The effect of a dense understory on the regeneration of tree species in the tropical forest of la Chonta, Bolivia

Bram Houben

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Preface

This report is the result of my thesis at the Forest Ecology and Forest management chair group of Wageningen University. This thesis is set up in cooperation with the Bolivian Forest Research Institute (IBIF due to acronym in Spanish).

In September 2004, I started the preparations for my thesis and from October till May 2005 I did my field work in the tropical forest of La Chonta, Bolivia. From September till January 2006, the data were analysed at the Wageningen University.

This study was a challenge for me to get a better understanding of the tropical ecosystem. The broad subject, including vegetation, herbivory and micro climate, gave me the opportunity to gain an insight in the ecology of the tropical rainforest.
For this opportunity, I thank the Forest Ecology and Forest Management group of Wageningen University, especially my supervisors, Prof. Dr. Frans Bongers and Dr. Marielos Peña-Claros, whose guidance has helped make this thesis a reality.
Frans Bongers helped me with the set up the project and to finish it. Marielos Peña-Claros was the director of IBIF and she gave me the possibility to work in their research plots of the beautiful rainforest of La Chonta, Bolivia. She supervised my thesis in Bolivia but she also helped me to make my stay in Bolivia much easier. I am grateful for all the help they gave me.

Also I would like to thank Dr. Ir. Lourens Poorter and Dr. Ir. Jan Den Ouden of the Forest Ecology and Forest Management group of Wageningen University for the support they gave me during the analyses of my data and to keep me focused during this process.

In La Chonta I lived in the field station together with other students and researchers from IBIF. I enjoyed the life at the field station very much where I experienced for the first time the life in the tropics. I will never forget the great joy and wonderful experiences I had in the tropical forest of La Chonta.

I am grateful to the staff of IBIF especially the “materos” or guides. They taught me many things of the forest and helped gathering my data.

Finally, and importantly, I would like to thank my family for all the support in the difficult days of this period. And for the stimulation and support you gave me to go back to Bolivia and to finish my field work.

Summary

In the tropical humid forest of La Chonta, Bolivia tree species cannot regenerate under dense understory vegetations of *Erytrochiton fallax*, *Heliconia sp.* and ferns. In the present study we investigated the different ways in which the dense understories influence tree seedling density and composition by modifying the micro environmental variables, such as light availability, soil moisture, soil temperature and litter distribution. Finally we determined the effect of a dense understory on the herbivory of seedlings.

In the control habitat and in the habitats with *Erytrochiton fallax, Heliconia sp.,* and ferns the measurements were done in plots of 4 x 4m (25 plots per habitat). A plot of an understory vegetation should contain more than 80% coverage of that specific understory, respectively *Heliconia sp., Erytrochiton fallax* and fern. The control habitat contained less than 20% coverage of *Heliconia sp., Erytrochiton fallax* and fern. The control habitat was the reference for environmental conditions without dense understory vegetation.

The most important effect of the dense understories of *Erytrochiton fallax*, *Heliconia sp*. and ferns on the microclimate is the reduction of light availability for seedlings. Dense understory vegetations of fern reduce the light availability by 70% and dense understory vegetations of *Erytrochiton fallax* and *Heliconia sp.* up to 90%. Another important effect is found in the *Heliconia sp.* habitat; this dense understory vegetation creates habitats with a higher thickness of litter.

In the present study, we counted 969 seedling individuals in total, divided over 53 species. Most seedlings that are found are shade tolerant and partial shade tolerant species. Seedlings of shade tolerant species can germinate and survive under low light conditions of 1-2 % of the full sun. This explains that most of species can occur in the different habitats and that there is no specific species composition for each habitat.

The number of seedlings and species is affected by the amount of sunlight available. The highest number of seedlings (16 per plot) in the control habitats can be explained by the high light condition (3 - 6 % of full sun). *Erytrochiton fallax* reduced light availability to 0.51 % of full sun, which explains the very low number of seedlings found (2 per plot). The intermediate number of seedlings (6 per plot) was found in the *Heliconia sp*. and ferns dominated habitat, and it may be related to the fact that these habitats have intermediate light levels (1 - 3% of full sun). *Heliconia sp*. produces also huge leaves which cause an increase in litter depth. The accumulation of litter can result in a physical barrier which inhibits seedlings to germinate and establish. These two factors together create an unsuitable habitat for seedlings and may inhibit the regeneration of tree seedlings under *Heliconia sp.*

The amount of herbivory on tree seedlings was lower in the *Erytrochiton fallax* and *Heliconia sp.* dominated areas, while it was highest in the fern habitat and the control areas. To be able to determine the differences in seedling density and composition in the four habitats based on herbivory, more specific research is necessary over a longer time period.

In general, species forming a dense understory create environmental conditions that are unsuitable for seedling establishment by decreasing light availability and in some cases increasing leaf litter depth, resulting in a decrease of overall seedling density and diversity below their canopies.

1. Introduction

1.1 The importance of sustainable forestry in Bolivia

Bolivia consists of three main geographical regions. The Altiplano is the high, mountainous and plateau region of the Andes, this area has very little forest cover. The Yungas is a sub-tropical zone, which has extensive forest cover and few inhabitants. The Oriente is the Amazon Basin and this region contains a lot of tropical rainforests, especially in the north.

Bolivia is the fifth biggest country of South America and the total land surface is 1 098 581 km². Of this total surface approximately 45 % is covered by forest. Forestry in Bolivia is a big sector of the countries economy and is still expanding. Wood production grew by almost a third from the late 1970s to the late 1980s, and timber exports have surpassed several other agricultural exports. The export of forest products is growing rapidly and these booms in timber exports have met numerous challenges. These include 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 hectares a year is recognized as the nation's most urgent environmental concern (Guzman 1998).

Fortunately natural forest management in Bolivian tropical rainforest has improved rapidly in recent years due to the implementation of a new forestry law, which was passed in 1996 and a movement by the Bolivian forestry sector to obtain forest certification under the Forest Stewardship Council (FSC) system (Fredericksen 2000). Bolivia's forestry sector is even forming a model for community forestry management in Latin America (Quevedo 1998). The 1996 Forestry Law recognizes that communities may be better stewards of the land than large, private concessionaires (Quevedo 1998). It gives communities preferential rights to utilize forested areas on agricultural properties that they possess. The Forestry Law gives indigenous people the opportunity to buy land parcels and 25 % of the forest area is already managed under a sustainable, community-based model (Quevedo 1998).
Nowadays the Forest Stewardship Council has certified over two million hectares of tropical forest in Bolivia, which makes Bolivia the country with the most certified tropical forest in the world (web page CFV).

Despite this big amount of FSC certified forest and many improvements in the Bolivian forestry sector, silviculture in Bolivia still rarely goes beyond selective harvesting. Evidence from research indicates the need to apply silvicultural treatments to improve regeneration and maintain stand quality. Bolivian forest managers have little experience with silviculture in natural tropical forest and little capital is currently available for investment in treatments that will yield silvicultural benefit only in long term. Small-scale research has been conducted to develop cost–effective treatments, but there is a need to conduct research on larger operational scales to determine the feasibility and cost effectiveness of recommended silvicultural systems (Quevedo 1998)

The Bolivian Forest Research Institute (IBIF, due to acronym in Spanish) is in charge of continuing the Long-Term Silvicultural Research Project (LTSRP) started in 2000 by the Sustainable Forest Management Project (the BOLFOR project, funded by USAID and the Bolivian government). The LTSRP consists in installing permanent, large-scale silvicultural research plots that would serve the general goal of contributing to the sustainable forest management of Bolivian forests (Fredericksen 2000). These plots are established in the most representative Bolivian tropical forests: the tropical dry forests, tropical humid forests and Amazonian wet forest. The plots allow researchers to determine the impacts of silvicultural treatments on biodiversity, stand dynamics, and forest ecosystem functions over long periods.

1.2 Problem description

Selective logging systems rely on the natural regeneration to produce the next crop of timber. These systems seek to maintain commercial productivity of logged forest by minimizing damage to residual trees and by conserving the potential natural regeneration of the forest. In natural regeneration systems it is assumed that the regeneration will occur naturally, beginning with an acceptable production of seedlings and some of these will eventually become harvestable adult trees (Mostacedo and Fredericksen 1999, Jansen 2003, Costa and Magnusson 2002).

In the tropical humid forest site of the LTSRP, several studies have found that commercial tree species are not regenerating adequately due to several reasons (such as small logging gaps, gaps covered by dense vegetation). Several researchers of IBIF have also noticed that there is almost no tree regeneration under patches of dense understory vegetation. Certain understory species can create very dense patches of vegetation, particularly species like *Heliconia sp., Erytrochiton fallax* and ferns. Dense understory vegetations are expected to influence the environment in such a way that it is unsuitable for the regeneration of tree species (George and Bazzaz 1999, Den Ouden 2000, Poorter and Yáskara 2000 Yáskara 2000, Cournag et al 2002). The goal of this study is to investigate the effect of dense understories of *Heliconia sp., Erytrochiton fallax* and ferns on tree regeneration.

1.3 Research objectives & questions

Based on the previous problem description, the general objective of this study is to determine the effect of dense understories of *Heliconia sp.*, *Erytrochiton fallax* and ferns on the regeneration of tree species. As reference point a control situation is set up; the values of this situation are an indication of the environmental values when no dense understory vegetation is present. Dense understories of *Heliconia sp.*, *Erytrochiton fallax* and ferns and the control situation are called habitats.

The aims are to:

- Investigate if dense understories modify the micro environmental conditions, such as light availability, soil moisture and temperature and litter distribution. Changes in these micro variables may play an important role in the establishment of tree seedlings.
- Determine if dense understories of *Heliconia sp.*, *Erytrochiton fallax* or ferns have an influence on tree seedling density and composition.
- Determine the herbivory pressure on seedlings of tree species in the different habitats

The following research questions were set up to answer this:

Central research question

Do dense understories of *Heliconia sp.*, *Erytrochiton fallax* or ferns affect seedling regeneration, seedling growth and seedling herbivory?

Research questions

Research question 1:
What effect has *Heliconia sp.*, *Erytrochiton fallax* or fern on leaf litter, soil humidity, soil temperature, and light availability?

Research question 2:
Does the occurrence of *Heliconia sp.*, *Erytrochiton fallax* or fern affect the density, the composition and growth of the tree seedlings?

Sub research questions for research question 2:

- What is the impact of the microclimate variables on seedling density and composition?

Research question 3:
Does the occurrence of *Heliconia sp.*, *Erytrochiton Fallax* or fern affect seedling herbivory?

2. Important factors and processes

2.1 Dense understories and regeneration of seedlings

In this study *Heliconia sp., Erytrochiton fallax* and ferns have one important feature in common. All the three species are common in the understory of the Bolivian tropical humid forest, where they form dense patches of vegetation (Fredericksen 2000). Because of their abundance in big parts of the forests, the species may interfere with seedling establishment through resource competition and environmental modifications (Denslow et al 1991, Svenning 2001). If patches of dense vegetation of these species correspond to lower seedling densities, then the distribution of these dense vegetation patches may affect the abundance, distribution of the seeds and seedling of the tree species.

Conceptual design of the process

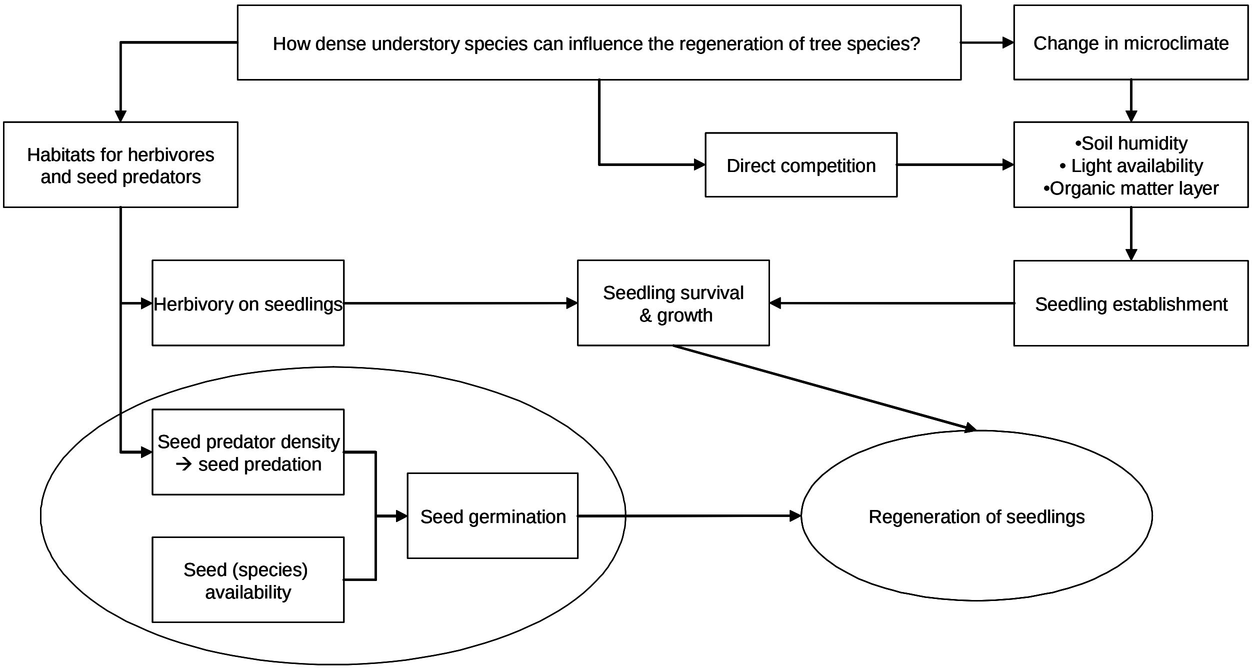

Fig. 1. Conceptual design of the process: How dense understories influence the regeneration of tree seedlings. The factors that are marked by the circle are not included in this study but they are also a part of the process. These factors are examined in another study (van der Heide, unpublished data).

