. If woody debris was present within 2 cm of the ruler, the height of the woody debris would be taken as litter depth.

Table 1. Topography classes (left) and soil types (right).

Class	Topography
1	Valley
2	Foot of slope
3	Low slope
4	Medium slope
5	Strong slope
6	Top of slope

Type	Soil texture	Loam (%)
1	Sand	0-20
2	Loamy sand	20-40
3	Sandy loam	40-60
4	Loam	60-80
5	Loamy clay	80-100

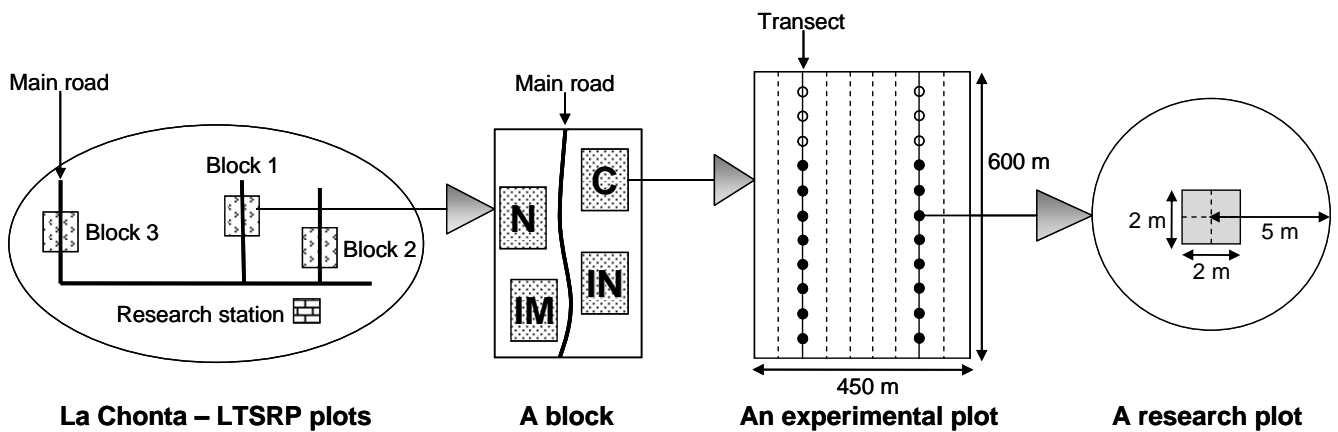


Figure 6. Schematic presentation of the experimental setup. This setup is designed to answer research question 1 & 2. The figure gives an overview of the experimental situation but do not represent reality at scale. The research plot shows the situation of block 1, closed circles represent planned research plots, open circles represent possible research plots, used when necessary. Trails are 600 m long, every 50 meters a trail was created by IBIF which resulted in 8 trails within the plot and 2 at the periphery. In block 2 and block 3 the experimental plots are turned 90° compared to the main road. Trails in these blocks are consequently only 450 meters long, and are created perpendicular to the 600 meter side, resulting in 11 trails within the plot and 2 at the periphery. Research plots were set-up next to a trail; all measurements (% ferns, *Heliconia spp.*, *Erythrochiton fallax*, etc.) were done in these plots.

### 3.3 Experimental design 2 - seed removal

The general design to answer research question 3 “Is seed removal influenced by dense understories of ferns, *Heliconia* spp. and *Erythrochiton fallax*?” is a seed removal experiment with seeds of several tree species prone to removal within numerous patches of the three understory groups.

#### 3.3.1 Seed species

Seeds of six tree species were included in the seed-removal experiment (Figure 7, Table 2). Species choice depended mainly on local and periodic availability in the area, although one species was already collected in the preceding year on behalf of another study (*Swietenia macrophylla* King.). These seeds were air dried and subsequently stored in a dark place. Others were collected during dispersal, but before conduction of the seed-removal experiment (*Schizolobium parahyba* (Vell.Conc.) S.F. Blake, *Sapindus saponaria* L., and *Cariniana ianeirensis* R. Kruth). Seeds were found in the experimental blocks in the vicinity of seed trees during transect-measuring in November and December 2004. These seeds also had some time, about a month, to dry before



Figure 7. Seeds of the 6 species used for the seed removal experiment. In alphabetical order: (1) *Cariniana ianeirensis* R. Kruth (without wings) (2) *Margaritaria nobilis* L.f. (3) *Pouteria nemorosa* Baehni (4) *Sapindus saponaria* L. (5) *Schizolobium parahyba* S.F. Blake (6) *Swietenia macrophylla* King.

being used in the experiment. The two remaining species (*Margaritaria nobilis* L.f. and *Pouteria nemorosa* Baehni) were collected during the dispersal period, which matched more or less with the experimental period of this experiment. Consequently, these seeds were unable to dry properly. Seeds of one species were always collected underneath several seed trees. If needed, fruit flesh was removed from the seed. Only undamaged seeds were used, except for *Cariniana* and *Swietenia*, these seeds were dewinged before storage. Subsequently, species will be referred to by generic name. Life history strategy, seed weight and fruit characteristics are summarized in Table 2.

Table 2. List of tree species used in the seed-removal experiment. The table includes scientific name, family, strategy, mean field weight and fruit characteristics. LLP = long-lived pioneer, PST = partial shade tolerant. Seed mass data sources: top three by Dr. Ir. L. Poorter, bottom three are field weights. (Sources: Poorter *et al.*, 2006, Hooper *et al.*, 2004).

Scientific name	Family	Bolivian name	Strategy	Seed mass (mg)	Fruit characteristics
<i>Cariniana ianeirensis</i> R. Kruth.	Lecythidaceae	Yesquero blanco	PST	0.16	Winged seeds. Wind-dispersed. Are frequently eaten by birds and animals.
<i>Margaritaria nobilis</i> L.f.	Euphorbiaceae	Cafecillo	LLP	0.013	Blue-metallic coloured seeds. Fruits dispersed by birds.
<i>Pouteria nemorosa</i> Baehni	Sapotaceae	Coquino	PST	1.66	Fruits are eaten by arboreal species. Primary dispersal by gravity. Secondary dispersal by vertebrates.
<i>Sapindus saponaria</i> L.	Sapindaceae	Isotouvo	PST	1268	Seeds are round, approximately 10 mm long, surrounded by a sticky fruit. Dispersal by big birds.
<i>Schizolobium parahyba</i> S.F. Blake	Caesalpiniaceae	Serebó	LLP	830	Wind-dispersed.
<i>Swietenia macrophylla</i> King.	Meliaceae	Mara	PST	472	Large, brown, winged seeds. Primary dispersal by wind. Potential (secondary) seed dispersal by vertebrates.

### 3.3.2 Plot characteristics and design

Seed removal was measured for the three different understory groups and a control "type" during January and February 2005. The three understory group were:

1. *Erythrochiton fallax*:  $\geq 80\%$                        $\& \leq 20\%$  ferns,  $\leq 20\%$  *Heliconia spp.*
2. Ferns:  $\geq 80\%$      $\& \leq 20\%$  *Erythrochiton fallax*,  $\leq 20\%$  *Heliconia spp.*
3. *Heliconia spp.*:  $\geq 80\%$                                        $\& \leq 20\%$  *Erythrochiton fallax*,  $\leq 20\%$  ferns

A fourth "type" served as control:

4. Control:  $\leq 20\%$  *Erythrochiton fallax*,  $\leq 20\%$  ferns,  $\leq 20\%$  *Heliconia spp.*

These understory groups and the control type were at least present in an area of 2x2 m, although preferably more (about 4x4 m) but this was hard to realize for every plot. Plots were located mainly in the control treatments of block 1 and 3, but it was impossible to install plots with a very high cover of *Erythrochiton fallax* in the control treatments, so these plots were established in the intensive treatment of block 2. To account for the variability between control and intensive treatments, control plots were established in both the control treatment of block 1 and the intensive treatment of block 2. In total, 233 plots were established, 95 were used twice (in different periods) and this makes a total of 328 seed stations. Seed depots were used to prevent washing-away of seeds during heavy rainfall. In an ideal situation 15 control plots, 15 fern plots, 15 *Heliconia* plots and 15 *Erythrochiton* plots would have been established and investigated for every seed species. In reality (Table 3), seed depots were sometimes missing, due to gap-formation or miscalculation, and this resulted in different numbers. Seed depots were made of metallic-wired mosquito-maze in a triangular shape, with the sides up folded and measured more or less 21x21x30 cm (Figure 8). In every seed depot, 10 seeds were placed, and seed depots were

filled with sand and a little bit of litter from the area, to make it look more natural. Seed depots were fixed to the ground with three cramps and marked with (mostly orange) flagging tape to a little plastic tube (+/- 30 cm high) about half a meter away from the depot, to decrease searching time (for researcher and assistants) of a seed depot.

Table 3. Number of seed depots used per seed species and treatment. Grand total and totals per seed species and understory group are also presented. A zero means the group is left out of the experiment, due to limited amount of seeds.

	<b>Control</b>	<b><i>E. fallax</i></b>	<b>Ferns</b>	<b><i>Heliconia spp.</i></b>	<b>Total</b>
<i>Cariniana</i>	14	16	15	0	<b>45</b>
<i>Margaritaria</i>	15	15	15	15	<b>60</b>
<i>Pouteria</i>	16	15	15	14	<b>60</b>
<i>Sapindus</i>	13	0	14	15	<b>42</b>
<i>Schizolobium</i>	16	15	16	15	<b>62</b>
<i>Swietenia</i>	16	15	13	15	<b>59</b>
<b>Total</b>	<b>90</b>	<b>76</b>	<b>88</b>	<b>74</b>	<b>328</b>

### 3.3.3 Seed assessment

Seeds were considered viable, if they were still present or had germinated while being present. Some forms of damaged seeds were also considered viable; when the seed coat or wing was partially eaten by either animals or insects so germination would not be affected, when they were entered by insects (termites), or when they were partially covered with fungi. Seeds were considered removed if they were indeed gone, or could not be seen within the vicinity (about 1 m) of the seed depot. When they could be seen in the direct vicinity, which was unusual, seeds were placed back in the seed depot. Seeds were considered



Figure 8. Seed depot with *Schizolobium* seeds. Photo is taken at the end of experimental period; one seed already germinated.

dead/predated if the embryo of the seed was partly or totally eaten by either animals or insects, or if the embryo was totally infested by fungi. Depots were checked after 0, 2, 4, 7, 10, 13 and 26 days. Seed depots were at least 25 meters apart and seed species were assigned to a depot randomly in the field. Damage to experimental plots and surrounding vegetation was reduced by entering the plots carefully and using one place to enter the plot. Moreover seeds were mainly analyzed and counted from a distance (0.5 meter), preventing damage in the direct vicinity of the seed depot. Seeds were handled with large tweezers, held by gloved hands and inspected at a white plate, which had a high contrast with the, mostly, dark seeds. All these precautions were taken to prevent body odours passing to the seeds.

### **3.3.4 Habitat characteristics data**

Environmental and vegetation variables were also measured in these experimental plots, mainly during the end of February and the beginning of March. This data could be linked to the seed removal rate of the seeds. Plots of 2x2 m were established around the seed depots, in such a way that the seed depot ended up in the centre. The following variables were measured; percentage cover of ferns, *Heliconia* and *Erythrochiton*, cover of *Costus spp.*, herbs and lianas, total vegetation cover, litter cover, woody debris cover, number of *Heliconia* stems and canopy openness. Cover is visually estimated and is defined as the vertical projection of the shoot area to the ground surface. Canopy openness was again measured with a densiometer in the centre of a plot. Number of woody stems, categorized by *Erythrochiton* and "other", were also counted according to four height classes. Height classes were 0-30 cm, 30-150 cm (both seedlings), 150 cm – 10 dbh (saplings) and 10-20 dbh (small trees). Habitat characteristics, like the variables measured in this study, are believed to contribute, positively or negatively, to the attractiveness of the site for animals, birds as well as insects (Peña-Claros and De Boo, 2002; Den Ouden, 2000).

### **3.4 Data analysis – silvicultural treatments**

#### *Exploring density distributions*

Primarily, data is explored with Excel to evaluate density (cover) distributions of the three understory groups within the forest. This was done by assigning all data points for fern, *Heliconia spp.* and *Erythrochiton fallax* cover to one out of 11 cover categories. Cover categories were 1-10%, 11-20%,....., 91-100% and one category with zero-values (no cover at all).

#### *Differences between treatments and blocks*

The second step in the analysis was checking the data for normality. None of the variables proved to be normal (Kolmogorov-Smirnov test for normality) and none of the dependent variables, covers of the three understory groups, had equal variances (Levene's test in two-way ANOVA). Transformations (arcsine and square root) also could not change the non-normal data to normal. Data analysis was therefore done using untransformed data (%) and non-parametric tests.

Differences between groups, for block and treatment, were subsequently analysed with a Kruskal-Wallis test, a non-parametric test. If the test-outcome was significant, pairwise comparisons were performed to find differences between pairs of treatment. The Bonferroni correction was used to correct the P value for multiple pairwise comparisons (P value for treatment-analysis: 0.0083 and for block-analysis: 0.0167). A Scheffe post-hoc test was used to double-check on the outcome of the multiple comparisons with Kruskal-Wallis tests (Field, 2005).

#### *Interaction effect of block x treatment*

A two-way ANOVA was performed to check for interaction effects of block x treatment. Understory groups which showed a significant interaction-effect were subsequently analyzed for differences between treatments per block. Again, this was done by using Kruskal-Wallis tests with a Bonferroni correction and double-checking by running a Scheffe post-hoc test with ANOVA.

### **3.5 Data analysis – environmental variables**

#### *Correlations and regressions*

Relations between environmental and vegetation variables were explored with correlation-tests. The spearman's rho test was used, because none of the variables proved to be normal (Kolmogorov-Smirnov test). Dummy variables were made for the topography classes and soil types, in this way the categorical variables were suitable for a linear regression. Separate linear regressions were performed to search for significant relation between individual variables and a dependent variable understory group. These significant variables were consequently entered in one linear multiple regression with the corresponding understory group. Afterwards, multiple linear regressions were checked for normality with the standardized residuals.

#### *Group differences*

Besides correlations and regressions, some extra tests were performed for soil type and topography class. In all cases, a Kruskal-Wallis test was executed to search for differences between topographic or soil categories per understory group. Pairwise comparisons with a Bonferroni correction were used to find significant differences. In the case of topographic categories the Bonferroni correction resulted in a very low p-value of 0.0023, while for soil categories this p-value was 0.005. This p-value for topography was too low to find significant differences, and therefore differences were analyzed with an ANOVA and Games-Howell post-hoc test. This is the most powerful post-hoc test when variances are unequal and it is still accurate with unequal sample sizes (Field, 2005).

### **3.6 Data analysis – seed removal**

#### *Exploring characteristics of understory groups*

First of all the data was checked for normality with Kolmogorov-Smirnov tests for every variable. None of the variables showed normality and variables also proved to have unequal variances with Levene's tests. Therefore non-transformed data were used in non-parametric Kruskal-Wallis tests. These tests were performed for every variable measured in the field to explore the characteristics of plots of the three understory groups and the control type. Again, pairwise comparisons with a Bonferroni correction ( $p=0.083$ ) were used to find differences between pairs of understory groups.

#### *Seed removal rate – Cox regression*

After analyzing the characteristics of the different types of understory plots, Cox regression was used to search for differences in survival rate per understory habitat (control, ferns, *Heliconia spp.* and *Erythrochiton fallax*). Habitat was entered as "covariate", day as "time" and census as "status", using 0 when seeds were not removed and 1 when seeds were removed. When habitat is entered (no entry criteria, except tolerance) as a covariate, Cox regression tries to shape the cumulative survival slope to a slope which matches more to the data per understory group. This was tested with simple contrasts to search for significant differences (Wald statistic) of seed survival per understory groups. These tests were performed per seed species separately and for all species together.

*Seed removal rate related to environmental characteristics – linear regression*

The seed removal rate is computed as a linear regression of the log-number ( $x + 1$ ) of surviving seeds against time (day) with inclusion of an intercept through the origin. This was necessary because otherwise seed depots which have their seeds removed at a higher rate have a lower seed removal. Seed removal rates were computed using Excel for every seed depot. This seed removal rate subsequently was regressed to different environmental and vegetation characteristics in a linear regression of SPSS. Standardized residuals were checked for normality with Kolmogorov-Smirnov tests.

## 4. Results

### 4.1 Influence of silvicultural treatments on the occurrence of the groups

Hardly any dense stands of ferns, *Heliconia spp.* and *Erythrochiton* occur in the forest. Mean covers were 25% for ferns, 16% for *Heliconia spp.* and 1% for *Erythrochiton*. Figure 9 shows that only 1% of the forest exists of very dense stands of ferns (> 80%), although 14% of the forest contains stands of ferns with a cover of 50% or more. In 6% of the plots ferns were absent. Only 3% of the forest is covered with a dense understory of *Heliconia*, while 9% is covered with patches of 50% or more *Heliconia*. However, in a large part of the forest, more than 40% of all plots, *Heliconia* was not present at all. *Erythrochiton fallax* occurred only in 10 plots and none of these 10 plots had a cover higher than 50% (not shown in figure 9).

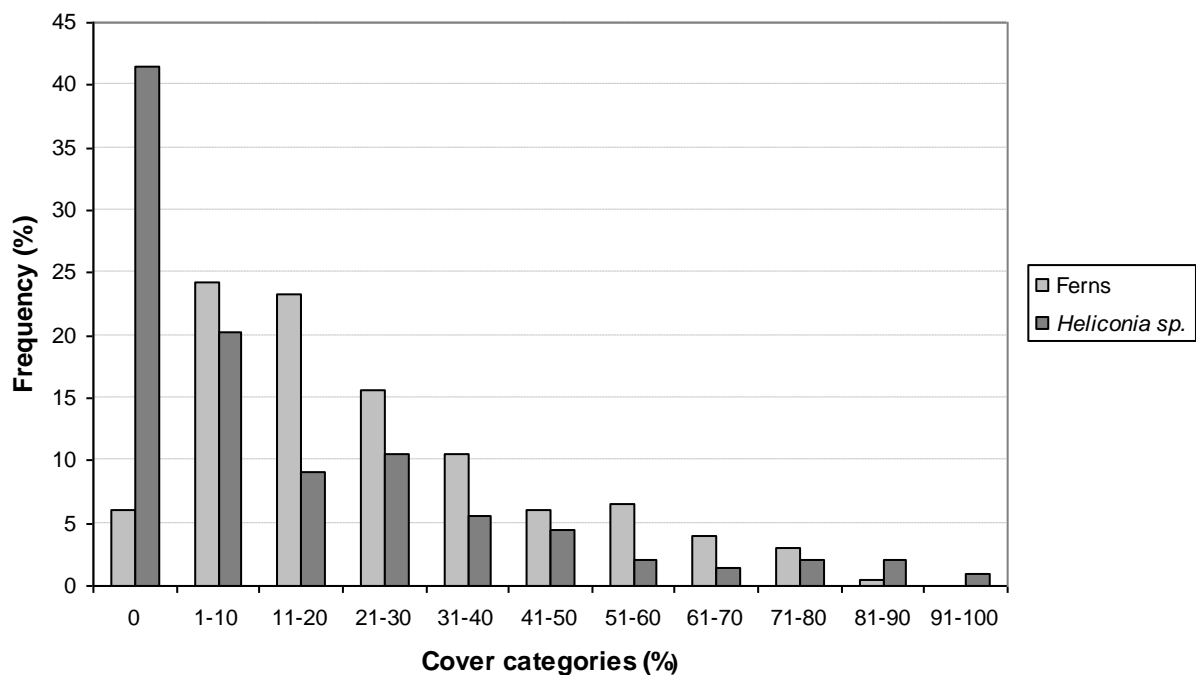


Figure 9. Density distributions of ferns and *Heliconia spp.* in La Chonta. Densities are clustered in cover categories of 10% each and a zero-category for absence of these groups. Total fern and *Heliconia* cover of all 198 plots are used. *Erythrochiton fallax* is not presented here, because numbers of plots where *Erythrochiton fallax* was present are minimal (10 out of 198 plots).

#### 4.1.1 Treatment effect

The three understory groups were successively analyzed with Kruskal-Wallis tests. Only ferns showed a significant difference in mean cover between treatments (Kruskal-Wallis with Bonferroni correction, sign. 0.000). This test pointed out that the control treatment differed with a higher mean from all other treatments, except for the normal treatment (Figure 10). The remaining understory groups, *Heliconia spp.* and *Erythrochiton fallax*, did not show significant differences among silvicultural treatments (Figure 10).



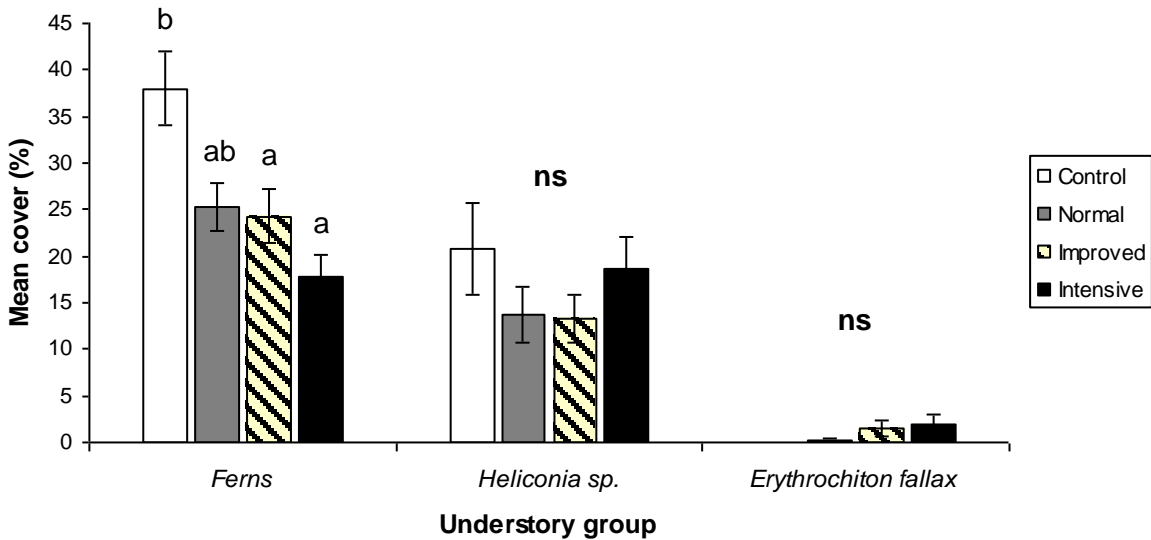


Figure 10. Mean covers of the three understory groups per silvicultural treatment. Mean cover is given in percentage (%), based on plots established along transects. Letters indicate significant differences among treatments (Ferns Kruskal-Wallis with Bonferroni correction, sign. 0.000). ns = not significant (*Heliconia spp.* sign. 0.671; *E. fallax* sign. 0.067)

#### 4.1.2 Block effect

Ferns proved to have a significantly higher mean cover in block 1, compared to block 2, block 3 did not differ from the other two blocks (Kruskal-Wallis, sign. 0.024). *Heliconia spp.* showed another picture, block 3 contained the highest cover of *Heliconia spp.*, while block 1 and 2 were significantly lower, but did not differ from each other (Kruskal-Wallis, sign. 0.001). A Kruskal-Wallis also showed a difference for *Erythrochiton fallax* (Kruskal-Wallis, sign. 0.019). Multiple pairwise comparisons with a Bonferroni correction indicated that the difference could indeed be found; *Erythrochiton fallax* was not present at all in block 3 and this block differed significantly from block 2. Block 1 and 2 did not differ significantly from each other. A Scheffe post-hoc test could not find this difference. Shortly, ferns are mostly present in block 1 and *Heliconia spp.* in block 3, while *Erythrochiton fallax* shows only questionable differences (maybe because ranges of mean cover of *Erythrochiton fallax* go from 0.0 till 2.0% for the intensive treatment).