2.2 The three different “problem” species

Much research is done about the biology and ecology of ferns. But *Heliconia sp.* and *Erytrochiton fallax* have not been thoroughly studied in the past. Little is known about their ecology, especially in the tropics.

Ferns and fern allies are known for the fact that they can carpet much of the forest herb layer in the tropics (Kricher 1997). Due to its clonal growth, longevity and persistence, ferns can build a dense understory canopy of fronds that may dominate the forest floor for decades or even centuries. Such dense ferns may effectively compete for water and nutrients and reduce growth of canopy trees. However, the most important consequence for forest dynamics of the presence of fern vegetation is its effect on the regeneration of tree species. Under conditions that are favourable for fern growth, the long term failure of tree regeneration may eventually results in the disappearance of the tree canopy. Examples can be found all over the world, like in Mexico and Great Britain. Often ferns have persisted after large scale disturbance events like fire or clear cutting. Ferns can quickly invade the disturbed sites and prevents new colonisation of trees. Due to the lack of efficient control measures, ferns are regarded as one of the world’s most troublesome weeds (Den Ouden 2000)

Heliconias (*Heliconia sp*., family *Heliconiaceae*) are recognized by their huge, elongate, paddle-shaped leaves (heliconias are closely related to bananas, *Musa sp.*) and their distinctive, colourful red, orange, or yellow bracts surrounding the inconspicuous flowers. Some *Heliconia sp* 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 and form dense patches of vegetations. All *Heliconia sp* have a Neotropical origin, with approximately 150 species distributed throughout Central and South America (Kricher 1997). Most Heliconias are 1-2 meters long, but a few species can be 5 meters or even longer (Gentry 1996).

Erytrochiton fallax is believed to be a clonal tree (M. Peña-Claros, personal communication), which belongs to the Rutaceae family. It is a typical understory species, has dark green leaves and small branches. The individuals grow very close to each other, forming dense stands. This plant can grow up to 5m high and can become 5 cm in diameter.

2.3 Seed dispersal by plants

Seed dispersal by plants is one of the most critical periods in a plant’s life. In this stage it is important for the plant to have a successful dispersal. The dispersal involves the greatest losses of individuals, as only very few or even none of the millions of seeds that an individual plant may produce during their lifetime will successfully establish and become reproductive. Successful dispersal creates the opportunity for species to pass genes to the next generation. By dispersal failure, on the other hand, presence of the species or individuals in the next generation can be nil. Dispersal therefore has a profound effect on vegetation composition and even structure of the forest (Wang and Smith 2002, Jansen 2003).

Large- seeded trees whose seeds are dispersed by mammals often have high levels of seed dispersal but high losses due to seed predation. Consequently, seedling establishment is influenced by the impact of mammalian seed predators as well as by the ability of seedling to survive where the seed is dispersed (Sork 1987).

2.4 Patterns of seedling establishment

When the seed dispersal is successful the seed will germinate and start to grow up. A common source of seedling mortality is unsuitable environmental conditions at the time of germination. Light availability below canopies is the principle limiting factor of tree recruitment and growth in forests (Cournag et al 2002).

Tree seedling germination and establishment have shown to be sensitive to light availability (Sork 1987, George and Bazzaz 1999, Cournag et al 2002) and light quality, soil moisture and temperature, nutrient supply (Burslem 1996, Poorter and Yáskara 2000), and quality and quantity of leaf litter (Den Ouden 2000, Poorter and Hayashida 2000, Molofsky and Augspurger 1992). Biotic factors like herbivory and competition from other plants, may effect seedling survival as well (Sork 1987). Some or even all of these factors may interact in complex ways to influence patterns of seedling establishment.

2.5 How dense understories can influence the regeneration of seedlings?

Light availability

The availability of light plays a major role in growth, survival and establishment of tropical seedlings. Mature tropical rain forests are dynamic communities with a high frequency of tree and limb falls which open gaps in the canopy resulting in a heterogeneous light availability on the forest floor (Capers and Chazdon, 2004). Small tree fall gaps are a common canopy disturbance where light availability on the forest floor typically reaches 8-10 % of full sun. The dense understories of shrubs and herbs intercept much of the remaining light in a forest, changing the light quality and quantity beneath their canopies. The understories can reduce the light availability to 1-2% of the full sun (George and Bazzaz, 1999). The survival of seedling under certain light conditions is dependent on the specific light requirements of the species. It is reported that species with greater seed size are associated with a higher degree of shade tolerance. Species with larger seeds have more resources in the seeds that allowed them to survive in low light conditions (Sork, 1987)

Effect of leaf litter

Germination and seedling establishment have been shown to be sensitive to temperature and moisture and to the quality and quantity of litter. To the extent that the understory modifies these micro environmental variables, temperature, soil moisture and litter distribution may also play an important role in the interactions between the understory and tree seedling (George and Bazzaz, 1999).

Litter production of the understory depends on the productivity of the plant species at a site but when the production is big and when decomposition is low, annual litter input will result in the build-up of an ectorganic soil profile. This is established by the increase in depth of the fermentation and the humus layer. These layers are considerably different from the litter layer, which only represents the youngest, physically and chemically unaltered, input of fallen organic material on top of the soil surface. As a result the fermentation and the humus layer contain much smaller particles and create more favourable moisture conditions when compared to the litter layer. The fermentation and the humus layer of the ectorganic profile create a physical and chemical barrier for seeds and seedlings after they have germinate in the upper layers and try to reach the “safe” mineral soil. The descending root of a seedling may be mechanically hindered by the ectorganic soil layers. Mechanical forces acting on the root tip have a strong impact on root development. So the mechanical properties of the ectorganic layer can be expected to have a potentially negative strong influence on the establishment of seedlings that have to germinate on the top of the ectorganic soil profile (Ouden 2000).

The presence and amount of leaf litter can also increase soil moisture and decrease soil temperature, which may affect seedling establishment (Molofsky and Augspurger 1992). Consequently, leaf litter of different depths within a tropical rainforest creates many different micro sites for seedling establishment.

Creating habitats for seed and seedling predators

Understory interference with tree seedling establishment may not only occur through resource competition or modification, but it may also occur indirectly through the understories influence on the behaviour of seed and seedling predators. A dense understory of herb or shrubs can provide habitats and shelter for both seed and seedling predators. Predators can feel themselves more secure in this kind of vegetations than in more open vegetation. Dense understories can change the availability of food resources and provide more fruits, seeds, seedlings or other food resources. The understory vegetation can be a food sources themselves or certain plant species that appear in combination with them, can be new food resources (Sork 1987). A higher density of seed and seedling predators may result in a higher rate of seed and seedling predation. This can lead to reduced seedling densities in the forest (George and Bazzaz 1999, Steven and Putz 1984). For example, within a given ecosystem, overall species composition of the rodent community, a common seed predator, is influenced by productivity and composition of the vegetation. The densities and species composition of rodent populations is however dependent on the structural characteristics of the habitat. Factors such as 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 utilization (De Jong 1979, Ouden 2000).

Herbivory on seedlings

When the seeds have germinated and the plant start growing, the seedling can be impeded and reduced in its growth by another biotic factor. Herbivory has been shown to be an important influence on seedling establishment. The effect of herbivory varies among sites, seasons and species. The survival of a species on a given site is depended on the density of the herbivores. Mammalian herbivores such as agoutis and pacas significantly decreased seedling densities of large seeded species in Panama (Sork 1987). It is possible that vertebrate herbivory on stem and leaves can reduce seedling height of seedling individuals. Insect herbivory, for example by leaf cutting ants, can also influence patterns of seedling establishment. Insect herbivory tends to be more sporadic with whole cohorts of seedling lost to herbivores in one season and none in the next one (Swaine 1996).

Tropical rain forest leaves are subjected to potential danger of herbivory and pathogens the whole year around. It is possible that these factors reduce the growth or the survival change, depending on the plant species defences against herbivory. Leaves of both tropical and temperate zone plants are laced with chemicals. These chemicals are called secondary compounds because most seem to lack any direct metabolic function. Plants contain many different kinds of secondary compounds. Because these compounds collectively help protect plants, they are commonly called defence compounds or allelochemics. Most plants species contain a variety of these, some defence compounds functions principally to protect against herbivores, some to protect against bacteria and fungi. Beside this, there are also other defence mechanisms. Tropical trees may protect themselves with spin, thorns, or may have leaves that are coated with very small “beds of nails”. Leaf toughness, nutrition value and fibre content affect also the rate of herbivory on a plant. Leafs with a high leaf toughness and fibre content and a low nutrients value are normally less predated. The typical tropical plants combines various depends compounds with other defence mechanisms (Kricher 1997).

3. Methods

3.1 Study area

This study was carried out in the forest concession La Chonta, one of the sites of the LTSRP. La Chonta is situated in the province of Guarayos of the department of Santa Cruz, Bolivia (15°45’ S, 62°55’ W; Fig. 2). The area experiences an annual mean precipitation of 1562 mm and an annual mean temperature of 25.3°C. The area is classified as a Subtropical Humid Forest according to the Holdridge system, and represents a transition between dry and Amazonian forests. Forest cover is seasonal with a dry season from May to October. Geologically it is a continuation of the crystalline shield chiquitano with fertile inceptisols. In La Chonta over 170 tree species are identified, of which 18 are considered to be of commercial value (Fredericksen 2000).

The treatment plots of the LTSRP installed in La Chonta were used to carry out this study. In LTSRP project, permanently installed, large-scale silvicultural research plots serve the general goal of contributing to the sustainable forest management of Bolivian forests (Fredericksen 2000). These treatment plots offer the opportunity to study the ecological impact of alternative silvicultural systems on biodiversity, forest community dynamics and ecosystem processes at more appropriate scales than small-scale treatment plots.
Treatment plots are 27 hectares and are situated in three blocks of the tropical humid forest. Each block contains four treatment plots, representing the four silvicultural treatments (Fig. 3). Further details, specific goals and the design of LTSRP can be found in Appendix 8.1.

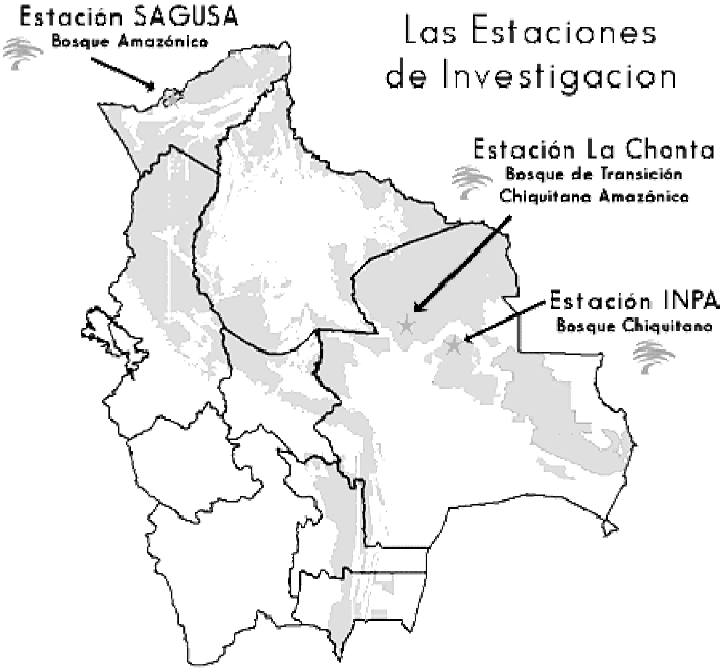

Fig. 2. The map of Bolivia. On the map the three research areas of IBIF are indicated. This study is conducted in the research area called “Estación La Chonta”.

3.2 Field methods

3.2.1 Plot establishment

For this study 25 4 x 4 m plots were established in each of the four habitats: dense understories of *Heliconia sp., Erytrochiton fallax* and ferns and the control situation. Consequently, there were 100 plots in total. The selection of the location of the plots was done by examining the following conditions; the plots of an understory should contain more than 80 % coverage of that specific understory, respectively *Heliconia sp., Erytrochiton fallax* and fern.
The control plots should contain less than 20% coverage of *Heliconia sp., Erytrochiton fallax* and fern.

The distribution of the plots:

- 25 plots contain more than 80 % coverage *Heliconia sp.*
- 25 plots contain more than 80 % coverage *Erytrochiton fallax*
- 25 plots contain more than 80 % coverage and fern.
- 25 plots contain less than 20% coverage of *Heliconia sp., Erytrochiton fallax* and fern.

These plots were spread over the 3 blocks of LTSRP, restricted by the selection criteria described above. Figure 3 gives an example of how the plots could be distributed in the LTSRP plots of La Chonta. The specific locations and coordinates of the plots in each block are given in Appendix 8.2.