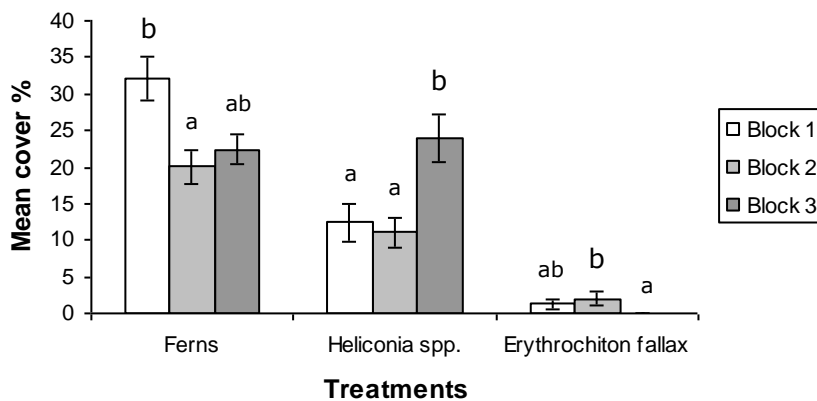


Figure 11. Mean understory cover for every understory group per block. Mean covers are given in percentages (%). Block 1 is shown in white, block 2 in grey and block 3 in dark grey. Letters above bars indicate significant differences among blocks. The bars show that every understory is more common in a different block (Kruskal-Wallis with Bonferroni correction, sign. ferns = 0.024, *Heliconia spp.* = 0.001, *Erythrochiton fallax* = 0.019).

#### 4.1.3 Block x treatment interaction

A two-way ANOVA was used to test for a block x treatment interaction. These ANOVA's (for every understory group separately) showed that there was not a block x treatment interaction for ferns, but that there was an interaction for *Erythrochiton fallax* ( $p < 0.000$ ) and *Heliconia spp.* ( $p < 0.000$ ; Figure 12).

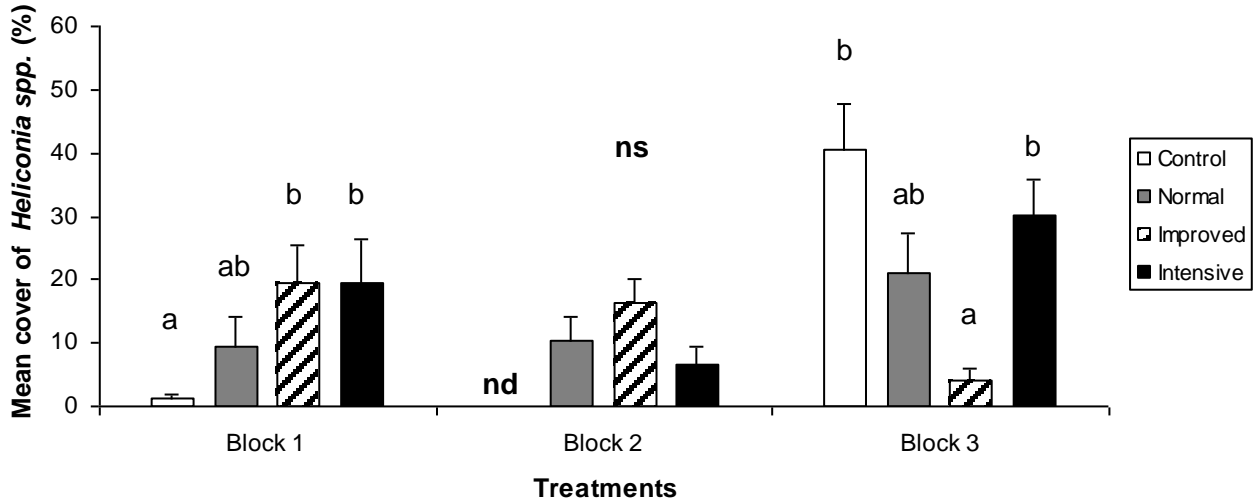


Figure 12. Mean *Heliconia spp.* cover per treatment and per block. Letters above bars indicate the significant differences (Kruskal-Wallis with Bonferroni correction, sign. = 0.017 for block 1 and 0.002 for block 3, block 2 = not significant). A two-way ANOVA indicated an interaction effect of block with treatment ( $p < 0.000$ ). Notice the different mean covers per treatment for block 1, compared to block 3 and block 2. ns = not significant, nd = no data

*Heliconia spp.* (Figure 12) are more common in the improved and intensive treatment compared to the control treatment in block 1 (Kruskal-Wallis, sign. 0.017), while in block 3 it shows the opposite trend (Kruskal-Wallis, sign. 0.002). *Heliconia spp.* do not show any differences between treatments in block 2.

*Erythrochiton fallax* is more common in the intensive treatment compared to the normal and improved treatment in block 2 (Kruskal-Wallis, sign. 0.001). However, this test-result is based on 198 data points of which only 10 are non-zero values. The other blocks do not show any significant differences.

## 4.2 Influence of environmental variables on the distribution of the groups

A lot of variables were measured and to reduce the number of variables, correlation tests were performed to explore the relations between understory groups and environmental variables (Table 4).

### Ferns

Ferns have a positive relation with topography and with maximum tree height. High cover of ferns is therefore related to higher places / steeper slopes and to a greater maximum height of the forest. These positive correlations are quite weak (Table 4). Fern cover is negatively related to *Heliconia spp.* and *Erythrochiton fallax*. These correlations mainly demonstrate that where ferns grow abundantly, *Heliconia spp.* and *Erythrochiton fallax* do not and visa versa. The negative correlation of the soil type shows that fern cover increases with a decreasing soil type number (decreasing loam content). Ferns are as a result growing at sandy or low loamy soils.

Table 4. Correlations of the most important factors. The upper table shows the relation of the three understory groups with vegetation types, the bottom table shows the relation of the three understory groups with environmental variables. Tested with bivariate correlations; Spearman's rho for non-normal and ordinal data. \*  $p \leq 0.05$ , \*\*  $p \leq 0.01$ , otherwise non-significant

	<b>Fern cover</b>	<b>Heliconia cover</b>	<b>Erythro. cover</b>	<b>Seedling cover</b>	<b>Seedling number</b>	<b>Liana cover</b>	<b>Herb cover</b>
<b>Ferns</b>	1	-0.219**	-0.260**	0.053	-0.017	-0.037	-0.083
	<b>Heliconia</b>	1	-0.143*	-0.075	-0.082	-0.087*	-0.094
		<b>Erythro.</b>	1	-0.165*	-0.018	-0.169*	-0.067

	<b>Canopy openness</b>	<b>Litter cover</b>	<b>Litter depth</b>	<b>Topo. class</b>	<b>Soil type</b>	<b>Max. height</b>	<b>Basal area</b>
<b>Ferns</b>	-0.060	0.116	0.083	0.174*	-0.135*	0.146*	0.075
<b>Heliconia</b>	0.308**	0.165**	0.113	-0.239**	-0.051	-0.020	-0.094
<b>Erythro.</b>	-0.219*	-0.134	-0.224**	-0.003	-0.186**	-0.090	-0.016

### *Heliconia spp.*

*Heliconia spp.* show positive correlations with canopy openness ( $r = 0.308$ ) and litter cover ( $r = 0.165$ ). This understory group hence grows in patches with abundant light and litter. Negative correlations are found for *Erythrochiton fallax*, ferns (as mentioned before), liana cover and topography. *Heliconia spp.* is thus more present in the valleys in contrast to the top or steep slopes. Places with a high *Heliconia* cover have a lower liana cover. The correlations with *Erythrochiton fallax* and lianas are quite weak (-0.143 and -0.087 respectively) (Table 4).

### *Erythrochiton*

No positive correlations could be found for *Erythrochiton fallax*, while negative correlations are abundant; seedlings, lianas, canopy openness, litter depth and soil type (Table 4). *Erythrochiton fallax* grows abundantly at places where seedlings and lianas are almost absent. Canopy openness is quite low at sites with a high cover of *Erythrochiton* and litter is not present in large quantities. The soil index decreases when *Erythrochiton fallax* increases in cover and this understory species is thus more situated on sandier, low loamy soils.

#### 4.2.2 Soil type and topography

Kruskal-Wallis tests were performed to find differences in mean ferns, *Heliconia spp.* and *Erythrochiton fallax* cover between soil index and topography index. In the case that these understory groups were indeed specialized to grow on for example poor soils or steep slopes, the differences could be pointed out with these tests.

For topographic class only *Heliconia spp.* showed differences between topographic categories ( $p = 0.022$ ). However, with pairwise comparisons and applying a Bonferroni correction ( $p = 0.0023$ ) the differences could not be found. An ANOVA with a post-hoc Games-Howell (for unequal variances) did show vague differences (Figure 13). *Heliconia spp.* grow well in valleys and low slopes, it is decreasing steadily on higher and steeper slopes. Differences are more obvious when classes 5 and 6 are compared with 1, 2 and 3.

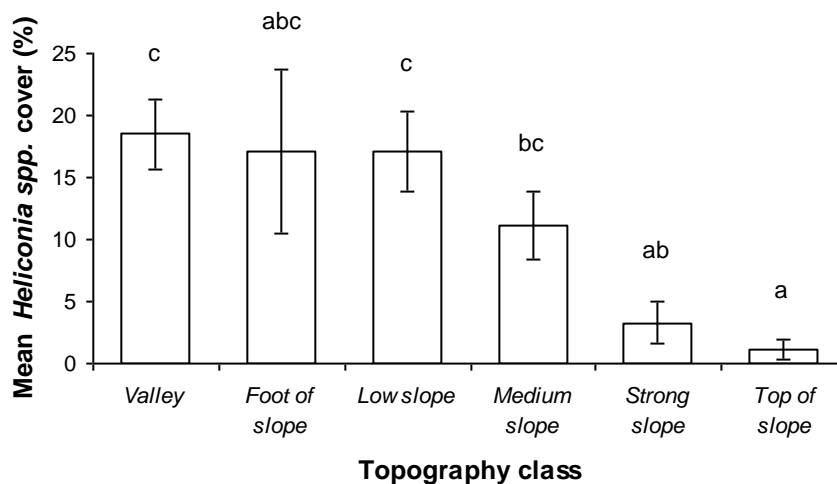


Figure 13. Mean differences of *Heliconia spp.* cover per topography category. Significant differences are computed with a post-hoc Games-Howell test.

For ferns differences could be found ( $p = 0.002$ ), with class 4 (loam) having a significantly lower mean compared to class 2 (loamy sand) and class 3 (sandy loam) (Figure 14). All other classes are not significantly different from the others (pairwise comparisons with Bonferroni correction,  $p = 0.005$ ), meaning real obvious differences could not be found. This may also be due to the large standard errors of class 1 and 5. Differences are more obvious when classes 1, 2 and 3 are compared with classes 4 and 5.

For *Heliconia spp.* no differences could be found (Kruskal-Wallis, 0.577). *Erythrochiton fallax* on the opposite does show differences among soil classes (Kruskal-Wallis, sign. 0.017). The highest mean occurred at soil index 1 (sand), while this category significantly differed with 4 (loam). Although *Erythrochiton fallax* hardly occurs at clayey soils (category 5) no significant difference could be found with category 1 because of the high standard errors of both classes (Figure 14).

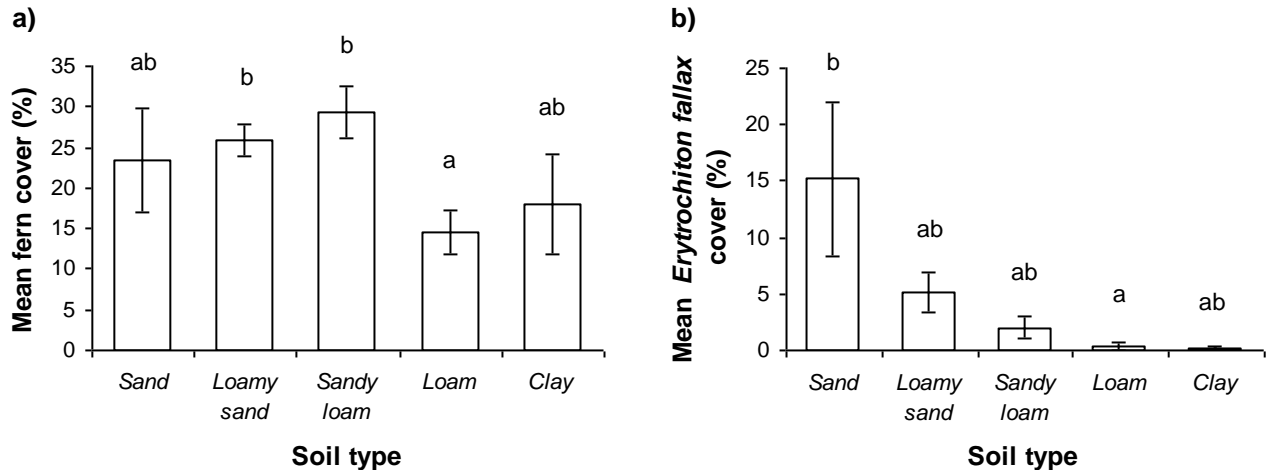


Figure 14. Mean differences of fern (a) and *Erythrochiton fallax* (b) cover per soil type. Columns with different letters are significantly different from each other.

#### 4.2.3 All environmental variables – multiple linear regression

Multiple linear regressions were performed to search for assumed causal relations between environmental variables and the presence of the three understory groups. Six environmental variables were used; soil type, topography classes, canopy openness, basal area, litter depth and maximum vegetation height. Vegetation variables were left out of the analysis because a trade-off could exist when measuring covers and the analysis would therefore not be reliable. These variables were first separately entered in a linear regression per understory group. Only variables that were significantly regressed to understory presence were subsequently used in a multiple linear regression. The dummy variables, for soil and topography, compare each category to the 0-category (always assigned zeros - the baseline). For both indexes the first category was chosen as baseline; 'sand' for soil and 'valley' for topography (Field, 2004).

##### *Erythrochiton*

*Erythrochiton* cover was negatively related to soil type and litter depth (Table 5). The negative relation with soil type indicates the higher occurrence of *Erythrochiton* on sandier soils (category 1). The negative relation with litter depth means *Erythrochiton* cover is higher when litter depth is lower.

##### Ferns

Both topography and soil type are regressed in the model for ferns. Topography was positively regressed to ferns, meaning fern cover increases on higher, steeper places compared to the valleys. Soil type is positively and negatively regressed to ferns, therefore soil type is important in determining fern cover. Intermediate soil types have the highest fern cover.

##### *Heliconia spp.*

The model for *Heliconia spp.* includes canopy openness and litter depth. Canopy openness has a positive effect on *Heliconia spp.* (Table 5). Litter depth also has a positive effect on *Heliconia spp.* cover. Neither topography, nor soil type showed a significant relation with *Heliconia spp.* cover.

Table 5. Important environmental variables affecting presence per understory group. Regression coefficients of *Erythrochiton fallax*, ferns and *Heliconia spp.* R-square and significance of regression model are shown on the last two lines. A multiple linear regression was used, all variables were entered. All b's of the included variables are shown, while related significance-values for every b are also shown. Significant p-values of concerning variables are shown in bold en italic. None of the regressions proved to have normal standardized residuals. See for soil type and topography class table 1.

Understory groups → Variables ↓	<i>Erythrochiton fallax</i> (n=198)		Ferns (n=198)		<i>Heliconia spp.</i> (n=198)	
	B	Sign.	B	Sign.	B	Sign.
<i>Canopy openness</i>	-	-	-	-	1.352	<b>.000</b>
<i>Litter depth</i>	-1.008	<b>.014</b>	-	-	1.165	<b>.049</b>
<i>Dummy soil type 1 vs. 2</i>	-8.622	<b>.028</b>	1.576	.766	-	-
<i>Dummy soil type 1 vs. 3</i>	-12.147	<b>.003</b>	4.591	.419	-	-
<i>Dummy soil type 1 vs. 4</i>	-13.879	<b>.002</b>	-9.275	.120	-	-
<i>Dummy soil type 1 vs. 5</i>	-13.939	<b>.016</b>	-3.778	.631	-	-
<i>Dummy topo class 1 vs. 2</i>	-	-	5.358	.371	-	-
<i>Dummy topo class 1 vs. 3</i>	-	-	2.986	.409	-	-
<i>Dummy topo class 1 vs. 4</i>	-	-	8.664	<b>.021</b>	-	-
<i>Dummy topo class 1 vs. 5</i>	-	-	7.004	.398	-	-
<i>Dummy topo class 1 vs. 6</i>	-	-	10.532	.228	-	-
<b>r<sup>2</sup></b>	0.090		0.087		0.136	
<b>P</b>	0.001		0.028		0.000	

### Seedlings

A regression on seedlings was also performed because the effect of these understory groups on regeneration was the primary starting point of this research. Again, all variables were separately tested with a linear regression. Significant variables were entered together in a regression model. Soil type exerted a positive effect on seedling cover and *Erythrochiton fallax* and litter height a negative effect. Ferns and *Heliconia spp.* had not a significant effect on seedling abundance ( $r^2 = 0.148$ ,  $p = 0.000$ ).

### 4.3 Influence of the groups on seed removal

First of all, understory groups differed in every variable measured in the different treatments (control, *Erythrochiton fallax*, ferns and *Heliconia spp.*), except for number of trees 10-20 cm dbh (Table 6). Control plots are really different from all other plots, because control plots have a very low total cover and low covers of the understory species. Ferns and *Heliconia spp.* do occur a little bit more in these plots compared to *Erythrochiton fallax* plots. Moreover, control plots contain the highest covers of herbs, lianas and seedlings 30-150 cm in height (Table 6).

Table 6. Habitat characteristics for each understory group. All characteristics are tested using a Kruskal-Wallis test. Significant differences were found with pairwise comparisons using a Bonferroni correction ( $p=0.0083$ ).

Variable	Habitat types				Sign.
	Control	<i>Erythro.</i>	Fern spp.	<i>Heliconia spp.</i>	
<i>Erythrochiton</i> cover	a	b	a	a	0.000
Fern cover	b	a	c	b	0.000
<i>Heliconia spp.</i> cover	b	a	b	c	0.000
Herb cover	c	a	b	b	0.000
Liana cover	c	a	b	b	0.000
<i>Costus spp.</i> cover	b	a	b	b	0.001
Total vegetation cover	a	bc	c	b	0.000
Woody stems number	b	a	a	a	0.000
• Seedlings 0 – 30 cm	b	a	ab	b	0.000
• Seedlings 30 – 150 cm	c	a	bc	b	0.000
• Saplings 150 cm – 10 cm dbh	b	b	b	a	0.000
• Trees 10 – 20 cm dbh	-	-	-	-	NS
<i>Erythrochiton</i> seedling number	a	b	a	a	0.000
Litter cover	b	a	ab	b	0.008
Woody debris cover	a	b	ab	ab	0.031
Canopy openness	c	a	d	b	0.000

*Erythrochiton* plots contain far more *Erythrochiton* than all other plots. All other variables evaluated in this understory patch exhibit low numbers, except for litter cover. This is probably due to the fact that litter cover is what remains if woody debris cover is subtracted from 100 %.

Fern plots are characterized by a significantly higher mean cover (75%) of ferns, compared to all other plots, although fern cover is also significantly higher in control and *Heliconia spp.* plots (10%) compared to *Erythrochiton* plots. Together with control and *Heliconia* plots, fern plots have a higher presence of *Costus spp.* Canopy openness is highest in fern plots compared to the other groups although this is probably due to the fact that it was not possible to measure light conditions beneath the ferns with a densiometer.

*Heliconia spp.* plots have a significantly higher *Heliconia* cover (71%) than all other plots (2%). These plots furthermore contain intermediate numbers of woody debris, *Costus spp.*, litter, ferns, herbs and lianas. In all other cases *Heliconia spp.* plots have low covers, but notable is the significantly lower numbers of saplings 150 cm in height – 10 cm dbh compared to the three other groups.