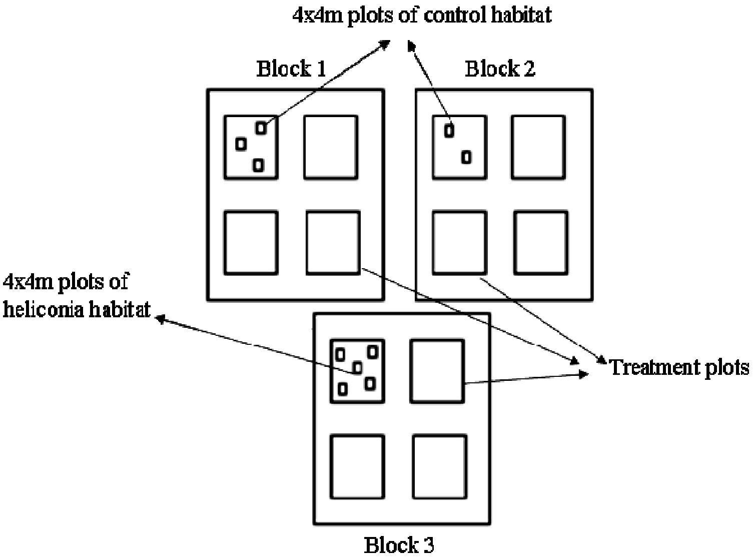

Fig. 3. Illustration of the design of LTSRP. Each block contains 4 treatment plots. The plots of this research are randomly spread over the blocks, only restricted by the selection criteria. As example some plots are indicated.

3.2.2 Abiotic factors

For each of the 100 plots a number of abiotic factors were measured to determine if there are different microclimatic conditions under dense vegetation of *Heliconia sp., Erytrochiton fallax* and ferns. The microclimatic conditions under these vegetations are compared with conditions in situations where these vegetations are not abundant (control plots). In this way we get an indication how these dense understory vegetations influence the microclimate. The abiotic factors that were measured are litter layer and cover, soil humidity and temperature, and light availability.

Litter layer and litter cover

The average litter depth was measured at 4 points of the plot (Fig. 4) by using a metal stake, which was forced into the litter till the bare soil was reached. Then the depth needed to reach the bare soil was measured by using a ruler. An average litter layer per plot was calculated based on these 4 measurements. The litter cover was estimated for each plot and is expressed in percentage.

Soil humidity

In the tropical forest, most of the length and mass of tree roots is concentrated in the upper 20 cm of the soil. So the soil moisture content over that range is a good indication of the soil humidity in the root zone of the plant (Poorter and Hayashida 2000). For each plot one soil sample was taken in the middle of the plot on a depth of 10 to 15 cm (Fig. 4). At this location, less edge effects are expected. The samples were taken with a small instrument, a little spade that has such shape that you always get the same amount of soil. The collected soil was put in plastic bag to prevent that the samples would dry out, and were taken to the lab. To determine the soil humidity, first the fresh weight of the sample was measured and then the sample was dried in an oven for 92 hours at 70 °C to determine the dry weight. Then the percentage soil humidity was calculated as:

$$\% \text{ soil humidity} = (A-B)/B*100$$

A= fresh weight of sample
B= dry weight of sample

Soil temperature

The soil temperature was measured once at two places in the middle of the plot, 1 m apart (Fig. 4). At this location, less edge effects are expected. This was done with two different thermometers, which were thrust 10 to 15cm in the ground. The two measurements were compared and the average was taken. In this way we get an indication of the ground temperature in the plot, uninfluenced by a local effect in the root zone of the plant (10 to 15cm deep)

Light availability

To get consistent information about the light availability in the different habitats, the photosynthetically active radiation (PAR) was measured. This measurement gives the best information about light availability in the forest (Ferment et al 2001). Two data loggers, the model Li-1400 and the Li-1000 with LI-COR quantum sensors, were used and the measurements are expressed in micromol/m^2/s.

Three different light samples were measured in the field:

- Sample A= light measurement 10 cm above the dense understory of *Heliconia sp., Erytrochiton fallax* and ferns.

- Sample U= light measurement under the dense understories, 30 cm aboveground. When the dense understory was lower than 30 cm, then this measurement was taken minimum 10 cm under the vegetation.
- Sample C= control sample, light measurement in an open area.

Sample A was not measured in the control habitat because there was almost no understory vegetation. Sample U was measured in each plot. Sample A and sample U were measured on four different locations in the plots (Fig. 4) with the Li-1400 data logger and LI-COR quantum sensor. Each measurement was done for 30 seconds to include any extreme influence of the sun (sunbeams). The four measurements were averaged. To get a reference point of the light availability on a certain day, a control measurement (sample C) was made continuously outside the forest in the open air by using a Li-100 data logger with a LI-COR quantum sensor.

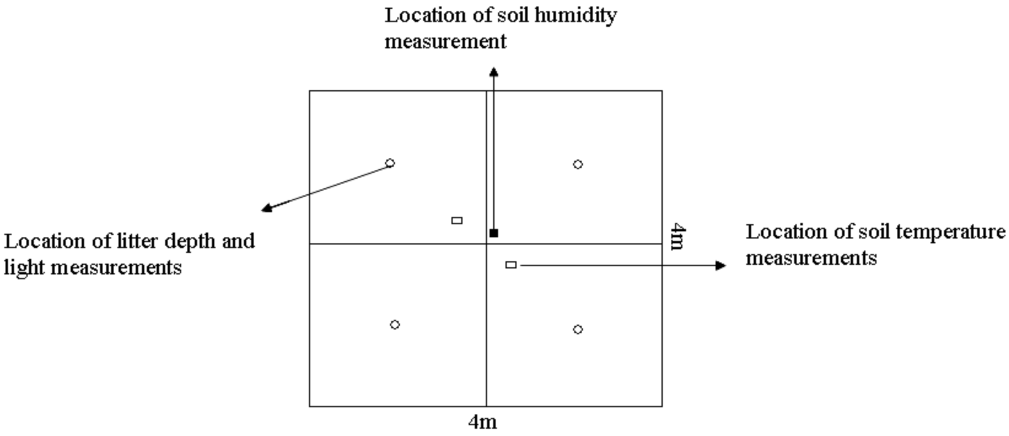

Fig. 4. The location of the measurements of the abiotic factors in a 4x4m plot.

3.2.3 Inventory of the natural regeneration

In the 100 plots of 4 x 4m seedlings of all tree species were counted, identified and measured in height. Additionally the height of the understory of *Heliconia sp.*, *Erytrochiton fallax* and ferns was measured.

Seedlings are considered as individuals between 10 cm and 200 cm in height, including relatively young plants but excluding most newly germinated seedlings (Harms et al., 2004). The tree seedlings were divided in 10 height classes (Table 1) to get an overall idea of the height that the seedlings achieve in the different habitats. When we compared the height of the seedlings with the height of the understories we can find seedlings higher then the dense understory. In this way we can get an idea if seedlings are able to break through the understory and grow bigger.

Table 1. Different classes of seedling heights.

Height Class	**Height of the seedling**	**Height Class**	**Height of the seedling**
1	10cm-28cm	6	105cm-123cm
2	29cm-47cm	7	124cm-142cm
3	48cm-66cm	8	143cm-161cm
4	67cm-85cm	9	162cm-180cm
5	86cm-104cm	10	181cm-199cm

3.2.4 Seedling growth and herbivory

1) Transplant experiment

The herbivore density and seedling growth was investigated by transplanting seedlings of *Swietenia macrophylla* and *Margaritaria nobilis*. These seedlings were planted and tagged with labels. Each plant received a unique number.

Because of lack in number of seedlings, we used a limited number of plots and no seedlings were planted in the *Heliconia sp.* habitat. Two seedlings of *Swietenia macrophylla* and one seedling of *Margaritaria nobilis* were planted in 45 plots: 15 plots with *Erytrochiton fallax*, 15 plots of the control habitat and 15 plots of the fern habitat. Consequently, we transplanted 90 *Swietenia macrophylla* seedlings and 45 *Margaritaria nobilis* seedlings. All measurements for this experiment were done at the beginning of the experiment (15/02/2005) and after 72 days.

<u>Seedling growth</u>

The shoot height and length was measured for each transplanted seedling using a ruler. The height is defined as the distance from the ground to the highest point of the plant. The length is determined as the distance from the ground to the top bud. The shoot length was used to calculate the relative growth rates (RGR) of the 2 species. The Relative Growth Rates (RGR) was calculated as: RGR= $[\ln(\text{lenght}_{t2}) - \ln(\text{lenght}_{t1})]/(t2 - t1)$. T1 and t2 are the two measurements periods (t1-t2= 72 day).

<u>Herbivory</u>

Percentage herbivory on a seedling was measured at the two newest leaves. At each seedling the two leaves were tagged and the leaf proportion that was eaten was estimated by using overhead sheets with grid on it. The sheets were placed over the tagged leaf and the numbers of intersection of lines were counted for each leaf separately. Also the number of intersections in the damaged part of the leaf was counted. Then percentage herbivory was calculated as

Percentage herbivory= (damaged part/surface leaf)*100;

and the herbivory rate was calculated as:

Herbivory rate: (% herbivory at time 1- %herbivory at time2)/time

There are 72 days between t2 and t1. All missing leaves at the end of the experiment are considered as eaten.

2) Natural regeneration

The percentage herbivory was also measured on the seedlings of the natural regeneration. The percentage herbivory of the two most upper leaves was measured once with the help of the grid system (as described in the previous chapter). This gives an indication of the herbivory on that moment. Of these seedlings the number of predated leaves and unpredated leaves were counted to get an indication of the percentage of leaves that are predated.

3.2.5 Vegetation density

For each of the 100 plots the density of the vegetation in the understory was determined. The following values were computed:

- The average height and cover of the *Heliconia sp.*, *Erytrochiton fallax* and ferns were estimated.
- The number of individuals of *Heliconia sp., Erytrochiton fallax* and ferns were counted.
- The cover of seedlings was estimated and the number was counted.
- The cover of lianas and herbs was estimated.

3.3 Methods of analysis

To answer the first research question ´What is the effect of *Heliconia sp., Erytrochiton fallax* or fern on leaf litter, soil humidity and temperature and light availability for seedlings” the following analyses were done.

The differences in the micro climate values among the habitats were statistically tested by using the program SPSS. A one-way ANOVA, tukey test was used for normal distributed data. When the data were not distributed normally, a Kruskal-Wallis (KKW) test and a Mann Withney-U (MWU) test were applied. The Mann Whitney-U test was used to test the differences between 2 habitats. We have 4 different habitats, when we compare them separately; you have to make 6 comparisons (1-2, 1-3, 1-4, 2-3, and 3-4). Because we compared them separately the chance was bigger that they were different. Therefore the significance level for the test was p=0.02.
When the data was not normally distributed, data transformations were applied. Mainly log transformations were used. But for the transformation of proportions to a normal distributed data set, the arcsin transformation was used.

For most measurements the number of plots is 25 in each habitat. But for the soil temperature measurements the number if plots in the control habitat is 12 and in the other habitats the number of plots is 25.

The measurements for soil humidity were done at two different time periods. Before the second measurement it had rained and this had influenced the results. Eight plots were measured in both periods (period 1 and 2). With these plots a correction factor was calculated for the results measured in the second period, which excluded the environmental influence, rain. The correction factor was equal to the sum of the differences of result 1 & 2/8 = 4.52. The corrected results of period 2 and the results of period 1 had almost the same mean and standard deviation. Therefore, they could be compared with each other and this data was used for regression analyses. To measure the differences in humidity between the habitats only the data points of the first measurement (before the rain) was used. We had 16 plots for *Erytrochiton fallax* habitat, 25 for the fern habitat, 25 for *Heliconia sp.* habitat and 16 for the control habitat.

To investigate the effect of the dense understory vegetations on light availability, we had calculated different light values; the light available for the seedlings, the light available for *Heliconia sp., Erytrochiton fallax* or ferns; and the absolute and relative light absorption of these dense understory vegetations. The first three values are expressed in % of the full sun. Using the data collected in the field (see chapter 3.2.2), we calculated four different light values:

1. Light S = light available for the tree seedlings, absorption of the forest and the understory vegetation = (sample U / sample C) * 100%
2. Light U= Light available for *Heliconia sp., Erytrochiton fallax* or ferns
   = (sample A / sample C) * 100%
3. Light abs= Light absorption of *Heliconia sp., Erytrochiton fallax* or ferns
   - Absolute absorption of the understory vegetation = light U – light S
   - Relative absorption of the understory vegetation (%) = (the absolute absorption / Light U) * 100

Sample A was not measured in the control habitat because there was no dense understory vegetation. Logically we did not have the Light U and Light abs values for the plots of the control habitats.

The numbers of plots used for measuring the different light values were 16 for the *Erytrochiton fallax* habitat, 25 for the habitat with ferns, 15 for the *Heliconia sp.* habitat and 25 for the control habitat.

The analysis of the second research question “Does the occurrence of *Heliconia sp., Erytrochiton fallax* or fern affect the density, composition and growth of the tree seedlings” was divided in several parts. If these factors are different between the habitats was investigated and also the impact of the micro climate variables on seedling density and composition was computed. The data analyses that were used can be summarized as follows.

Seedling density

To investigate the differences in seedling and seedling species density between the different habitats, we compared the average number of seedlings and seedling species of each habitat with each other. A one-way ANOVA with Tukey was applied.