4.3.1 Seed removal - Cox regression

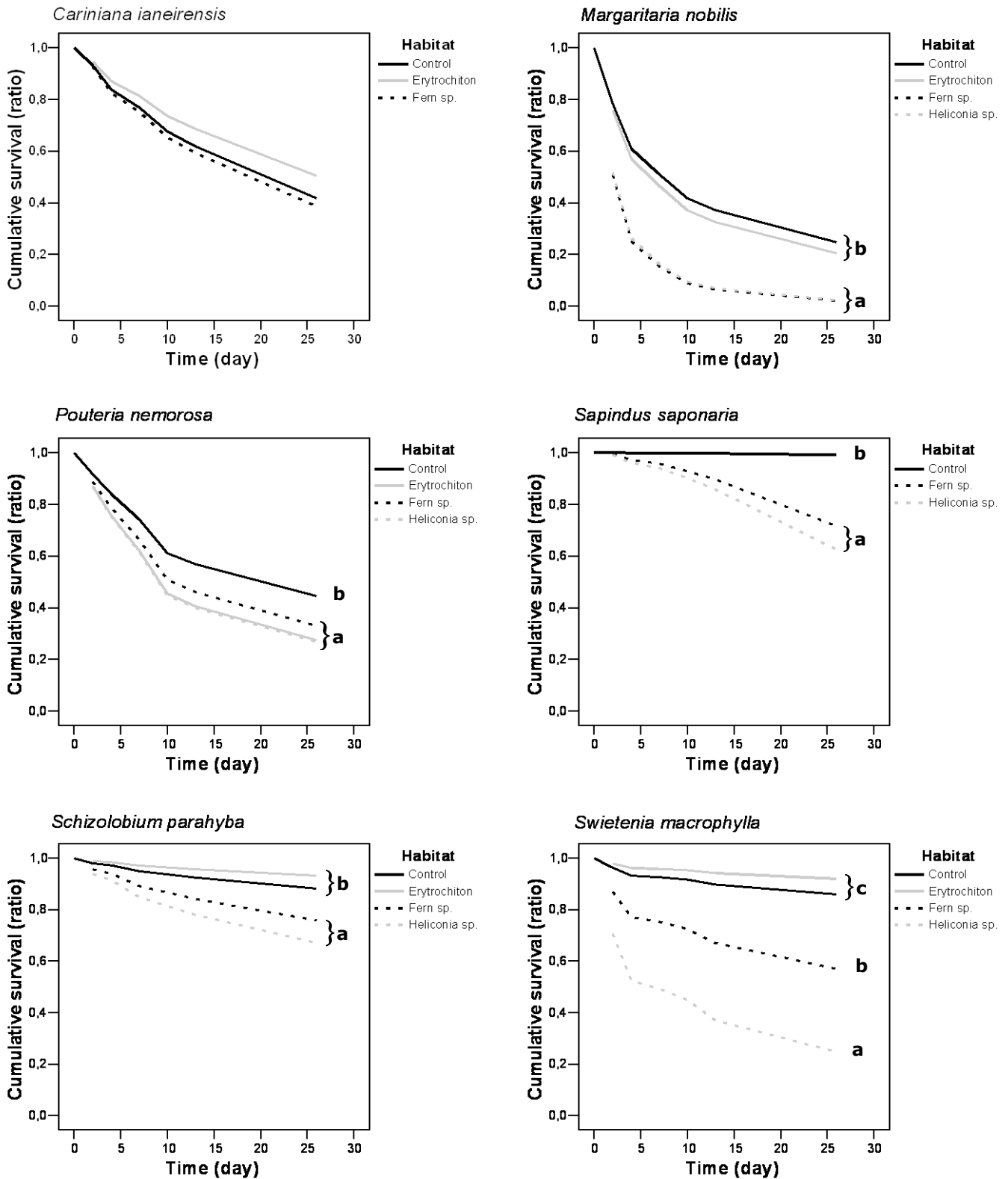


Figure 15. Seed removal rate per seed species. Different cumulative survival functions are given per habitat-type. Habitat types with different letters significantly differ from each other. Note that there are only three habitats for *Cariniana ianeirensis* and *Sapindus saponaria*.



### Seed removal per seed species

All seed species, except *Cariniana*, show significant differences ( $p < 0.05$ ; Figure 15) among habitats (the three understory groups and a control group). In all these five cases, the control group experiences the highest seed survival. In three cases the control group is accompanied by *Erythrochiton fallax* (*Margaritaria*, *Schizolobium* and *Swietenia*). Ferns and *Heliconia spp.* are in most cases placed in the same group, with a lower survival compared to control, except for *Swietenia*, where seeds showed a significantly higher survival in ferns than in *Heliconia spp.* In the case of *Pouteria*, *Erythrochiton fallax* is not significantly different from ferns and *Heliconia spp.*

### Seed removal total

For all seed species, seed survival is significantly different, with control plots having the highest survival, and *Heliconia spp.* plots having the lowest survival. *Erythrochiton fallax* has a slightly lower survival than control, and ferns have a survival intermediate to that of *Erythrochiton fallax* and *Heliconia spp.* (Figure 16).

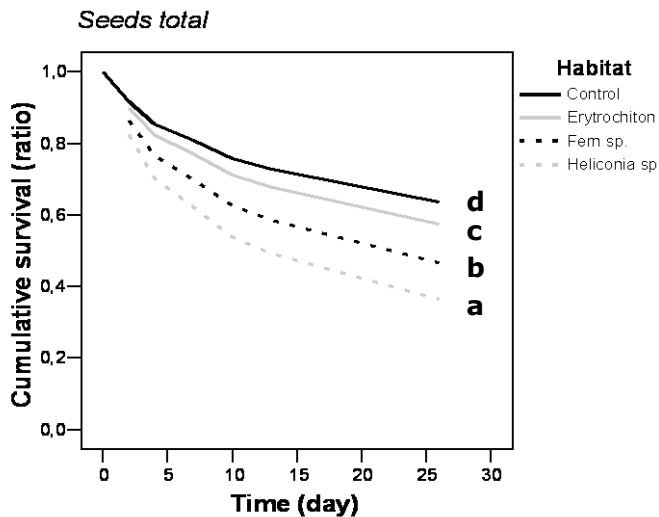


Figure 16. Seeds removal rate lumping all seeds together. Different cumulative survival functions are given per habitat-type. All habitats are significantly different from each other ( $p < 0.001$ ).

### 4.3.2 Variables influencing seed removal –multiple linear regression

Not all variables are regressed to removal rate. Canopy openness was not included because this was measured below the vegetation except for ferns (these were too low to use a densitometer beneath the vegetation), this could bias the results from a multiple linear regression. Only the lumped woody stems number (including all seedling, saplings and small trees) were included, not all the classes separately. This resulted in a regression with the following variables; ferns, *Heliconia spp.*, *Erythrochiton fallax*, *Costus spp.*, herbs, lianas, woody stems, litter and woody debris (see table 7).

Every species, except *Cariniana*, was related to more than one variable. Removal rate of all species, except *Cariniana*, was related to fern cover and *Heliconia spp.* cover. *Cariniana* is related to liana cover, but this variable explains little of the variation found in the data. *Pouteria* is furthermore related to *Erythrochiton* cover and herb cover. This could correspond with the COX-regression, which showed that all three understory groups were significantly different compared to the control plots but not compared to each-other. *Sapindus* was, besides to ferns and *Heliconia*

*spp.*, related to woody stems number. *Schizolobium* was also related to liana cover. Seed removal of all species together was related to fern and *Heliconia spp.* cover, as well as to *Erythrochiton* cover, woody stems number and liana cover (explaining together only about 10 % of the variation).

Table 7. Effect of microhabitat variables on seed removal rate. Results are shown per seed species and for all species together. Only characteristics that did influence the seed removal for one or more species are listed, standardized slopes (beta's) for these characteristics are shown in the table. A backward multiple regression was performed.

Species	N	Fern cover	Helico. cover	Erythro. cover	Herb cover	Woody stems number	Liana cover	r <sup>2</sup>	P
<i>Cariniana</i>	45	-	-	-	-	-	0.311	0.097	0.037
<i>Margaritaria</i>	60	0.392	0.377	-	-	-	-	0.230	0.001
<i>Pouteria</i>	60	0.357	0.442	0.513	0.443	-	-	0.180	0.026
<i>Sapindus</i>	42	0.467	0.384	-	-	0.458	-	0.361	0.001
<i>Schizolobium</i>	62	0.260	0.413	-	-	-	0.238	0.246	0.001
<i>Swietenia</i>	59	0.298	0.700	-	-	-	-	0.501	0.000
All species	328	0.272	0.353	0.245	-	0.136	0.174	0.105	0.000

*Swietenia* seed removal has the largest explained variation, about 50 %, with only two variables. All other seed-species have an explained variance between approximately 20 and 30 %. Regressions were highly significant (Table 7), except for *Cariniana* and *Pouteria*. The b-values (not shown here), are all in the order of  $10^{-3}$  to  $10^{-4}$ , indicating why  $\beta$ 's are shown. These values show the number of standard deviations the outcome (in this case removal rate) will change as a result of one standard deviation change in the predictor. These  $\beta$ 's are directly comparable with each other; therefore, they provide a better insight into the "importance" of a predictor in the model (Field, 2005). It is interesting to look at the  $\beta$ 's of *Swietenia*, because the difference between the  $\beta$ 's of fern cover and *Heliconia* cover is quite large, therefore *Heliconia* cover ( $\beta = 0.700$ ) is more important in the model compared to fern cover ( $\beta = 0.298$ ). In the other seed-species these two  $\beta$ 's are far more comparable.

## 5. Discussion

At first sight, the understory groups did not seem to represent a large part of the forest at La Chonta. In La Chonta more than 40% of the plots did not contain any *Heliconia spp.*, for *Erythrochiton* this was even approximately 95%. On the contrary, in a study of Costa (2004), *Heliconia acuminata* occurred in 95% of the inventoried plots. In La Chonta, it also appeared that “dense” understories of more than 50% foliage cover only occurred in a small portion, about 10%, of the forest. The non-native invasive shrub buckthorn (*Rhamnus frangula* L.), for example, was found to occur in more than 40% of the study area in high densities (>50%) (Fagan and Peart, 2004). Other studies only mention the total cover in the study area, which varies considerably. In Ghana, the weedy perennial *Chromolaena odorata* Linn. covers 95% of the study site (Honu and Dang, 2000); in the 1626-ha Coweeta Basin *Rhododendron maximum* increased from 15% (1976) to 32% (1993) occupancy (Beckage *et al.*, 2000) and at La Selva dwarf palms have a mean cover of 21% (Wang and Augspurger, 2004). Monocots (including Heliconiaceae) covered only about 8% percent of the area at La Selva. Costa (2004) found Heliconiaceae (12.7%) and pteridophytes (11%) to be in the top four of the total understory cover and in a study of Poulsen and Balslev (1991) *Heliconia velutina* had the second highest cover of all herbs, while two fern species had the second and third most individuals. The total ground herb cover, however, was only 2.5% of a 1-ha plot, which is very low compared to this study. In La Chonta, the foliage cover of ferns is 25%, for *Heliconia* 16% and for *Erythrochiton* only 1%. Taking everything into consideration, the understory of La Chonta may indeed be considered “dense”, although other species have been found to form larger patches.

### 5.1 Impact of treatment and canopy openness

Treatments had some effect on the abundance and occurrence of the understory groups, but this was not extremely evident for every understory group. The treatments are a reflection of various compounding results of silvicultural interventions and I expected that the treatments would, most visually noticeable, be differing in canopy openness throughout the plots. The hypotheses were mainly based on this assumption (Chapter 1). This assumption, though, proved to be wrong (Appendix II). The three blocks have very dissimilar mean canopy openness for analogous treatments (Figure 20). This raises the question if blocks are in fact comparable. Small differences may occur between blocks due to differences in time since logging. Within one block however there are also no significant differences in mean canopy openness between the treatments (figure 20). I however expected to find a positive correlation of canopy openness with an increase in management treatment.

A possible explanation can be that my results are biased; I sampled relatively small plots along two random trails in every treatment plot, while a random or regular sample distribution within the treatments could have been more representative of the area. My results can also be biased because my total sample consisted of 0.03% of the area. Goddings (2005) came to similar conclusions; no differences between silvicultural treatments compared to the control treatment and she also thought her sample size might be too small (6% of the area). Canopies are known to close quite rapidly after disturbance (logging), and this, together with the time elapsed after the initiations of the blocks, 3-4 years, might have caused the quite homogeneous results (Asner *et al.*,

2004; Broadbent *et al.*, 2006; Costa and Magnusson, 2003; Denslow *et al.*, 1998; Dirzo *et al.*, 1992; Flores *et al.*, 2001).

Not many studies have focused on the effect of logging on understory plants; especially not in the tropics (see also Costa *et al.*, 2002 and Royo and Carson, 2006). In the temperate regions of the world, however, some studies have investigated the role of logging on the establishment of dense understories. In temperate forests in Chile, dense thickets of understory bamboo are formed after burning or selective logging (Reid *et al.*, 2004). Oregon grape (*Berberis nervosa*) and salal (*Gautheria shallon*) both increased in thinned areas compared to unthinned areas (Huffman and Tappeiner II, 1997). Hay-scented fern is partly forming dense understories due to thinning, and partly due to browsing (De la Cretaz and Kelty, 1999). North American devil's club (*Oplopanax horridus*) had highest stem recruitment in clearcut stands, while it was more numerous in maturing stands (Lantz and Antos, 2002). This result implicates that time, as well as state (clearcut, partially cut or mature/control) influence understories (Lantz and Antos, 2002; Tappeiner *et al.*, 1991; Reader and Bricker, 1992).