Composition of the seedling species over the habitats

The difference in seedling species composition was investigated with the use of the program TWINSPAN. With this analysis we tried to determine if dense understory of *Heliconia sp., Erytrochiton fallax* or fern influences the seedling species composition in such way that a specific seedling species composition occurs under *Heliconia sp., Erytrochiton fallax* or ferns. The Two-Way Indicator Species Analysis (TWINSPAN) (Hill 1979b, Gauch and Whittaker 1981) is a method of simultaneously classifying both species and sample units. In addition it produces two-way ordered tables and a dendrogram. In the table and dendrogram groups of plots with comparable species composition will be clustered. In the two-way ordered table, species names are arrayed along the left side of the table, while sample numbers are along the top. The pattern of zeros and ones on the right and bottom sides define the dendrogram of the classifications of species and samples, respectively. The interior of the table contains the abundance class of each species in each sample. Abundance classes are defined by pseudospecies cut levels. TWINSPAN does not analyse abundance data directly but is based on presence/absence data. However, it approximates quantitative abundance data by creating a variable number of "pseudospecies" representing abundance classes. The "pseudospecies cut levels" are used to define the ranges of the abundance classes. In the table 9 (Fig. 7) the maximum of 9 classes is used.

The biodiversity of the habitats

We had determined if the 3 dense understory vegetations have also an influence on the seedling biodiversity. The Shannon diversity index was calculated to determine if seedling diversity varied among habitats. The Shannon's index accounts for both abundance and evenness of the species present. The proportion of species *i* relative to the total number of species (p_i) is calculated, and then multiplied by the logarithm of this proportion ($\log p_i$). The resulting product is summed across species, and multiplied by -1 (Magurran 1988):

$$H= -\sum_i p * \log p_i$$

The impact of the microclimatic variables on the seedling composition and density

To investigate which microclimatic variables determine the presence of a seedling species, we explored the data using a canonical correspondence analysis (CCA) (ter Braak 1988a). This method uses multiple regression to select the linear combination of environmental variables that explain most of the variation in the species scores on the axes. The result of this analysis is presented in an ordination diagram, which also gives the ranking of samples along the axes, based on the species composition in each sample. In the CCA analysis, the following environmental factors were included: cover and height of the litter, available light for the seedlings and the cover of three dense understory vegetations.

We also investigated which microclimatic factors have the most influence on the number of seedlings and seedling species in general (seedling density, n=81). This was done using a forward multiple regression analysis (SPSS). In the multiple regression analysis the following variables were included: available light for the seedlings, and litter cover and depth.

Soil humidity and temperature were not included in the two analyses because these are static measurements. These results show the differences between the habitats but these static results could not be related to germination or seedling composition.

Seedlings growth

The effect of the understory vegetations on the growth of the seedlings was investigated in the transplant experiment. *Swietenia macrophylla* seedlings and *Margaritaria nobilis* seedlings were planted. The seedling length was measured at the beginning and at the end of the experiment. The Growth Rates (GR) of these seedlings was calculated and the differences between the habitats were measured with an ANOVA.

$GR = [\ln(\text{lenght}_{t2}) - \ln(\text{lenght}_{t1})] / (t2 - t1)$

$t1$ and $t2$ are the two measurements periods ($t2$-$t1$= 72 day)

Herbivory

To answer the last research question "Does the occurrence of *Heliconia sp.*, *Erytrochiton Fallax* or fern affect seedling herbivory?" three herbivory values were calculated: the herbivory rate, percentage herbivory on a leaf and the % predated leaves (see chapter 3.2.4).
The herbivory rate was calculated for the seedlings of the transplant experiment and the percentage herbivory was computed for all seedlings (seedlings of transplant experiment and natural regeneration). The percentage of leaves that are predated was calculated for all natural regenerated seedlings (>10cm <200cm).

The differences in herbivory rate, percentage herbivory and percentage of eaten leaves among habitats were calculated with a one way ANOVA test and a Tukey when the data were normally distributed. When the data were not normally distributed, a Kruskal-Wallis test and a Mann Whitney-U test (with a significance level of 0.02) were applied.

Summary of analyses

Table 2. The different data analyses that are used.

Research parts	**Normally distributed**	**Not normally distributed**
Differences in microclimate, seedling densities and herbivory	ANOVA, tukey	Kruskal-Wallis, Mann Withney-U (p=0.02)
Seedling composition	Two-Way indicator Analysis (TWINSPAN)	
Biodiverstiy of a site	The Shannon diversity index	
Impact of the environmental variables on the seedling composition (exploration)	Multi-Variate analysis: Canocical correspondence analysis (CCA)	
Impact of the microclimate variables	Multi regression analysis (stepwise)	

5. Results

5.1 The micro climate under the three dense understory vegetations

Litter depth was different among habitats (ANOVA, F= 23.796, df= 3 p= 0.00). The litter depth of *Heliconia sp.* habitat was significantly higher (6.8 cm) than the litter depth of all other habitats (range between 3.9 cm and 4.7 cm) (Fig. 5.1.). The other habitats did not differ among each other in terms of litter depth.

Although the mean litter cover per habitat ranged between 95 and 100%, there were significant differences among habitats (Kruskal Wallis, X^2= 14.172, df= 3, p=0.003). The habitat with *Erytrochiton fallax* had the lowest litter cover, while the habitat with ferns and *Heliconia sp.* had the highest values (Fig. 5.2).

Soil temperature was significantly different among habitats (Kruskal Wallace, X^2= 36.227, df=3, p=0.00). The soil temperature from *Erytrochiton fallax* was approximately 24.5°C and this was significant lower than the soil temperature in the other habitats. But difference was only 0– 1.5°C. (Fig. 5.3)

Soil humidity varies between 12 and 16.5 %, and habitats showed a significantly different soil humidity (ANOVA, F=5.059, df=3, p=0.003). The soil humidity of the ferns habitat is the lowest and the humidity of the *Heliconia sp.* habitat is the highest. The humidity of these two habitats are significant different (p= 0.002). The other two habitats have intermediate values (Fig. 5.4).

The light availability for *Erytrochiton fallax*, ferns or *Heliconia sp.*, differs significantly (ANOVA, F = 9.399, df=2, p = 0.00) (Fig. 5.5). The light availability for the *Heliconia sp.* is 14.5 % of the full sun and it is significantly higher than the light available in the *Erytrochiton fallax* habitat (p=0.031) and ferns habitat (p=0.00), respectively 5.3 and 3.2 % of the full sun.

The light absorption of the dense understories was expressed in an absolute and relative value. The absolute light absorption of *Erytrochiton fallax*, ferns or *Heliconia sp.* is highly significant different from each other (ANOVA, F=10.891, df=2, p=0.00). The absolute light absorption of the *Heliconia sp.* is 12.8% of the full sun and is significantly higher than the light absorption of the *Erytrochiton fallax* (p=0.046) and the ferns (p=0.00) (Fig. 5.6). This is 4.7 and 2.3% of the full sun. The relative light absorption of the three understory vegetations differs also highly significant among the habitats (Kruskal Wallace, X^2=26.391, df=2, p=0.00). The relative light absorption is higher in the habitats with *Erytrochiton fallax* and *Heliconia sp.* (approximately 90%), and it is lower in the ferns habitats (71%) (Fig. 5.7).

This leads to different amount of light available for the seedlings under the dense understories. The difference in light availability for the seedlings among the habitats is highly significant (Kruskal Wallace, X^2=38,556, df=3, p=0.00). The light availability for seedlings is the highest in the control habitats (3 - 6 % of the full sun), and it is the lowest in the habitats with *Erytrochiton fallax* (0.5% of full sun) (Fig. 5.8).

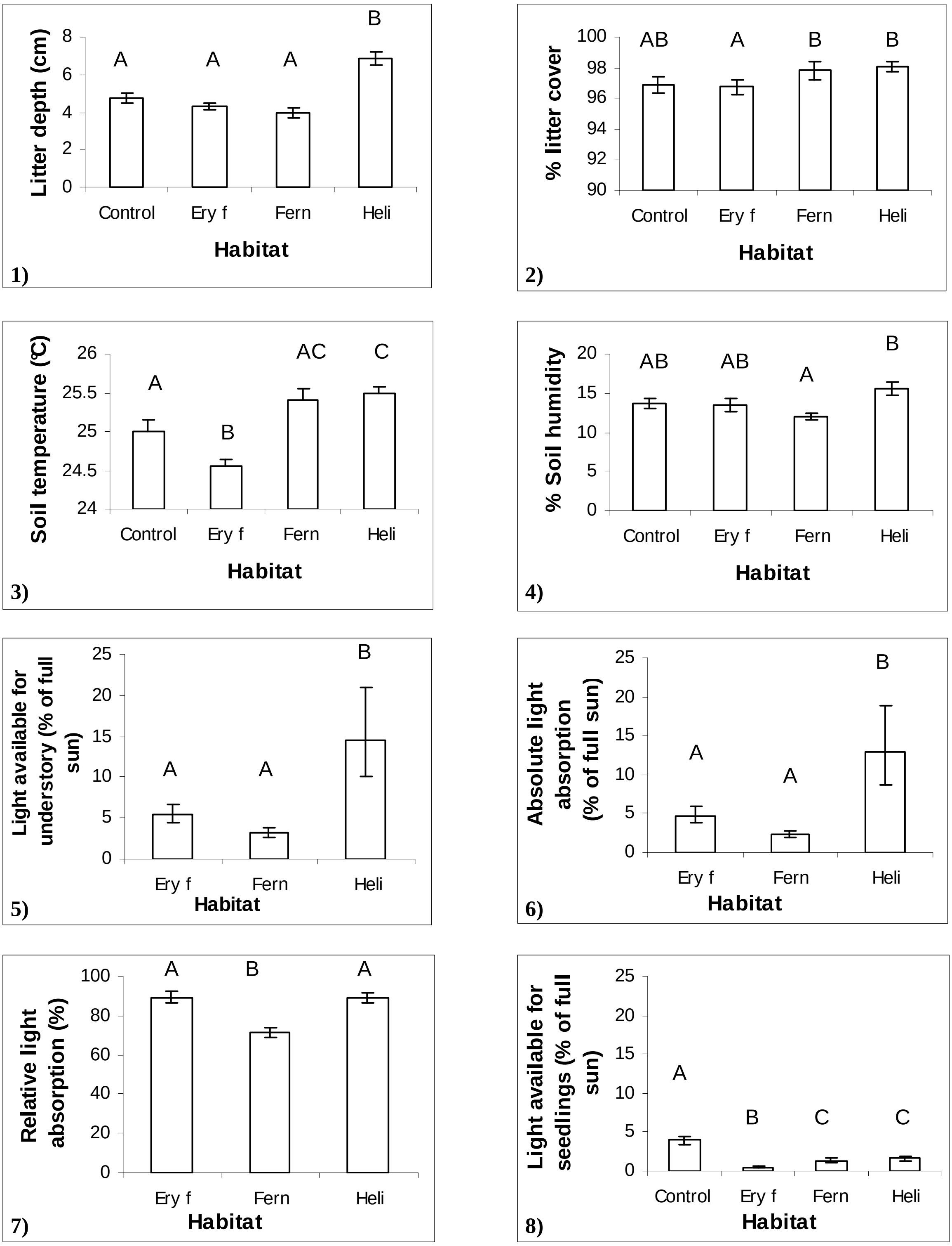

Fig. 5. Abiotic factors compared between the four habitats. Identical letters above bars indicate statistical homogeneity (ANOVA with tukey, $p > 0.05$ and Kruskal Wallis with Mann Withey- U, $p > 0.02$). The data in graph 1, 4, 5 and 6 is normal distributed and in graph 2, 3, 7 and 8 the data is not normal distributed. Error bars indicate the standard error of the mean.

5.2 The effect of dense understory vegetations on tree seedlings

5.2.1 Seedling density

In the 100 plots, we counted 969 seedlings in total, divided over 53 seedling species (Table 3). The number of seedlings/ plot of the 4 habitats are highly significant different (ANOVA, df=3, F=33.733, p=0.00).The number of seedlings is higher in the control plots, and lower in the *Erytrochiton fallax* habitat (Fig6. A).

The number of seedling species per plot (Fig. 6) differed also significantly among habitats (ANOVA, df=3, F=48.211, p=0.00). All the habitats are significantly different from each other (p=0.00) except the habitats with the ferns and the *Heliconia sp.* Figure 6 shows that the number of seedlings and seedling species is the highest in the control habitat and the lowest in the habitat with *Erytrochiton fallax*.

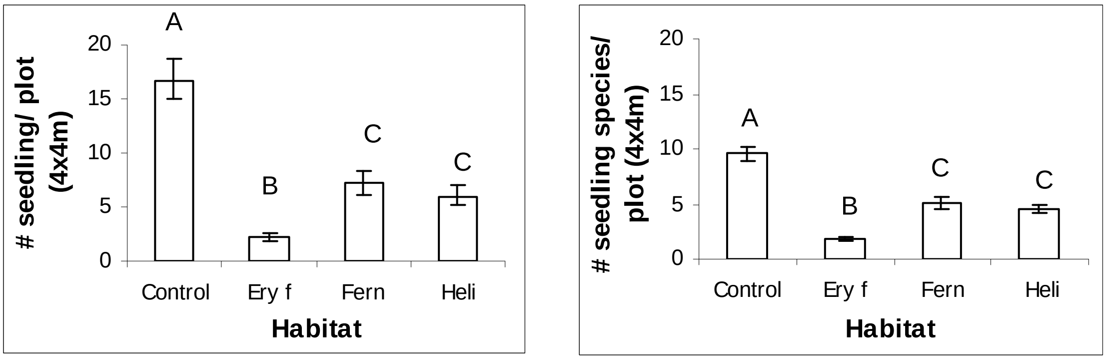

Fig. 6. The average number of seedlings/plot and seedling species/plot for each habitat. Identical letters above bars indicate statistical homogeneity (ANOVA with tukey, p >0.05). Error bars indicate the standard error of the mean.

Table 3. All the seedling species that are found in the 100 plots with their common name, scientific name and family name. Species that are printed bold are commercial species. The species numbers are used in the TWINSPAN vegetation table and in the ordination graph.

Nr	Common name	Scientific name	Family
1	aivaivillo	*Piper sp.*	Piperaceae
2	ajo ajo	*Gallesia integrifolia*	Phytolaccaceae
3	aliso	*Stylogyne ambigua*	Myrsinaceae
4	amarguillo	*Picramnia sellowii*	Myrtaceae
5	amarillo	*Vochysia mapirensis*	Vochysiaceae
6	ambaibillo	*Suessenguthia multisetosa*	Acanthaceae
7	arraigan	*Eugenia cf. florida*	Myrthaceae
8	arraigan hoja grande	Myrciaria sp.	Flacourtiaceae
9	blanquillo	*Ampelocera ruizii*	Ulmaceae
10	cari cari blanco	*Poeppigia procera*	Fabaceae
11	cari cari colorado	*Acacia* sp.	Mimosaceae
12	**cedro**	***Cedrela fissilis***	Meliaceae
13	conservilla	*Alibertia verrucosa*	Rubiaceae
14	**coquino**	***Pouteria nemorosa***	Sapotaceae
15	gabetillo amarillo	*Aspidosperma* sp.	Apocynaceae
16	gabetillo colorado	*Simira rubescens*	Rubiaceae
17	huevo de perro	*Peschiera australis*	Apocynaceae
18	isotouvo	*Sapindus saponaria*	Sapindaceae
19	jichituriqui	*Aspidosperma cylindrocarpon*	Apocynaceae
20	laurel	*Nectandra* sp.	Lauraceae
21	lucuma	*Pouteria macrophylla*	Sapotaceae
22	mani	*Sweetia fruticosa*	Fabaceae
23	manicillo	*Machaerium* sp.	Fabaceae
24	mapabi	*Neea hermaphrodita* [a*]	Nyctaginaceae
25	mapabi hoja grande	*Neea hermaphrodita* [b]	Nyctaginaceae
26	mapajo	*Ceiba samauma*	Bombacaceae
27	**mara**	***Swietenia macrophylla***	Meliaceae
28	momoqui	*Caesalpinia pluviosa*	Caesalpiniaceae
29	Mora	*Maclura tinctoria*	Moraceae
30	murure	*Batocarpus amazonicus*	Moraceae
31	negrillo plateado	*Ocotea guianensis*	Lauraceae
32	negrillo tropero	*Licaria triandra*	Lauraceae
33	**ochoo**	***Hura crepitans***	Euphorbiaceae
34	**ocorocillo**	***Spondias mombin***	Anacardiaceae
35	ojoso blanco	*Sorocea saxicola*	Moraceae
36	ojoso colorado	*Psudolmedia laevis*	Moraceae
37	pablo diablo	*Triplaris americana*	Polygonaceae
38	pacay	*Inga edulis*	Mimosaceae
39	paichane blanco	*Suessenguthia multisetosa*	nk
40	picana	*Cordia alliodora* [a*]	Boraginaceae
41	**picana negra**	***Cordia alliodora*** [b]	Boraginaceae
42	sama blanca	nk	nk
43	sama colorada	*Cupania cinerea*	Sapindaceae
44	sapaimo blanco	*Trichilia pallida*	Meliaceae
45	sapaimo colorado	*Hirtella triandra*	Chrysobalanaceae
46	Sauco Amarillo	*Zanthoxylon sprucei*	Rutaceae
47	sawuinto	*Myrcianthes sp.*	Myrtaceae
48	**serebo**	***Schizolobium parahyba***	Caesalpiniaceae
49	sirari	*Ormosia nobilis*	Fabaceae
50	trompillo	*Guarea guidonia*	Meliaceae
51	**verdolago**	***Terminalia oblonga***	nk
52	yerbo	*Dendropanax arboreus*	Araliaceae
53	**yesquero blanco**	***Cariniana ianeirensis***	Lecythidaceae

nk= not known

* The a or b indicates that the b is a variation of the species a

5.2.2 Seedling species composition

Most species appear in the different habitats, although species number varies significantly among habitats (Fig. 6). Almost all species found in habitats with dense understory vegetation are species that are also found in the control habitat. Only a few species appear in a specific habitat but the abundance of these species is very low.

In two-way ordered table (Appendix 8.3) of the TWINSPAN analysis it was not possible to distinguish a clear cluster of plots with comparable species, representing a given habitat. The TWINSPAN analysis indicates that specific species composition under the dense understory vegetation of *Heliconia sp., Erytrochiton fallax* or fern does not exist. As an illustration of the results of the TWINSPAN analyses, Table 4 presents the 12 seedling species that appear in more than 20 % of the 100 plots (overall frequency >20%). These species occur in the control habitats and in the habitats with an understory, only *Nectandra sp.* and *Pschiera australis*, are not found in the habitat with *Erytrochiton fallax*. The frequency (percentage plots with that species) and average number of a species in a plot differs among habitats. This illustrates that there is no specific species composition under *Erytrochiton fallax, Heliconia sp.* or ferns but that there are differences in terms of frequency of the different species. It is evident that the control plots have the highest frequency and the habitat with *Erytrochiton fallax* the lowest one. The fern and the *Heliconia sp.* plots have intermediary numbers. The seedling species that are most abundant in the habitats are all shade tolerant or partial shade tolerant species.

Table 4. The 12 seedlings that appear in 20 % or more of the 100 plots (overall frequency). The frequency for each habitat or percentage plots with that species in a habitat and average number of a species in a plot are calculated for 12 seedling species. Light classes: ST= shade tolerant, PST= partial shade tolerant, nk= not known. Ery f= *Erytrochiton fallax*

Species		**light**	**overall frequency**	**frequency for each habitat**				**average number of a seedlings/ plot**			
Scientific name	**Common name**	**class**	**all sites**	**Ery f**	**Control**	**Ferns**	**Heliconia**	**Ery f**	**Control**	**Ferns**	**Heliconia**
Licaria triandra	negrillo tropero	nk	52	44	68	72	24	0.8	1.44	1.08	0.28
Ampelocera ruizii	blanquillo	ST	39	12	68	40	36	0.16	3.04	0.84	1.04
Nectandra sp.	laurel	PST	35	0	36	60	44	0	0.68	1.44	0.64
Stylogyne ambigua	aliso	ST	33	12	56	40	24	0.24	1.12	0.76	0.48
Pouteria nemorosa	**coquino**	PST	31	4	44	40	36	0.04	0.76	0.48	0.52
Batocarpus amazonicus	murure	PST	31	4	60	24	36	0.04	1	1.04	0.4
Psudolmedia laevis	ojoso colorado	ST	31	12	48	28	36	0.16	0.92	0.48	1.08
Hura crepitans	**ochoo**	PST	26	20	20	28	36	0.24	0.32	0.4	0.88
Inga edulis	pacay	nk	24	4	56	24	12	0.04	0.88	0.28	0.12
Myrcianthes sp.	sawuinto	PST	23	8	52	20	12	0.08	1.56	0.4	0.16
Eugenia cf. florida	arraigan	ST	21	4	32	28	20	0.04	0.76	0.36	0.4
Peschiera australis	huevo de perro	ST	20	0	44	32	4	0	1.08	0.56	0.04

The Commercial species

The two-way ordered table (Fig. 7) and table 5 indicates that the most commercial species are rare but distributed over all four habitats. Most commercial species are found in the control habitat, where they have the highest number of seedling per plot (except for *Hura crepitans*). The species that are light demanding (LLP) seem to appear more in the control plots. *Pouteria nemorosa* and *Hura crepitans* are the most numerous commercial species and are found in all habitats. Only the frequency and the relative abundance in which they appear are different among the habitats (Table 5).

Table 5. The average number per plot for the commercial seedlings found in the 4 habitats. Light classes: LLP= long lived pioneer (light demanding), PST= partial shade tolerant, nk= not known. Ery f= *Erytrochiton fallax*

Species	**Light class**	**Average number of a seedling/ plot** **Control**	**Ery Fal**	**Ferns**	**Heliconia**
Cedrela fissilis	LLP	0.04	0	0.04	0
Pouteria nemorosa	PST	0.76	0.04	0.48	0.52
Swietenia macrophylla	PST	0.04	0	0	0
Hura crepitans	PST	0.32	0.24	0.4	0.88
Spondias mombin	LLP	0.16	0.04	0	0
Cordia alliodora	NK	0.08	0	0.08	0
Schizolobium parahyba	LLP	0.04	0	0	0
Terminalia oblonga	PST	0.2	0.04	0	0.08
Cariniana ianeirensis	PST	0.16	0	0.04	0.2

5.2.3 Seedling biodiversity

The Shannon diversity index (*H*) is the index that was used to characterize the species diversity of tree seedlings in the habitats. A high value of the Shannon index means that there is a greater number of species present and the individuals are distributed more equitably over the species First the index was measured for each plot. The index value of a habitat is the average of his 25 plots.

Table 6. The Shannon index for each habitat (± Standard deviation)

Habitat	**Shannon index**	**Standard deviation**
Erytrochiton Fallax	0.52	0.47
Control	2.02	0.31
Fern	1.38	0.56
Heliconia	1.31	0.43

The four habitats differed in species diversity (Kruskal Wallis, df= 3, X^2= 61.45, p= 0.00). The diversity of species is highest in the control habitat and the lowest in the habitat with *Erytrochiton fallax* (Table 6). The habitats with ferns and *Heliconia sp.* have similar species diversity.

5.2.4 The impact of the environmental variables on the seedling composition.

The first axis of the CCA explains 21% of the variation, and the second axis explains 17 % (Table 7). The Monte Carlo test indicate that these axes explain the distribution of the species (p=0,002) significantly. The first axis is strongly correlated with environmental factors, cover of *Heliconia sp.* (0.53) and litter depth (0.50), while the second axis is strongly correlated with the cover of *Erytrochiton fallax.*

Table 7. Correlation of species ordination axes with environmental factors and eigenvalues. Ery f= *Erytrochiton fallax*

Factor	**Axis 1**	**Axis 2**
Cover ferns	-0.0065	-0.1936
Cover Heliconia	0.5319	-0.2283
Cover Ery f	0.1595	0.6801
Litter cover	0.3808	-0.1127
Litter depth	0.5014	-0.0501
Available light	0.0262	-0.1124
Eigenvalue	0.214	0.168

The numbers represent the seedling species and the arrows represent the environmental factors (Fig. 7). The length of the arrow is proportional to the magnitude of change in the direction, and for interpretation purpose, each arrow can also be extended backwards through the central origin. The environmental factors, cover of *Erytrochiton fallax,* cover of *Heliconia sp.* and litter depth, have long arrows and this indicates that they have more influence on the species composition. Species near or beyond the tip of the arrow will be strongly positively correlated with and influenced by that environmental factor. Those at the opposite end will be less strongly affected.

The ordination diagram indicates that at a high cover of *Erytrochiton fallax* or *Heliconia sp.* some seedling species are not present and that a high cover of *Erytrochiton fallax* is negative correlated with the factor available light for seedlings. Many seedling species are also negative influenced by the litter depth and this factor is correlated with the cover of *Heliconia sp.* The Canoco analyses indicate that the factors cover of *Erytrochiton fallax*, cover of *Heliconia sp.* and litter depth have an influence on the seedling composition. Few species are standing alone in the ordination diagram, but when we look in the TWINSPAN table, you can see that these species are very rare.

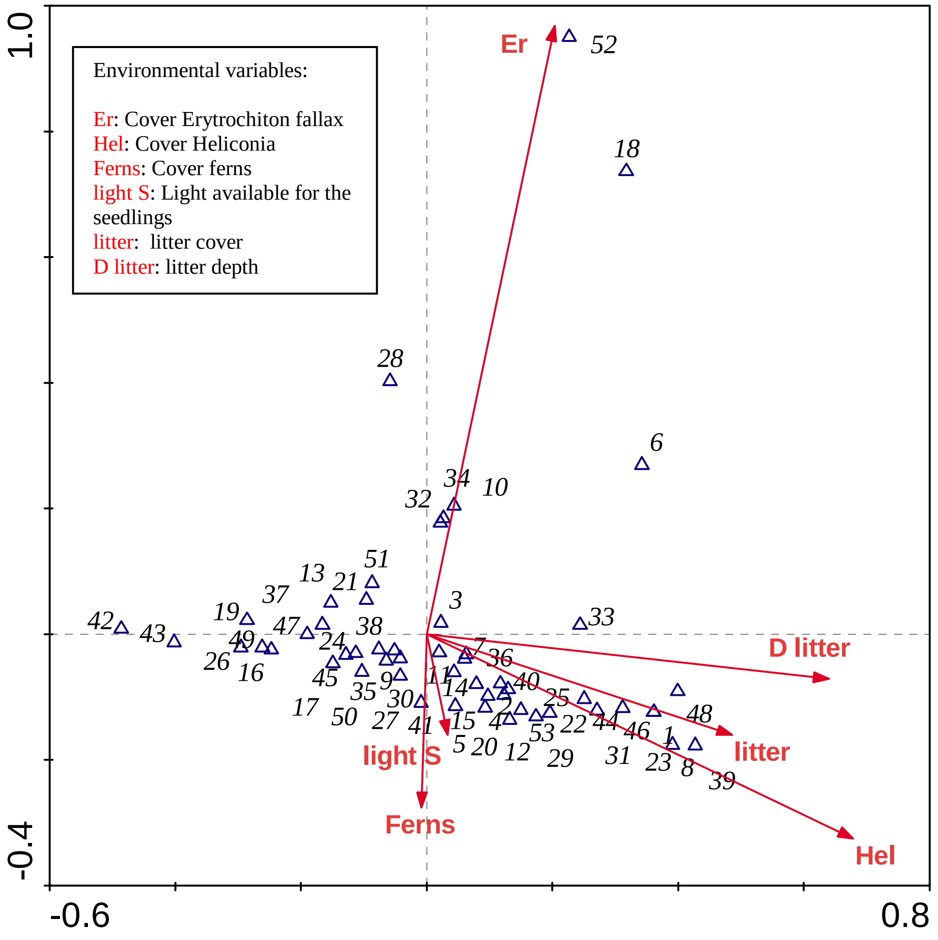

Fig. 7. Ordination diagram, from a CCA analysis. The numbers represent species (table 3)

5.2.5 The impact of the micro climatic variables on seedling density

In this part of the analyses, we have investigated if the micro climate factors, available light for the seedlings and litter cover and depth, have an influence on the number of seedlings and species, in general (n=81).