Studies in the tropics focus more on herb community composition and richness, instead of one dense understory group/species (Costa and Magnusson, 2002). Other studies focused on gap-phase regeneration (Denslow *et al.*, 1990; Dirzo *et al.*, 1992; Levey, 1988; Martins and Rodrigues, 2002). Dirzo *et al.*, (1992) found young gaps to be more variable in understory plant composition, compared to older gaps which showed really dense understories of 50% cover of more. This indicates that time also plays a role in the establishment of dense understories in tropical systems. Unfortunately, I could find only one study from the tropics focusing on the effect of logging on a specific understory species (Costa *et al.*, 2002). In the latter study the density of reproductive individuals increased with logging intensity, but logging intensity did not influence total densities. In my own study, logging (intensity) did influence fern density negatively; effects on *Heliconia spp.* and *Erythrochiton* were more complex. These results will be discussed in more detail for every understory group separately.

### **Ferns**

It was hypothesized that ferns would be more abundant in the control treatment compared to the other treatments. In the case of La Chonta it was indicated beforehand that ferns were more abundant in the control treatment compared to the other treatments (M. Peña-Claros, pers. communication). For ferns there indeed proved to be a difference in cover between silvicultural treatments, with the control treatments having the highest mean fern cover (Figure 10).

In other studies, ferns are commonly associated with the forest understory (Royo and Carson, 2006; Page, 2002). However, ferns are also known to colonize new canopy gaps (Royo and Carson, 2006; De la Cretaz and Kelty, 1999; Norton, 1994; Page, 2002). Although the light conditions are only slightly different among treatments in La Chonta, it can be that the fern species in La Chonta are not able to colonize environments with higher light conditions or are competing with other understory species (monocots) in occupying the new gap (Dirzo *et al.*, 1992). The analysis for research question 2 (environmental variables) however, showed that fern cover is not related to canopy openness but to soil type and topography (Table 4 and 5). Furthermore, data from La Chonta (Park, 2003) shows that both *Heliconia spp.* and ferns increased in newly-formed gaps, the cover of ferns in these gaps was even higher than *Heliconia spp.* cover. Royo and Carson (2006) found that mostly shade-intolerant fern species could monopolize large areas. My own data of research question 3 (Table 6) furthermore shows that ferns can occupy, partly, highly contrasting

patches (ferns occur in the fern, as well as the *Heliconia spp.* and control plots). According to Page (2002), ferns are very quickly light saturated, and therefore an existence beneath the much larger, light-blocking, *Heliconia spp.* would be possible.

The individual fern species in La Chonta may however show differences in their reaction to treatments and proliferation according to environmental variables. Costa and Magnusson (2002), for instance, found a fern species, *Lomariopsis prieuriana*, to decline in abundance in logged areas while another fern species, *Trilophyllum dicksinoides*, increased in abundance. Hill and Silander (2001) found very different reactions to light for two fern species (*Dennstaedtia punctilobula* and *Thelypteris noveboracensis*) in the same temperate forest. In this study, the most abundant fern species in La Chonta (Figure 17) is the particular species which does not show any correlation with



Figure 17. The most abundant (left) and second most abundant (right) fern species in La Chonta.

canopy openness. According to an investigator at IBIF (C. Pinto, pers. communication), this fern is also present in the dry period, although foliage cover becomes lower, while the second most important species disappears totally. This observation could indicate a relatively high tolerance to drought, as well as to increased light availability, for the most common species (Page, 2002). The abundance of ferns per treatment, consequently, does not seem to stroke with the results of research question 2. I therefore suggest that the lower mean covers of ferns in the non-control treatments only reflect a temporal set-back in cover, due to compounding effects of silvicultural measurements, like mechanical stresses (treefall), compaction and scarification of the soil (Costa and Magnusson, 2002; Page, 2002). Another possible explanation could be that the establishment of other species, typically present after disturbance (like *Urera baccifera* L.), interferes with the establishment of ferns through resource competition.

### ***Heliconia spp.***

*Heliconia spp.* showed a very low density in the control treatment of block 1 and a very high density in the control treatment of block 3 (Figure 12). It was expected that *Heliconia spp.* would be more abundant in the improved and intensive treatments compared to the control and normal treatments. The first two treatments should have a more open canopy due to logging and applied silvicultural treatments (BOLFOR, 2000). Vroomans (2003) also detected a large abundance of *Heliconia spp.* in the control plot of block 3. A superficial comparison of the *Heliconia spp.*-maps produced by Vroomans (2003) leads to a more or less similar distribution of *Heliconia spp.* among treatments to the one it was found in this study.

According to Stiles (1975) most *Heliconia spp.* can not tolerate deep shade and occur mostly in canopy gaps. Several other studies have also found an increase of *Heliconia spp.*, or related species, in high-light environments. In a study of Costa *et al.*, (2002), two species of Marantaceae, *Calathea altissima* and *Ischnopsiphon arouma*, did indeed increase in total and adult density on the

long-term (11 years), while on the short term (5 years) only *I. arouma* showed a response. Costa and Magnusson (2002) found an increase of *Heliconia acuminata* in logged areas, as well as a high abundance of flowering *H. acuminata* after 5 years (Costa and Magnusson, 2003). Dirzo *et al.*, (1992) also mention a high leaf area of herbaceous monocots in the gap understory (including *Heliconia spp.*). At Barro Colorado Island, *Heliconia spp.* were one of the first plants invading disturbed areas (Hooper *et al.*, 2004, following Kenoyer, 1929). Bruna *et al.*, (2002) observed in 50% of the cases a very abundant *Heliconia acuminata* growth near forest edges, although not all plants were healthy.

The main explanation of the contradictory results found in this study can be deduced from the actual mean light availability, which differed between blocks and their corresponding treatments. Light availability in control treatment block 3 was much higher compared to the light availability control treatment block 1 (Appendix II). The range in which 100% of the data points occurred was very narrow, and consequently nearly every plot had the same large canopy openness (except for two small outliers).

Another reasonable explanation can be the differential establishment of *Heliconia spp.* occurring in La Chonta (Appendix II, Table 10). Four main species of *Heliconia* were recorded in the field; all of these species were given morphospecies names (Figure 18). The species *Heliconia sp.* "garzia" was almost absent from block 1 and 2. In block 3 it is mostly present in the control treatment. Besides *Heliconia sp.* "garzia", *Heliconia sp.* "farol" also had a very high presence in the control treatment of block 3 (Appendix II, Table 10). According to Berry and Kress (1991) some species of *Heliconia* are better adjusted to low light circumstances (partial shade). Architectural adaptations like leaf shape, leaf size, leaf number and petiole length, to low-light environments are a general feature of understory plants (Kimura and Simbolon, 2002). All these adaptations could lead to minimization of self-shading in the crown and maximization of assimilative ability. *Heliconia spp.* are also adapted to different light regimes including the forest understory (Rundel *et al.*, 1998; Valladares *et al.*, 2002). Both studies mentioned the growth form to be of specific importance (zingiberoid for shaded versus musoid for lighter environments). Possibly, *Heliconia sp.* "garzia" is a species that is more adapted to the generally higher shade in the understory compared to the other species. Results that support this suggestion are the dissimilar growth form compared to the musoid form (pers. observation) and a non-existing relation with canopy openness when zero-values are excluded (Linear regression, enter,  $p=0.076$ , Appendix II). The other abundant species in this treatment, *Heliconia sp.* "farol", shows a very strong relation with canopy openness when zero-values are excluded (Linear regression, enter,  $p < 0.01$ , Appendix II). The combination of the presence of these two species in this block, a consistently large canopy openness, and the lower elevation (Figure 13 shows *Heliconia spp.* having a higher abundance on lower parts) of block 3 compared to the other blocks (Vroomans, 2003) could explain the high abundance of *Heliconia spp.* in this block.

However, the correct species of La Chonta's *Heliconia spp.*, growth forms, as well as data on species' reaction to light remain imprecise. All these aspects should be studied in more detail to draw more accurate conclusions. Nevertheless, a general positive relation with light (Table 4), as hypothesized, was found among La Chonta's *Heliconia spp.*, even though these results did not correspond with the treatments.



Figure 18. Four of the many *Heliconia* spp. in La Chonta. From left to right (morphospecies names): *Heliconia* sp. "toucan", *Heliconia* sp. "lorro", *Heliconia* sp. "farol", *Heliconia* sp. "garzia". Notice the large differences in inflorescences.

### ***Erythrochiton fallax***

Explaining the presence of *Erythrochiton fallax* among treatments or blocks presents some difficulties. It was not really expected to find this understory group in a certain treatment. The highly patchy distribution it showed in this research was not expected as well. In block 3 *Erythrochiton fallax* was totally absent, while the intensive treatment of block 2 was the only treatment with a respectable abundance of *Erythrochiton fallax*. From the edges of this treatment, *Erythrochiton fallax* continued into the forest in high densities (personal observation).

Poorter *et al.*, (2006) measured architectural traits among 54 tree species in Bolivia and *Erythrochiton fallax* had the lowest juvenile crown exposure ( $CE_j = 1.27$ ).  $CE_{juv}$  increased in his study from shade-tolerant to pioneer species, and for that fact, *Erythrochiton fallax* should be highly tolerable to shade. My results indeed showed a significant negative correlation with canopy openness for *Erythrochiton*, even though it mainly grows in the intensive treatment. According to Mery Ocampo (studying *E. gymnanthus*), in an interview of Bustos (2006), *Erythrochiton gymnanthus* grows in places with high abundance of trees, but the most important aspect for this species is a constant light environment. My findings would then be highly contradictory with that statement, because I performed my study in a semi-deciduous forest and light fluctuations could be occurring on a seasonal basis, except when *Erythrochiton* is solely growing below trees which are not deciduous. Moreover, the intensive treatment could have experimented light fluctuations during the past years after installation, this however also depends on where the logging occurred exactly.

## **5.2 Effect of topography and soil**

Many studies have examined the effects of environmental characteristics on the distribution of understory species, mainly to correlate species richness to these characteristics (Tuomisto and Poulsen, 1996; Costa *et al.*, 2005; Poulsen *et al.*, 2006). In these studies, species and species groups have been related to, mainly, topographic and edaphic factors (Gibbons and Newbery, 2002; Valencia *et al.*, 2004; Poulsen and Balslev, 1991). My study species were indeed influenced

by environmental characteristics as was hypothesized. The effect of canopy openness is already discussed, but other environmental characteristics were also important.

In this study, a positive relation was found between fern cover and topography class (Tables 4 and 5). Poulsen and Balslev (1991) also found a positive correlation between topography and the fern *Adiantum terminatum*. However, the other 24 fern species encountered in their research area did not show a correlation. Norton (1994) states that ferns are probably quite sensitive to topographical position and indicated in his study that many species show differences in abundance with respect to topographic position. In addition, he found several pteridophytes to be linked to a different topographic position in undisturbed forests compared to disturbed forests. Furthermore, the gametophyte phase of ferns is very dependent on water and ferns may therefore be greatly affected by water availability (Costa *et al.*, 2005; Page, 2002). Norton (1994) suspects the study species are more related to soil wetness inherent to the topographical position. Costa *et al.*, (2005) suggest that ferns have a higher presence at slopes, because they can not compete with the large herbs in the valleys, but also can not withstand the low water availability in the uplands. In La Chonta, *Heliconia spp.* are more abundant in the valleys (Figure 13, Table 4), and consequently ferns may be competing with them for water.