Available light for the seedlings and litter depth show a significant relation with log number of seedlings (n=81, R^2=0.191, p=0.00) and the number of seedling species (n=81, R^2=0.209, p=0.00) (Table 8). The regression coefficients indicate that the variable available light has a positive effect on the number of seedlings and the number of seedling species but litter depth has a negative effect on these numbers (Table 8). This means that with an increase of light available for the seedlings the number of seedlings and the number of species increase but with an increase of the depth of the litter, these numbers decrease.

At species level, we have investigated if these variables have also this influence on the number of seedlings for the 5 most abundant species in the habitats. Available light has a positive effect and litter depth has a negative effect on the number of *Ampelocera ruizii* seedlings (n=81, R^2=0.10, p=0.006). This species was the only one of the 5 investigated species, which had its density affected by these abiotic variables (Table 8).

Table 8. The effect of the micro climate on the number of seedling species the number of seedlings and for the 5 most abundant species. A forward stepwise multiple regression analysis was performed. The regression coefficients for the different micro climate characteristics included in the regression models are given.

Dependent variable	**n**	**Available light**	**litter depth**	**litter cover**	**R^2**	**P**
Number of seedling species (not normal distributed)	81	0,697	-0,611	~	0,209	0,00
Log(Number of seedlings)	81	0,058	-0,068	~	0,191	0,00
Licaria triandra	81	~	~	~	~	~
Ampelocera ruizii	81	0,276	-0,387	~	0,10	0,006
Nectandra sp.	81	~	~	~	~	~
Stylognyne ambigua	81	~	~	~	~	~
Pouteria nemorosa	81	~	~	~	~	~
	For the 5 species: data not normal distributed					

5.2.6 The effect of the understory vegetations on the growth of the seedlings

Transplant experiment

After 72 days an amount of seedlings had survived but of the seedlings that survived only a few have grown. Most of the seedling had been eaten, did not survive because of shade or drought or disappeared (Table 9).

Table 9. The results of the transplant experiment. Ery f= *Erytrochiton fallax,* Cafe= Cafecillo, Sw m= *Swietenia macrophylla.* Growth rate= Growth rate (cm/day).

Habitat	**Control**		**Ery f**		**Fern**	
Species	**Cafe**	**Sw m**	**Cafe**	**Sw m**	**Cafe**	**Sw m**
Planted	15	30	15	30	15	30
After 72 days:						
Dead	3	3	7	6	0	2
Disappeared	1	16	2	8	1	4
Eaten, dead	2	4	0	5	1	11
Survived	9	7	6	11	13	13
Grown (of survived)	1	1	4	6	1	1
Growth rate	0.009	0.003	0.0008	0.002	0.01	0.0004

In the *Erytrochiton fallax* habitat 6 *Swietenia macrophylla* and 4 *Margaritaria nobilis* seedlings had grown. In the control and fern habitats only 1 *Swietenia macrophylla* and 1 *Margaritaria nobilis* had grown. Of these seedlings growth rates of the 2 species is calculate. In all habitats the growth rates of the species are low. The growth rate of *Margaritaria nobilis* in the fern habitat seems to be the highest but this value is only based on one seedling (Table 9).

The numbers of seedlings that had grown are too low for making a statistical comparison among the habitats. So the effect of the growth on seedlings of the different understory vegetations cannot be statistically tested.

Natural regeneration

Table 10. Height of understory vegetations.

Habitat	**Height understory (cm)**	**Standard deviation**
Fern	62.8	11.37
Erytrochiton fallax	302.2	63.84
Heliconia	254.8	52.85
The understory vegetation cover >80%		

The height of the seedlings that are present in the plots was measured and divided in 10 height classes (Table 10). Most seedlings that were found in the 4 habitats are seedlings of height class 1 and 2. The control habitat is the only habitat where seedlings of all classes were found. In the fern habitat seedlings were divided over seedling class 1 - 8. Most seedlings of the *Heliconia sp.* habitat were seedlings of height class 1 to 4. In the habitat with *Erytrochiton fallax* the major part of the seedlings that were present are seedlings of height class 1 (Fig. 8).

The average height of the fern understory is only 62 cm. In this habitat seedlings found were in average higher than the fern understory, suggesting that they are able to break through the fern carpet and grow higher (Fig. 8). The average height of *Erytrochiton fallax* and *Heliconia sp.* is higher then 2 meters (Table 10). No seedlings were measured higher then 2 meters and nothing can be said about the possibility that seedlings break through these understory vegetations.

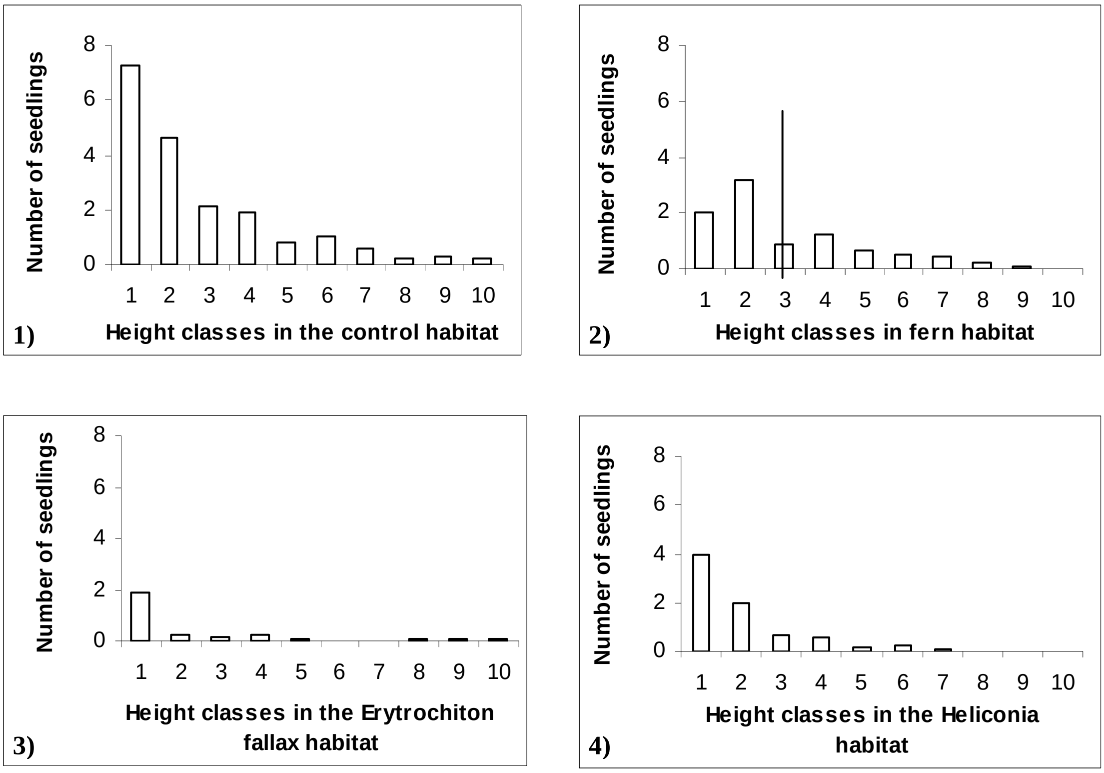

Fig. 8. The average number of seedlings in a height class of each habitat. The horizontal line in height class 3 of graph 2 represents the height of the fern understory.

5.3 Herbivory on tree seedlings

Transplant experiment

In this analysis we used the seedlings of the transplant experiment that survived and that were dead caused by predation (Table 9). The herbivory rate on *Margaritaria nobilis* (ANOVA, df=2, F=1.654, p=0.20) and on *Swietenia macrophylla* (ANOVA, df=2, F=1.980, p=0.144) is not significantly different among the habitats. However, the herbivory rate under *Erytrochiton fallax* tends to be a bit higher then in the other habitats (Fig. 9).

Natural regeneration

The percentage herbivory on a leaf and the percentage predated leaves (at the moment of measuring) were calculated for the four habitats. There is a significant difference among the habitats as a whole for the two variables (Kruskal-Wallis, X^2=21.741, df=3, p=0.00 and X^2= 18.229 df=3, p=0.00). The percentage herbivory on a leaf is significantly higher in the control habitat (23%) than in the other habitats (12-17%) (Fig. 9). The percentage predated leaves is significantly different among almost all habitats except between habitats with *Erytrochiton fallax* and *Heliconia sp.* The percentage of predated leaves is the highest in the habitat with ferns (75%) and in the control habitat (69%) (Fig. 9). In general the percentage herbivory and percentage predated leaves are lower when *Erytrochiton fallax* and *Heliconia sp.* are present and they are higher in the control and the fern habitat (at the moment of measuring).

At species level, we investigated differences in herbivory on *Licaria triandra, Stylogyne ambigua* and *Amphelocera ruizii*. These are the three most abundant seedling species in the four habitats. First, we had determined if one of the species is preferred. In general, the percentage herbivory is lower on *Licaria triandra* and higher on *Amphelocera ruizii* (Fig. 10).
Licaria triandra is lowest preferred but the percentage herbivory and percentage predated leaves is still the highest in the control and the fern habitat, indicating the high level of herbivory in these habitats. *Stylogyne ambigua* has the same percentage herbivory and percentage of predated leaves in all habitats. The herbivory on *Amphelocera ruizii* is significantly the lowest in the *Heliconia sp.* habitat and the highest in the habitat with *Erytrochiton fallax* (Fig. 10). These results suggest that herbivory differs between species and habitats.

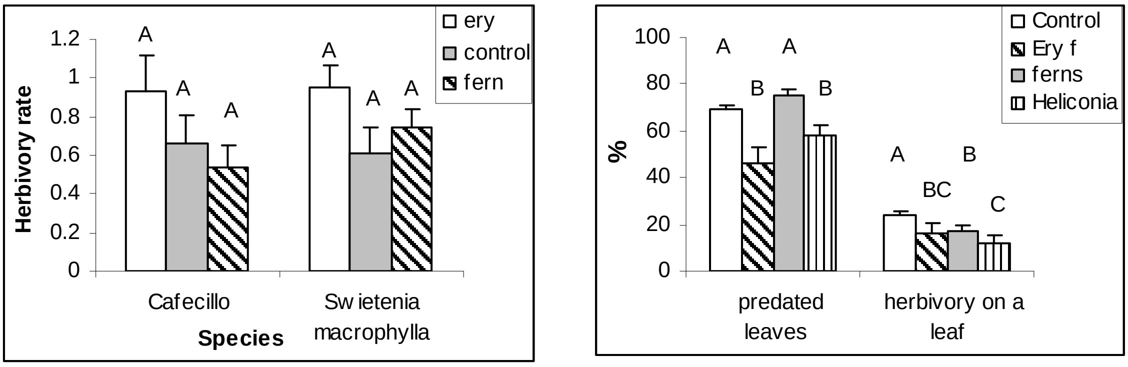

Fig. 9. Graph1= percentage herbivory of a leaf/day of *Margaritaria nobilis* and *Swietenia macrophylla.* Graph 2= The % leaves with predation and the average % herbivory on a leaf of the seedlings of the four habitats. Identical letters above bars indicate statistical homogeneity (ANOVA with tukey, p >0.05 and Kruskal Wallis with Mann Withey- U, p >0.02). The data in graph 1 is normal distributed and in graph 2 data is not normal distributed. Error bars indicate the standard error of the mean.

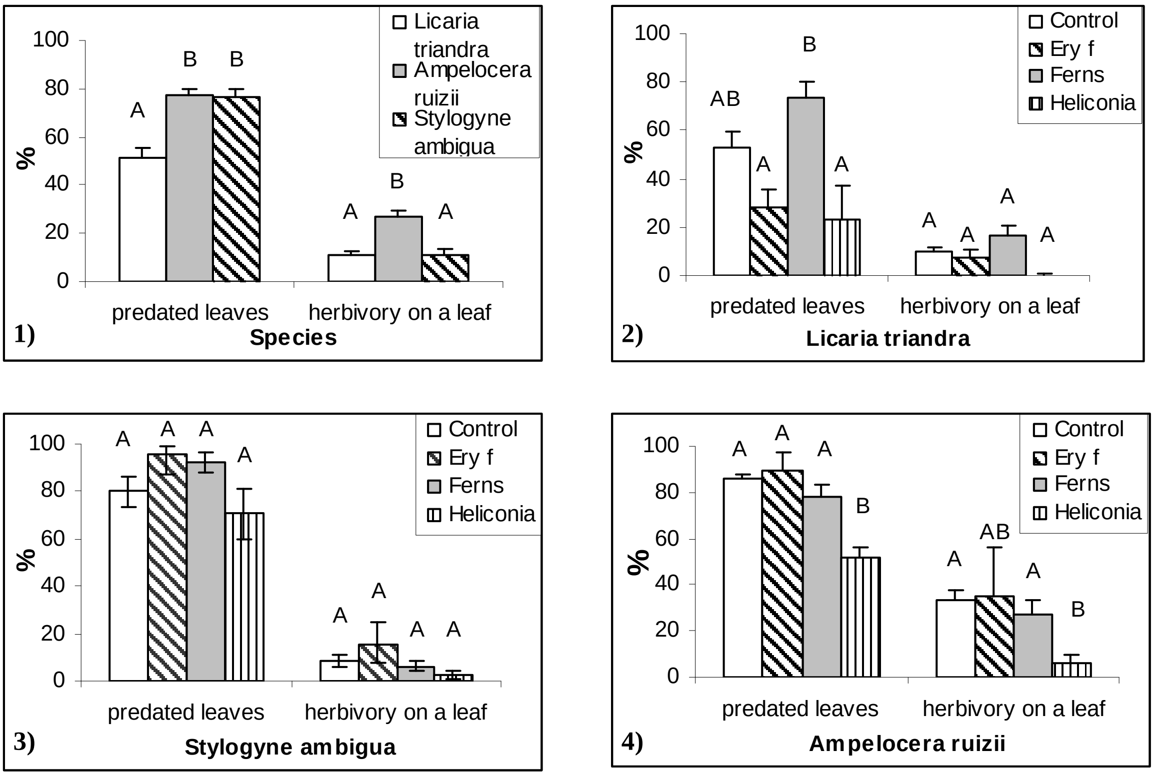

Fig.10. The herbivory (percentage herbivory and % leaves with predation) on *Licaria triandra*, *Stylogyne ambigua* and *Amphelocera ruizii.* Graph 1= comparison of herbivory between the species in general. Graph 1, 2 and 3= comparison between the habitats on species level. Identical letters above bars indicate statistical homogeneity (ANOVA with tukey, p >0.05 and Kruskal Wallis with Mann Withey- U, p >0.02). The data in graph 2 and 4 is normal distributed and in graph 1 and 3 data is not normal distributed. Error bars indicate the standard error of the mean.

6. Discussion

In the present study we have investigated the effect of three dense understory vegetations, *Erytrochiton fallax, Heliconia sp*. and ferns on the regeneration of tree species. Higher densities of this kind of understories in the forests correspond to lower seedling densities; this would suggest that the distribution of these three understory species may affect the abundance and distribution of seedlings of tree species.

6.1 The micro climate under the three dense understory vegetations

In the comparison of the effect of the three understory vegetations, *Erytrochiton fallax, Heliconia sp*. and ferns on the regeneration, the micro climate and environmental conditions play an important role. The way in which dense understories vegetations modify the micro climate or environmental conditions are determine the germination and establishments of tree seedlings (George and Bazzaz 1999, Poorter and Yáskara 2000, Cournag et al 2002, Capers and Chazdon 2004).

The litter cover in the four habitats is more or less the same and varies between 95 and 100 % but we have found differences in litter depth that can affect seedling density. The thickness of the litter layer is dependent of the litter production of the vegetation that is in a given area (Facelli & Picket 1991). In the plots with *Erytrochiton fallax, Heliconia sp*. and ferns, these species cover more than 80% of the plot, and consequently, they are most determining for the litter production. The litter depths in the control habitats and the habitats with *Erytrochiton fallax* and ferns are more or less the same. The litter depth in the habitat with *Heliconia sp.* is higher than in the other habitats. *Heliconia sp.* have huge, elongate, paddle-shaped leaves and they grow quickly, clumps spreading by underground rhizomes (Kricher 1997). Annual litter production of these leaves is so high that the litter layer increases and becomes higher than in the other habitats.
The impact of leaf litter on seedling establishment varies with species, habitat type and timing of germination, suggesting a complex interaction (Molofsky & Augspurger 1992). For example, in a study on seedling response to litter depth, the smaller seeded species were negatively affected by litter but to different degrees. The presence of medium litter reduced the number of seedlings of *Luehea seemannii*, *Cordia alliodora* and *Ochroma pyramidale* but C*eiba pentranda* seedlings were only affected by the deepest treatment (Molofsky & Augspurger 1992).

The soil temperature is the lowest in the habitat with *Erytrochiton fallax* which can be explained by the low light conditions under this vegetation. This low temperature of 24°C of is only 1 or 2°C lower than in other habitats and this small difference has probably no effect on the nutrient supply for the roots. An increase of root zone temperature of 10°C (from 25°C to 35°C) decreased the concentrations of leaf nutrient elements in *Luctuca sativa* (Tan et al, 2002).
The soil humidity in the four habitats varies between 12 and 16.5 %. The differences are small and no remarkable differences among the habitats are noticed. In a similar study, on the effects of fern on the establishment of tree seedlings, the fern cover did not affect soil humidity (George and Bazzaz 1999). The soil temperature and humidity measurements of our study cannot explain the appearance and abundance of species in a habitat. Because these are static measurements for that moment and they examine the differences between habitats (at the moment of measuring). For relating soil temperature and humidity with seed germination, other long term repeated measurements have to be accomplished at specific germination moments (Molofsky & Augspurger 1992).

Light availability for the seedlings is different for each habitat. *Erytrochiton fallax* occurs at shady parts of the forest (5.3 % of full sun) and the light that reaches the understory is further reduced for 90%. This causes very low light conditions under *Erytrochiton fallax* patches (0.51 % of the full sun). Ferns are also found in shady parts of the forest but the reduction in light caused by ferns is only 70%, from 3.2 % of full sun to 1.3 - 3 % of full sun. *Heliconia sp.* grows in high light condition like gaps. But these species also reduces the light by 90 % and the light level decrease from 14.5 % of full sun to 1.6 - 3 % of full sun, which causes low light conditions. In similar studies, the dense understories of shrubs and herbs intercept much of the remaining light in a forest, changing the light quality and quantity beneath their canopies. The understories can reduce the light availability to 1-2% of the full sun (George and Bazzaz 1999, Cournag et al 2002, Capers and Chazdon, 2004).

6.2 The effect of dense understory vegetations on tree seedlings

We found that dense understory vegetation of *Erytrochiton fallax, Heliconia sp.* and ferns decrease the density of seedling and seedling species. The number of seedlings and seedling species is positively correlated with each other. Highest numbers of seedlings and seedling species are found in the control habitat, while the lowest numbers are found under *Erytrochiton fallax.*
Seedling diversity is related with the number of species and seedlings that are found in a habitat.
The lowest diversity was found in the habitat with *Erytrochiton fallax* and the highest in the control habitat. Diversity in the habitats with ferns and *Heliconia sp.* were lower than in the control habitat.

The canoco analyses indicate that an understory vegetation of *Erytrochiton fallax*, *Heliconia sp.* and fern have an influence on the seedling composition. Some seedling species do not occur under these understories but almost all species occur in the control habitat. Indicating that the species composition under a specific dense understory is not specific. Only few species appear in a specific habitat but the abundance of these species is very low.
For a fern understory in the Harvard forest in Massachusetts, USA also a reduction of seedling density and a change in seedling composition was found (George and Bazzaz 1999).

Two micro climate factors had a significant effect on the seedlings and seedling species.
The factor available light had a positive effect on the number of seedlings/ seedling species and the factor litter depth had a negative effect on the number of seedlings. The availability of light plays a major role in growth, survival and establishment of tropical seedlings. The survival of seedling under certain light conditions depends on the species light demand (or shade tolerance) (George and Bazzaz 1999, Capers and Chazdon 2004, Sork 1987, Cournag et al 2002, Capers and Chazdon 2004)

In the present study most seedlings that are found under the dense understory vegetation are shade tolerant and partial shade tolerant species. Seedlings of shade tolerant species can germinate and survive under low light condition of 1 - 2 % of the full sun but survival and growth increase rapidly when light gaps occur (Canham 1985, Poulson and Platt 1989, Kitajima 1994, Cournag et al 2002, Poorter and Arets 2003, Capers and Chazdon, 2004). This explains that most seedlings can occur in the different habitats. But the frequency and abundance of seedlings is affected by the amount of sunlight available.
The highest numbers of seedlings in the control habitats can be explained by the high light conditions that are found of 3 - 6 % of the full sun. Under *Erytrochiton fallax* there is a very low light condition (0.51 % of the full sun) which explains the very low number of seedlings and species. Light conditions of 1.3 - 3 % of full sun are found under fern vegetation, more light can reach the seedlings and this result in a higher seedling density. The density of the fern carpet is depended of the season, in the dry period leaf shedding can occur and temporary more light can reach the seedlings (Den Ouden 2000). Fern understories have negative impact on the regeneration but because of their low height and season dependent density, it is possible for seedlings to establish, gather enough sunlight and to break through the dense fern layer. Under the dense understory vegetation of *Heliconia sp.* light conditions are 1.6 - 3 % of full sun. But *Heliconia sp.* produces also huge leaves what causes an increase in litter depth. The accumulation of litter results in a build up of a thick ectorganic profile and this thick layer may present a physical barrier for

newly germinating seedlings to establish their roots into the soil or to emerge below the litter (Den Ouden 2000). These two factors together create an unsuitable habitat for seedlings and may inhibit the regeneration of tree seedlings under *Heliconia sp.* Because *Heliconia sp.* is found in high light conditions, it is possible for seedlings that can germinate in the thick litter layer to gather enough light (through sunbeams) and become bigger.

The effect of dense understories of *Erytrochiton fallax*, *Heliconia sp.* and ferns on the growth of tree seedlings could not been determined in this study. The methods we applied were not capable of answering this question. To determine this effect by way of a transplant experiment more seedlings have to be used in all the habitats and more repeated measurements have to be made over much longer time period. This will provide you with more data to investigate this effect.

6.3 Herbivory on tree seedlings

The herbivory on tree seedlings was lower in the *Erytrochiton fallax* and *Heliconia sp.* habitats and the highest in the fern and control habitats. On species level, we have investigated difference in herbivory on *Licaria triandra, Stylogyne ambigua, Amphelocera ruizii* and on the species of the transplant experiment *Margaritaria nobilis* and *Swietenia macrophylla.* The results varied among the species, so that no general pattern could be determined. These results may be due to the fact that the amount of herbivory of a seedling is determined by many factors. For example, species preference, seedling defences against herbivores, which herbivores occur below an understory vegetation, time of measuring, which food sources are available in a habitat, etc (Sork 1987, Kricher 1997, Cash and Fulbright 2005).

Tropical rain forest leaves are subjected to potential danger of herbivory and pathogens year-round. It is possible that these factors reduce the growth or the change of survival, depended of the plant species defences against herbivores. Many tropical plants have defence, like chemicals, spins and thorns against herbivores as well as against invasive pathogenic bacteria and fungi. Most seedlings, depending of the species, contain a variety of these (Kricher 1997).

A dense understory of herb or shrubs can also provide habitats and shelter for both seed and seedling predators. They can feel more secure in this kind of vegetations than in more open vegetations or even than in the natural regeneration of the forest. The dense understory can change the availability of food resources and provide more fruits, seeds, seedlings or other food resources (Sork 1987, Cash and Fulbright 2005) and will attract more predators.

To be able to investigate this kind of factors and to determine the differences in seedling density and composition in the four habitats based on herbivory, more specific research is necessary over a longer time period.

6.4 Conclusion and recommendations

The most important effect of the dense understories of *Erytrochiton fallax, Heliconia sp.* and ferns on the micro climate variables is the reduction of light available for the seedlings. Dense understory vegetations of ferns reduce the light availability by 70 % and the dense understory vegetations of *Erytrochiton fallax* and *Heliconia sp.* up to 90%. Another important effect is found in the *Heliconia sp.* habitat; this dense understory vegetation creates habitats with a higher thickness of litter.

In the present study most seedlings that are found in the four habitats are shade tolerant and partial shade tolerant species. Seedlings of shade tolerant species can germinate and survive under low light conditions of 1-2 % of full sun but survival and growth increase rapidly when light gaps occur (Canham 1985, Poulson and Platt 1989, Kitajima 1994). This explains that most of the species can occur in the four habitats and that there is no specific species composition in each of the habitats. But the number of seedlings and species is affected by the amount of sunlight available. The highest numbers of seedlings and seedling species are found in the control habitat which has the highest level of light availability (3 -6 % of the full sun). Under *Erytrochiton fallax* there are very low light conditions (0.51 % of the full sun) explaining the very low number of seedlings and seedling species. In general, dense understories create environmental conditions that are unsuitable for seedling establishment by decreasing light availability and in some cases increasing leaf litter depth, resulting in a decrease of overall seedling density and diversity below its canopy.

In the sustainable tropical forestry the selective logging systems rely on the natural regeneration to produce the next crop of timber. These systems seek to maintain commercial productivity of logged forest by conserving the natural regeneration potential of the forest. In natural regeneration systems it is assumed that the regeneration will occur naturally, beginning with an acceptable production of seedlings and some of these will eventually become harvestable adult trees. This study suggests, however, that under dense understories of *Erytrochiton fallax*, *Heliconia sp.* and ferns the natural regeneration, especially from light demanding species, is inhibited. The dense understories decrease overall seedling density and diversity below its canopy.

Consequently, if these dense patches of vegetation occur in large parts of the forest, it is recommended to remove or to decimate this understory vegetation when it is feasible and profitable, to guarantee a good natural regeneration of commercial tree species.