I found a clear negative correlation of *Heliconia spp.* cover with topography. Berry and Kress (1991) mention the fact that *Heliconia spp.* grow most abundantly on elevations below approximately 450 masl and inhabit roadsides and riverbanks. Stiles (1975) already mentioned that *Heliconia spp.* are probably correlated to topography and in the studies of Poulsen *et al.*, (2006) and Costa *et al.*, (2005) *Heliconia spp.* were more often found in the lower parts of the environment, while Poulsen and Balslev (1991) could not find preferences. Nevertheless, in La Chonta, Vroomans (2003) thought the high abundance of *Heliconia spp.* in block 3 could be explained by the low elevation of that block (mean elevations; block 1: 373, block 2: 362, block 3: 318). An explanation for the clear relation in La Chonta with the lower parts of the area may be that *Heliconia spp.*, and other large monocots, are relatively intolerant of dry-season water stresses, which are also prevailing in La Chonta (Bruna *et al.*, 2002). Another indication of their dependence on water availability is the protection of their seeds through groundwater-filled bracts (Bronstein, 1986). Growing mainly on the lower parts should provide the *Heliconia spp.* a more constant resource of groundwater.

Fern species and *Erythrochiton* were furthermore both negatively related to soil type. Ferns have been found to relate to soil type in various studies. Independent of what was measured (extractable bases, soil texture, soil cation content, inundation), several studies found fern species, even of the same genus, to all have their own niche with respect to soil properties (Tuomisto, 2006; Tuomisto *et al.* 2002; Tuomisto and Poulsen, 1996). More precise measurements should be more accurate in finding niche specializations for the ferns, and other understory species in La Chonta, especially because the range in texture is quite small for La Chonta (Park *et al.*, 2005).

For small trees, not much information about relation with soil properties is available. Valencia *et al.* (2004) state that, generally speaking, many neotropical tree species are generalist with respect to soil. *Erythrochiton gymnanthus* is a species to be highly adaptive with respect to soil, inundation or topography (Bustos, 2006). Auld (2001) found most Rutaceae species to occur on sandy soils, and not on clay soils. According to Kallunki (1992) *Erythrochiton fallax* has often been found on poorly drained or rocky soil. In this study, *Erythrochiton fallax* does not seem to be a generalist and it also did not occur on rocky soil.

The relation between topography and soil has been established often as a relation between topography and water availability (Costa *et al.*, 2005; Poulsen *et al.*, 2006). Although *Erythrochiton*



did not show a relation with topography, the low number of encounters (24 plots in total) caused by its very patchy distribution could have biased the results. Even among these 24 plots no relation could be found with topography (Appendix III), although topography did show a positive correlation with soil. Furthermore, none of these 24 plots were situated on the classes "strong slope" and "top". Consequently, it is difficult to state if there is no interference of topography at all. However, relying on these results, *Erythrochiton* seems to be a specialist regarding soil type and a generalist regarding topography. Gibbons and Newberry (2002) and Valencia *et al.* (2004) both found several abundant species that were growing independent of topography. However, the opposite was also true; both studies found some species to be clearly specialist. Harms *et al.* (2001) also found just a few tree and shrub species to be related to topography or habitat; these results are therefore in line with the results of this report. However, as Valencia *et al.* (2004) also suggested; patchiness could be due to dispersal limitation. To really unravel the ecology and reproductive biology/dispersal limitation of *Erythrochiton fallax* a more thorough research is necessary with a higher amount of plots in a larger part of the forest.

### 5.3 Seed removal

This research focused on seed removal in three different dense understory groups (80% cover of a given understory species). A control (<20% for every understory group) was incorporated in the experiment to have a really opposing habitat patch to compare the results of the dense understories with. On average the cover was far less than in the other plots (Table 6). Most of the few studies that have investigated seed removal beneath dense understories used a patch with a (partly) removed dense understory as control (Abe *et al.*, 2001; George and Bazzaz, 1999; Iida, 2004; Schreiner *et al.*, 2000). Others also used controls with less vegetation, or a sparse vegetation of the understory species (Alcántara *et al.*, 2000; Beckage *et al.*, 2000; Caccia and Ballaré, 1998; Den Ouden *et al.*, 2005). Due to time constraints and the existing experimental setup in La Chonta, using patches with less vegetation as controls was the only possible choice. Besides this control, the dense understories can also be compared to each other. As far as I know, this is the first study in which several dense understory groups in the same forest, relatively close to each other, have been used in a seed removal experiment. Moreover, I have not found any study including seed removal experiments within (and outside) dense understory patches in the tropics (see also Royo and Carson, 2006 and references therein). Therefore, I am forced to compare my results partly to studies in temperate areas of the world.

For *Heliconia spp.* and fern plots, my results were much alike, and average removal was higher than 50% after 28 days, although this differed strongly per seed species. However, my *Erythrochiton* plots were really dissimilar. Overall removal was a little bit more than 30% (Figure 16), while for 2 seed species (*Schizolobium* and *Swietenia*) removal was even lower than 10% (Figure 15). In only one case (*Pouteria*) seed removal in the *Erythrochiton* plots was significantly different from the control group. The results of temperate studies compared to my study are, however, strikingly similar. Although George and Bazzaz (1999) did not find differences in seed removal for all seed species, a significant higher seed removal for *Quercus* seeds (65% removed) was found in the fern plots. Caccia and Ballaré (1998) had similar results for *Pseudotsuga* seeds placed beneath dense saplings patches (90% removed). Alcántara *et al.* (2000) found 67% removal in dense patches against 33% in sparse patches. Schreiner *et al.* (2000) observed 50% of the seeds to be removed after 22 days in cut plots and after 10 days in dense plots. Iida (2004) even found an ultimate 98.9% predation within *Sasa* sites (dwarf bamboo) compared to outside these sites (84.1%).

Seed removal differences per seed species has been shown more often in studies (Briones-Salas *et al.*, 2006; George and Bazzaz, 1999; Guariguata *et al.*, 2000; Hulme and Borelli, 1999; Sánchez-Cordero and Martínez-Gallardo, 1998; Schreiner *et al.*, 2000), which underlines the importance of using different seed species in seed removal experiments before drawing general conclusions about the effects of seed removal on future tree regeneration or community composition. For this study, I suggest that the differences between the three understory groups are caused by the (absence or presence of) vegetation density and structural complexity (e.g. woody debris) near the ground (Figure 19). Understory density near the ground is much lower within *Erythrochiton* plots compared to fern and *Heliconia spp.* plots (personal observation). Other environmental characteristics (Table 6) are also less abundant. Taken everything together, near the ground, these plots may not be attractive to seed removers (Figure 19).

Understories or structurally complex vegetation (Anderson *et al.*, 2003) are believed to influence the behaviour of seed predators, primarily by providing shelter or suitable habitat to small mammals, mainly rodents (Abe *et al.*, 2001; George and Bazzaz, 1999; Iida, 2004; Royo and Carson, 2006; Wada, 1993). Moreover, around the world, rodents are among the most important



Figure 19. Density of *Erythrochiton* and *Heliconia spp.* plots near the ground. Near the ground *Erythrochiton* plots (a) are much more open than *Heliconia spp.* plots (b).

post-dispersal seed predators (Alcántara *et al.*, 2000; Brewer and Webb, 2001; Holl and Lulow, 1997; Hulme and Borelli, 1999; Notman *et al.*, 1996; Sánchez-Cordero and Martínez-Gallardo 1998; Wenny, 2000). Therefore, rodents may play an important role in the removal of the seeds beneath the dense understories in this study. Several factors, including rodent community, can influence seed removal, and much of these factors have been revealed by studies on gaps, forest age and rodents in the tropics.

Schupp *et al.* (1989) mentioned that lianas in gaps are possibly important hiding places for rodents. In a study of Peña-Claros and De Boo (2002) on seed removal among successional stages, liana density seemed to be the best predictor of seed removal rate. In my study liana density showed to be of importance in three of the seven cases (including all seeds together).

This study did not find litter to be a significant predictor for any species, in the study of Peña-Claros and De Boo (2002). On the other hand, litter depth is much higher in *Heliconia* plots compared to *Erythrochiton* plots, which is practically devoid of (deep) litter. Moreover, the litter in dense *Heliconia spp.* plots is constantly replenished by the *Heliconia spp.* itself, while in the rainy season (in which this study was executed) almost all litter beneath *Erythrochiton* decomposes. Cintra (1997) found, in a study specifically focusing on litter, that there was a positive relation between seed survival and litter depth, which is opposite to my own results. Animals would have more problems locating the seeds in the deep litter layer. The litter, however, also functioned as a barrier to successful seedling survival for one of the two species.

The presence of woody debris, as well as uprooted trunks, seems also to be correlated to the abundance of small mammals. This leads to a higher seed removal in, for example, gaps (Schupp and Frost, 1989) and managed forests (*temperate forests* - Manning and Edge, 2004), where woody debris is abundant. The latter study also found herbs and grasses to be important factors for small mammal survival. Iida (2004) discovered that woody structures were important, especially in the *Sasa*-removed sites, but not in sites with a high understory density. In my study, woody debris did not seem to be important, but herbs were important for one species. The results of the woody debris may, however, be due to the way of measuring woody debris. Woody debris was measured as the percentage cover other than litter and bare soil. It was, unfortunately, not qualified in terms of height or origin (fallen trees versus fallen branches), while woody debris between the different understory plots can be quite different (personal observation). In *Heliconia spp.* plots, woody debris often existed out of trunks or the plots were close to trunks, while in *Erythrochiton* plots woody debris was often smaller and consisted of fallen branches.

The differences between the understory groups may also be explained by other factors. First of all, *Erythrochiton* plots were the only plots located solely in the intensive treatment. *Heliconia spp.* and fern plots were all established in the control plots, *Heliconia spp.* plots however were restricted to the control treatment of block 3. Control plots were placed in the control treatment of block 1 and the intensive treatment of block 2. Therefore, differences in mammal community composition may occur due to distance or prevailing treatment (control versus intensive). Second of all, canopy openness was much higher for *Heliconia spp.* plots, seeds in gaps may be subjected to different predator pressures than in the understory of a forest. Some studies found a lower seed removal within gaps compared to the understory, due to for example an absence of seed removers (Cintra and Horna, 1997; Sánchez-Cordero and Martínez-Gallardo, 1998). Others (Schupp and Frost, 1989; Schupp *et al.*, 1989) found a higher seed removal within gaps, while Wenny (2000) could not find a difference between gaps and the understory. Seed rain, and therefore seed abundance, may also differ between gap and understory. Loiselle *et al.* (1996) found wind-dispersed seeds to

arrive more in gaps, but overall seed rain was higher in the understory, while others (Levey, 1988; Cintra and Horna, 1997) hypothesized the opposite.

Logging itself can also have an overall effect, but in this study this could only be tested for the control plots (which were both in the control treatment and the intensive treatment). For the control plots, logged versus unlogged forest did not seem to be important in most of the seed species, except for *Pouteria* seeds (Mann-Whitney U test,  $p = 0.050$ ). *Pouteria* seeds had a higher seed removal in unlogged forest, while other studies found the opposite; a higher seed removal in logged forests or secondary forests compared to unlogged or mature forest (Forget *et al.*, 2001; Guariguata *et al.*, 2002; Peña-Claros and de Boo, 2002; Andresen *et al.*, 2005). But this overall logging effect can be species-specific as shown by contrasting results for other seed species (Forget *et al.*, 2001; Guariguata *et al.*, 2002). Differences could be related to changes in vegetation, presence of woody debris or litter or to a different canopy tree composition (Forget *et al.*, 2001), which consequently can lead to a difference in animal or bird composition (Thollay, 1997). For La Chonta, differences in animal community between treatments and also between blocks have been observed (Soto and Herrera-Flores, 2003). Small mammals were more present in the intensive and normal treatment compared to the control treatment. Interestingly, the highest amount of small mammals was captured in the intensive treatment of block 2 (where *Erythrochiton* plots are situated). Despite the very high abundance of small mammals in this specific treatment, seed removal is very low. Medium-sized mammals are far more present in the control treatment of block 3 compared to other treatments, which may have resulted in the higher removal of the larger and/or harder seed species (*Sapindus*, *Schizolobium*, *Swietenia*) (Vieira *et al.*, 2003). Block differences existed for small mammals, the genus *Oryzomys*, for terrestrial birds and medium-sized mammals (Soto and Herrera-Flores, 2003). Differences in seed removal can therefore be partly induced by the block differences. Site-effects were also found in a study of Feer and Forget (2002), while the sites were less than a kilometre apart.

One seed species, *Margaritaria*, had a high overall removal in all four understory groups although the control and *Erythrochiton* group still had significant lower removal. This quite high seed removal is hard to explain, although it may partly be explained by inherent characteristics of the seeds. The seeds of this long-lived pioneer species were somewhat smaller and had softer seed coats; I therefore suggest that these species may have a significant part of their seeds removed by invertebrates. Many studies showed invertebrates could be important seed removers of small seeds (Briones-Salas *et al.*, 2006, Fornara and Dalling, 2005; Holl and Lulow, 1997; Hulme and Borelli, 1999; Terborgh *et al.*, 1993). Fornara and Dalling (2005) furthermore mentioned a combination of low seed mass, small size, high moisture content and soft seed coat may be favoured by invertebrates. In La Chonta, invertebrates may be present in all research plots and remove seeds of this species. In fact, *Margaritaria* was often found partly beneath the surface of the soil, which may be an indication of burial by invertebrates (personal observation). Especially ants and cochroaches were more abundant in the undisturbed forest compared to disturbed forest in La Chonta (Fredericksen and Fredericksen, 2002). Another explanation of the overall high removal of *Margaritaria* seeds can be that the bright metallic-coloured seeds may be more easily detected by terrestrial birds, as well as mammals.

I used removal as a proxy for seed predation, and therefore these results and the obvious conclusions should be taken with some care. Although some studies mention seed removal indeed nearly equals seed predation (Brewer and Webb, 2001; Den Ouden *et al.*, 2005, see Levey and Byrne, 1993, for ants) authors have shown that even a small proportion of scatterhoarded seeds can secure seed germination. In the last years more attention is paid to seed fate (Brewer and

Webb, 2001; Forget *et al.*, 2005; Schupp 1993; Vander Wall *et al.*, 2005; Wang and Smith, 2002) clearly showing and underlining the importance of tracking seed fate and identifying seed predators, instead of only observing the first step in survival (seed removal). Nevertheless, a lot of studies still use seed removal as a proxy for seed predation (Peña-Claros and De Boo, 2002; Cintra and Horna, 1997), as I did, and general conclusions about the influence of these understories can still be made.

As the three understories influence the degree in which the several seed species are being removed, they can affect future tree recruitment and, on the long term, tree canopy composition. The extent, however, to which this will happen, depends on several factors. Moreover, the arrival of seeds in fragments of ferns, *Heliconia spp.* and *Erythrochiton* can be influenced by the physical structure of the patch (Wang and Augspurger, 2004) as well as its place within gap versus intact forest. Including other processes, influenced by dense understories, starting after the seed period, like seedling emergence, competition, mechanical stresses and seedling herbivory, (Royo and Carson, 2005; see also a MSc thesis of Houben, 2006) the struggle for life of future canopy trees within these patches will be far from easy.

This study clearly showed that dense understories within tropical moist forests affect heavily seed removal, and therefore seedling recruitment. It furthermore shows that not all dense understories have a general similar influence on seed removal; the effects are, to a certain extent, understory specific.

## 6. Conclusions

*Erythrochiton*, ferns and *Heliconia spp.* indeed form dense patches in the tropical moist forests of La Chonta and had a fairly high presence in the forest. These patches varied in their distribution and were negatively influenced by silvicultural treatment in the case of two of the three understory groups (ferns and *Heliconia spp.*).

Light availability is an important factor in determining *Heliconia spp.* distribution, while ferns are less dependent on light availability. Soil type showed to be the main factor affecting the presence of ferns, together with topography. Topography also showed to profoundly affect the distribution of *Heliconia spp.* This could partly explain the high occurrence of *Heliconia spp.* in the control treatment of block 3, where the elevation is quite low. Specific differences between *Heliconia* species may also have played a role. *Erythrochiton* is negatively affected by canopy openness, although a clear relation with treatment could not be found. The distribution is much patchier compared to ferns and *Heliconia spp.* *Erythrochiton* was more abundant on sandy soils compared to loamy or clayey soils. It is therefore considered a clear specialist in this study with respect to edaphic factors.

Seed removal indeed proved to be higher in dense vegetations; presence solely did however not explain seed removal rates. The specific characteristics of the dense vegetation group also influence seed removal. The main difference was the generally lower seed removal in the *Erythrochiton* plots compared to the fern and *Heliconia spp.* plots, that was probably induced by the low ground cover in *Erythrochiton* plots, due to a virtually absence of any kind of herb or litter layer. Due to the differential seed removal rates within the understory groups and per seed species, the understories could potentially influence the future tree community composition.

## 7. Recommendations

Only taken into consideration the regeneration of the forest and its timber value, I would recommend removing patches of the three understory groups in La Chonta. Removal could improve the regeneration of tree species in La Chonta, which happened in several studies after removal (De la Cretaz and Kelty, 1999; George and Bazzaz, 1999; Honu and Dang, 2000; Slocum *et al.*, (2004). In addition, seed survival could also increase after removal of the dense vegetation (Abe *et al.*, 2001; Iida, 2004; George and Bazzaz, 1999; Schreiner *et al.*, 2000). Therefore removal could also be very beneficial for future tree crops of commercial tree species in La Chonta. *Heliconia spp.* would probably be the most economically profitable understory group to remove. The skid trails leading to the *Heliconia spp.* patches are already present in the forest because they grow mostly in gaps, preventing more damage to the forest. They inhibit the regeneration in the early stages of gap-phase regeneration, which immediately delays the growth of future crop trees. Moreover, many of the future crop tree species are light demanding or only partially shade tolerant, therefore they would benefit from an increase in light in gaps.

If I take other factors into consideration, my recommendations are quite different. In the case of *Erythrochiton* there are three factors to consider. First of all, *Erythrochiton* is restricted to a small area in Colombia and the lowlands of Peru and Bolivia east of the Andes (Kallunki, 1992) and therefore has a certain level of rarity or endemism. Secondly, I doubt *Erythrochiton* is going to form a considerable problem for regeneration after logging, since my own results and the results of Bustos (2006) show that the species would have more potential to disappear due to logging and fragmentation. Finally, *Erythrochiton* is largely an unknown species with respect to ecology and reproductive biology. Since many shrubs in the understory reproduce vegetatively rather than sexually (Kanno and Seiwa, 2004) and the balance between these two types of reproduction can vary with succession stage, stand type, basal area and species (Huffman and Tappeiner II, 1997; Kanno and Seiwa, 2004; Lantz and Antos, 2002; Lezberg *et al.*, 2001; Tappeiner *et al.*, 1991), it would be interesting to investigate this for *Erythrochiton*. Especially because Rutaceae is a family of which 75-100% species are reported to be clonal (Van Groenendael *et al.*, 1996). Consequently, the patchy distribution of *Erythrochiton* could also be due to a difficult sexual reproduction and a following horizontal clonal expansion into the area. Taking all these aspects into consideration I recommend investigating more thoroughly the ecology and reproductive biology of this species.

Furthermore I recommend investigating (dense) plots of ferns and *Heliconia spp.* also in the dry season. This will add valuable information about their (negative) influence on regeneration to the results of this report. The reasoning behind this recommendation is that the tropical moist forest of La Chonta experiences profound differences in precipitation during the year. This study was done during the rainy season, meaning that what happens in the other, distinctively different half of the year (May-September) is still unexploited. Differences may exist in mammal community, vegetation cover (Soto and Herrera-Flores, 2003) and seed rain (Sautu *et al.*, 2006). All these factors taken together will change the role, extent, method and direction of the dense understories on tree regeneration in the dry season (Wang and Smith, 2002).

I furthermore recommend studying the impact of removing understories on for example the vertebrate population depending on the understory species. *Heliconia spp.*, as well as *Erythrochiton* are dependent on hummingbirds for their pollination and therefore will attract numerous individuals and species of these birds (Seifert, 1982; Kallunki, 1992). Conservation of these bird (and possibly

other vertebrate and invertebrate) species (see also Seifert, 1982) may be more important than the economical losses associated with a temporal or qualitative setback in tree regeneration.

In conclusion, an assessment should be made between deploying financial and human resources to studying tree regeneration and its impact on forest fauna in a removal experiment or studying in further detail their additional impact in the dry season or ecology and reproduction. Such an assessment can not be done without considering the Msc-thesis report of Bram Houben and this report in conjunction.

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## Appendix I

### The organization IBIF (El Instituto Boliviano de Investigación Forestal) and the LTSRP

The LTSRP in La Chonta consists of twelve plots which are approximately 27 ha and are situated in a total of three blocks in this tropical humid forest. Each block contains four plots, representing the four silvicultural treatments. These treatments include an unharvested control plot, a plot harvested using traditional methods, a plot harvested using additional silvicultural treatments and a plot using intensive silviculture (Study Plan). The management of the treatments will be discussed in further detail.

#### Treatment 1: Control

These plots are not being harvested, but despite this fact, some lianas have been cut by La Chonta during forest inventories. The impacts of pre-harvest liana cutting in the plots will be minimal because of the small amount of lianas cut in relation to the total amount.

#### Treatment 2: Normal Management by La Chonta

This management system includes the following conditions:

- a. Planning of roads and logging based on a census of commercial trees.
- b. Harvesting above established diameter limits.
- c. Retaining 20% of commercial trees above diameter limit as seed trees and as a security factor to guard against high-grading.
- d. Cutting of lianas on commercial trees, this means cutting 1-4 lianas on the 1-2 harvestable trees per hectare, just as they did in treatment 1.
- e. Directional felling, mainly to protect logging crews and to facilitate log extraction.

#### Treatment 3: Improved Management

This includes the operations described in treatment 2, extended with the following operations:

- a. Flagging of future crop trees (FCT) before harvest for those species currently harvested at La Chonta. FCT's are defined as trees >10 cm dbh with well formed crowns.
- b. Cutting all lianas on the stem and crown of FCTs.
- c. Liberating a percentage of FCTs from overtopping, poor-formed non-commercial trees. The baseline goal for liberating FCTs will be 15 trees/ha. These non-commercial trees will be girdled by chainsaw, followed by application of 50% aqueous solution of the herbicide 2,4-D. Lianas will also be cut in girdled trees.

#### Treatment 4: Intensive Management

Follows the operations in treatment 3, with the following modifications and additions:

- a. Additional flagging, liana-cutting, and liberation from non-commercial tree species for lesser valued species that are listed in the management plan for La Chonta. The baseline goal for liberating trees will be 25 trees/ha.
- b. Lianas that sprout from the hanging stem will be treated with herbicide (2,4-D) two months after cutting.
- c. Increased intensity of harvest by 2x by relaxing diameter limits and/or harvesting of species currently not harvested by La Chonta.
- d. Timber stand improvement treatments including chainsaw girdling of all non-commercial tree species > 40 cm dbh, except for fig-species or trees otherwise important for wildlife.
- e. Soil scarification/competing vegetation removal in logging gaps using a skidder at the time of log extraction. Logging gaps incorporating scarification will be those with no advanced regeneration of current or potential commercial species and which have commercial seed and root sprout sources in the immediate vicinity. Scarification will include movement of the crown portion of the harvested tree towards the border of the gap.