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8. Appendix

8.1 The study design of the project LTSRP

Treatment plots are 27 hectares and are situated in a total of three blocks in the tropical humid forest. Each block contains four treatment 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 (Fredericksen 2000).

Specific goals of the LTSRP experiment include the following (Fredericksen 2000)
- Evaluate the sustainability and cost-effectiveness of individual silvicultural treatments and alternative silvicultural systems.
- Increase understanding of stand dynamics and other biological processes in Bolivian forests.
- Determine the impact of silvicultural treatments on biodiversity and forest ecosystem function.
- Assess the compatibility of forest management for timber with other forest management options.

LTSRP has also delineated some projects, which are likely to be conducted at each site, these are the following (Fredericksen 2000).
1. Treatment costs and timber yields.
2. Effects of treatments on tree growth, stand composition, and stand quality.
3. Recruitment and growth of regeneration.
4. Damage to residual stands and soils.
5. Impacts on plant and animal communities.

The study proposed here will mainly focus on the second and third specific goal of the LTSRP. This study also fits extremely well in the third delineated project and thus will indeed focus on recruitment and growth of regeneration.

The following table will show the species included as future crop trees in treatments and these species are the species of commercial value.

Table 11. Future crop tree species.

Species(latin name)	**Common name (Spanish)**
Swietenia macrophylla	Mara
Cedrela odorata	Cedro
Cedrela fissilis	Cedro
Ficus glabrata	Bibosi colorado
Hura crepitans	Ochoó
Cariniana ianeirensis	Yesquero blanco
Cariniana estrellensis	Yesquero negro
Hymenaea courbaril	Paquió
Centrolobium microchaete	Tarara amarilla
Cordia alliodora	Picana negra
Pouteria nemorosa	Coquino
Spondias mombin	Ocorocillo
Terminalia amazonica	Verdolago
Schizolobium amazonicum	Serebó
Tabebuia serratifolia	Tajibo amarillo

Management of the treatments

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 if 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. FCTs 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 sprouts 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.

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.

8.2 Plot locations in field

With the selection criteria described in Chapter 3.2 the 100 plots are set up in some treatment plots of the 3 blocks of the Long-Term Silvicultural Research Project (LTSRP) (Fig.3).
The distribution of the plots of the 4 habitats is as follows.

- The control habitat: 9 plots in block 1, LTSPR control treatment and 16 plots in block 2 LTSRP intensive treatment
- The *Erytrochiton fallax* habitat: 25 plots with in block 2, LTSRP intensive treatment
- The fern habitat: 25 plots in block 1, LTSPR control treatment
- The *Heliconia sp.* habitat*:* 25 plots. in block 3, LTSPR control treatment

The exact locations of the 100 plots in the treatment plots of LTSRP are expressed in coordinates (Table 11). The coordinates are used in the LTSRP.

Table 11 : The exact locations of the plots

		Blok	**LSRP**	**Coordinates**	
Habitat	**Plotnr**	**of LTSRP**	**Treatment**	**X**	**Y**
Erytrochiton fallax	1	2	Intensive	550	275
Erytrochiton fallax	2	2	Intensive	550	325
Erytrochiton fallax	3	2	Intensive	550	350
Erytrochiton fallax	4	2	Intensive	500	345
Erytrochiton fallax	5	2	Intensive	500	325
Erytrochiton fallax	6	2	Intensive	500	310
Erytrochiton fallax	7	2	Intensive	450	370
Erytrochiton fallax	8	2	Intensive	400	360
Erytrochiton fallax	9	2	Intensive	350	400
Erytrochiton fallax	10	2	Intensive	350	365
Erytrochiton fallax	11	2	Intensive	320	400
Erytrochiton fallax	12	2	Intensive	300	400
Erytrochiton fallax	13	2	Intensive	275	400
Erytrochiton fallax	14	2	Intensive	250	422
Erytrochiton fallax	15	2	Intensive	300	350
Erytrochiton fallax	16	2	Intensive	500	260
Erytrochiton fallax	17	2	Intensive	350	385
Erytrochiton fallax	18	2	Intensive	250	400
Erytrochiton fallax	19	2	Intensive	250	375
Erytrochiton fallax	20	2	Intensive	240	433
Erytrochiton fallax	21	2	Intensive	220	427
Erytrochiton fallax	22	2	Intensive	200	220
Erytrochiton fallax	23	2	Intensive	150	270
Erytrochiton fallax	24	2	Intensive	150	250
Erytrochiton fallax	25	2	Intensive	150	225
Control	26	2	Intensive	500	175
Control	27	2	Intensive	500	118
Control	28	2	Intensive	500	85
Control	29	2	Intensive	400	125
Control	30	2	Intensive	400	225
Control	31	2	Intensive	400	248
Control	32	2	Intensive	350	250
Control	33	2	Intensive	350	120
Control	34	2	Intensive	350	170
Control	35	2	Intensive	300	175
Control	36	2	Intensive	300	255
Control	37	2	Intensive	250	300
Control	38	2	Intensive	200	330
Control	39	2	Intensive	100	150
Control	40	2	Intensive	150	190
Control	41	1	control	50	340
Control	42	1	control	150	75
Control	43	1	control	250	50
Control	44	1	control	350	125
Control	45	1	control	350	240
Control	46	1	control	300	175
Control	47	2	Intensive	200	150
Control	48	2	Intensive	400	300
Control	49	2	Intensive	400	360
Control	50	2	Intensive	400	375

Habitat	**Plotnr**	**Blok of LTSRP**	**LSRP Treatment**	**Coordinates X**	**Y**
Fern	51	1	control	300	75
Fern	52	1	control	300	200
Fern	53	1	control	300	325
Fern	54	1	control	250	350
Fern	55	1	control	250	300
Fern	56	1	control	250	200
Fern	57	1	control	250	75
Fern	58	1	control	250	25
Fern	59	1	control	150	250
Fern	60	1	control	150	300
Fern	61	1	control	100	300
Fern	62	1	control	100	150
Fern	63	1	control	100	0
Fern	64	1	control	50	175
Fern	65	1	control	50	300
Fern	66	1	control	150	325
Fern	67	1	control	125	0
Fern	68	1	control	60	0
Fern	69	1	control	50	450
Fern	70	1	control	140	440
Fern	71	1	control	100	225
Fern	72	1	control	100	30
Fern	73	1	control	150	275
Fern	74	1	control	150	420
Fern	75	1	control	160	440
Heliconia sp.	76	3	control	600	15
Heliconia sp.	77	3	control	540	175
Heliconia sp.	78	3	control	535	345
Heliconia sp.	79	3	control	400	35
Heliconia sp.	80	3	control	400	55
Heliconia sp.	81	3	control	400	75
Heliconia sp.	82	3	control	370	0
Heliconia sp.	83	3	control	350	20
Heliconia sp.	84	3	control	360	145
Heliconia sp.	85	3	control	350	250
Heliconia sp.	86	3	control	350	300
Heliconia sp.	87	3	control	350	400
Heliconia sp.	88	3	control	300	375
Heliconia sp.	89	3	control	300	325
Heliconia sp.	90	3	control	300	270
Heliconia sp.	91	3	control	300	125
Heliconia sp.	92	3	control	250	200
Heliconia sp.	93	3	control	250	275
Heliconia sp.	94	3	control	250	315
Heliconia sp.	95	3	control	250	350
Heliconia sp.	96	3	control	250	425
Heliconia sp.	97	3	control	200	360
Heliconia sp.	98	3	control	180	475
Heliconia sp.	99	3	control	150	265
Heliconia sp.	100	3	control	320	0

8.3. TWINSPAN analyses: Two way ordered table

```
                                              1
              9 11233 23314995 34494222335566903445566778852588  1234444556666777777888889999918    11112566773122
              8607701532418147780799689395908205364837067915626126161245022459124578014580356753348934892316397204

10  Poeppigi  --1------------------------------------------------------1--1------------1----------------------------  00000
22  Sweetia   ---------11-------------------------------------1---------------------------11-2--------------------  00000
34  Spondias  ----1------------------1--------------------------------2---------------------------1---------------  00000
35  Sorocea   ------1---1----------1-1------------------------------22---------1----------------------------1-----  00000
 2  Gallesia  2-----4-----------------1--------------------------------------------1----1-1-1---------------------  000010
13  Aliberti  -------1-41----------------------1--3---------------------------------------------------------------  000010
16  Simira r  ----112--6-------------------------------------------1----1--2--------------------------------------  000010
21  Pouteria  --------111---1-------1--2----------------------------11-------------------------------------2------  000010
26  Ceiba sa  ------1--1------------------------------------------------------------------------------------------  000010
28  Caesalpi  -122114--23-1---------1---------------------------------------------------------------211-----------  000010
37  Triplari  ----------1-----------------------------------------------------------------------------------------  000010
45  Hirtella  -----1---21------13--1------------------------------------1----1----------1-------------------------  000010
51  Terminal  ----3-2-------------------------1------------------------------------1--------------------1---------  000010
52  Dendropa  --1-------------------------------------------------------------------------------------------------  000010
17  Peschier  ---------57----3-12---12-513-1---1-1--2-1----------------1--2--1-----1---------------------1--------  000011
19  Aspidosp  ------1--1-----------2-1----------------------------------------------------------------------------  000011
24  Neea her  ----------2----------1-----1----------------1-------------------------------------------------------  000011
47  Myrciant  -----171-12----11-32-23941---3-2-2---22---------------1-------2-------1--1--------------------------  000011
 3  Stylogyn  ---------43--------1-133111133-41--211-------------1--4211-125---11-1----41-------3-2----------1----  0001
53  Carinian  ----------1-111-----1--------1------------------------1--1--------------1------1--------------------  0001
 9  Ampeloce  -----22--29-991829666334-522213127111-1-1---1-----------1--1--------1------1--1---1---1--------1----  0010
30  Batocarp  ----213---112111-1-1--16--1--1---11211-1--119--------1----1------------2-1-11----1------------------  0010
38  Inga edu  ----11---11-11---214--3-2-22-1---1--11-11--1----------1---1------------1-------1-------------------  0010
43  Cupania   ------1---1-----------33---------1--1---------------------------------------------------------------  0010
14  Pouteria  ----1-1------21--1-----231121-1313311112-12-11--1------2----1--1---------1---1----------------------  0011
15  Aspidosp  --------------------1-----1-------------------------------------------------------------------------  010000
25  Neea her  -----------------------------------1----------------------------------------------------------------  010001
40  Cordia a  ---------------------------------------1------------------------------------------------------------  010001
42  sama bla  ----------------------2-----------------------------------------------------------------------------  010001
49  Ormosia   ---------------------1-411-------1--1--2----1-------------------------------------------------------  010001
41  Cordia a  ----------------------1----------1------1-------------------------1---------------------------------  01001
50  Guarea g  ------------------------1--1-----1--------------------------------------------------------------1---  01001
27  Swieteni  -----------------1----------------------------------------------------------------------------------  0101
29  Maclura   --------------4---------------------------------------------------------------------------------3---  0101
 4  Picramni  -----------------11-----------------------------1-----------------------------------------------1---  01100
20  Nectandr  ------------1--6-------21-111-1--44-1351--113-515-----211--12---2--2111112-----1-------------2------  01100
31  Ocotea g  -----------------1--1----------1------------------------1----------1--1-----------------------------  01100
36  Psudolme  ------------39432421--31----1---122--1------2----1--1--21112-12------2---11-1-11--------------------  01100
 7  Eugenia   -------------1-------9---1-------111---21---1---1--1-22---1--211-1--------1--6-1--------------------  011010
12  Cedrela   ----------------------------1-------------------------1---------------------------------------------  011010
18  Sapindus  --------------------------------------------------------------------------------11--------2---------  011011
32  Licaria   1-------------11-251-3514131-1---2--11--1---5-1---1-11212112112-2--2------11--2---231126111112111---  011011
46  Zanthoxy  ---------------------------------------------------------------------------------1--------------2---  011011
44  Trichili  ------------------------------------------------------2-----------------------------------------2---  011100
 1  aivaivil  ------------------------------------------------------1---------------------------------------------  011101
 5  Vochysia  ----------------------------------------------------------------1-----------------------------------  011101
 6  Suesseng  ------------------1------------1-------------3-2----------------------------1-----------------------  011101
 8  arraigan  ------------------------------------------------------------------------------2---------------------  011101
11  Acacia s  --------------------------------------------------------12------------------------------------------  011101
23  Machaeri  ------------------------------------------------------2---------------------------------------------  011101
39  Suesseng  ---------------------------------------------------------------------2-----1-1----------------------  011101
48  Schizolo  --------------------------------------------------------1-------------------------------------------  011101
33  Hura cre  --1--1-------4-1----------1-------3-1--------1---21---1-2----31121----1119-1-22--1------1-----------  01111
 0  Nothing   -------------------------------------------------------------------------------------------------111  1

              0000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000111
              0000000000011111111111111111111111111111111111111111111111111111111111111111111111111111111111111
              0111111111100000000000000000000000000000000000111111111111111111111111111111111111111111111111111
               000000111100000000000111111111111111111111111000000000000000000000000000000000000000111111111111111
               000111    000011111100000000000011111111111100000000000000000000000000000000000110000000000000001
                             01111101111111111100000000000100001111111111111111111111111111111
```

Two way ordered table of species versus plots, La Chonta. Values indicate abundance classes. 1= 1 individual, 2= 2 individuals… 9 ≥9 individuals.
Plot 1-25= plots with *Erytrochiton fallax*, plot 26-50= control plots, plot 51-75= plots with ferns, plot 76-100= plots with *Heliconia sp.*