TREE REGENERATION AFTER LOGGING IN A BOLIVIAN DRY FOREST

by
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Contents

Summary

Selective logging causes important changes in the forest microclimate/environment, which can affect regeneration of tree species. As tree species differ in ecological characteristics they will probably respond differently to changes in forest environment. This study focuses on the regeneration of a broad range of tree species in a dry tropical forest in Bolivia. The main objectives are 1) to find the ecological characteristics of commercial and common tree species on shade tolerance, habitat preference, growth response and mortality, and 2) to determine the response of these species to logging.

The study was carried out in a dry tropical forest in Eastern Bolivia. Saplings (<3 m height) of 24 tree species were measured in unlogged forest and in three logged areas in which different logging treatments were applied. The logging treatments were different in the logging intensity and a combination of silvicultural management. Height measurements were done in 2003 and 2005. The 2005 measurements also included presence of lianas, characterisation of the light environment Crown Illumination Index and the habitat.

Canopy openness and habitat composition were different between logged and unlogged forest areas / treatments, but not among logging treatments. Canopy openness differed significantly between habitats. The lowest canopy openness was found in undisturbed habitat followed by natural habitat, logging gaps and skidder trails. No significantly different canopy openness was found between logging gaps and skidder trails.

The study species strongly differed in distribution over light conditions: the percentage saplings in shade ranged from 24% to 94% among 24 species. Differences in light conditions among species were also apparent from height–light trajectories - curves that relate Crown Illumination Index to tree height. These trajectories differed considerably among 13 of the study species. A significant correlation was found between shade tolerance conditions of species and differences in growth in higher light environments.

Sixteen of the 24 study species had a lower density in the logging treatments compared to the control treatment while the density was higher in logging treatments for 6 species. Of the species with economic value, 6 had lower densities, while 4 had a higher density in the logging treatments. The 15 species that were found with more than 70% of its individuals in shade conditions only one species had a slightly higher density in logging treatments. While from 8 species, which were found with less than 70% of its individuals in shade conditions, there were 4 species with a higher density in logging treatments. These results have not been statically tested.

Nine of 22 tree species were non-randomly distributed over habitats, suggesting that these species have a preference for certain habitats. Four of those 9 species showed a preference in habitats created by logging (skidder trails and logging gaps) while the other five species showed preferences for natural habitats.

Only the species *P. rhamnoides* was found to have a significantly higher growth in the intensive treatments while *P. rhamnoides* was found to have a negative preference for habitats cause by skidders and logging. Six species were found to have significantly different growth rates between habitat categories. The growth rates were found to be generally higher in the habitats disturbed by skidder or logging. Strangely these higher growth rates in these habitats are not always reflected in habitat preference of these six species tree species, differences in densities were observed between the logged treatments and the control treatment.

These results show that tree species differ strongly in shade tolerance, growth and light-response. These ecological characteristics can be useful to understand logging effects on seedling regeneration however these results can’t give a straightforward prediction on how species will responded to logging. Furthermore most species have a preference for a natural habitat and 66% of the species have a higher density in the control treatment. A logging system in which undisturbed areas, small gaps and large clearings with soil compaction are combined so different species with different habitat preferences will be both favoured is recommended. The results suggested that regeneration of trees species in the dry tropical forest is slightly decreased due to logging.

1. Introduction

Tropical forests are generally considered as one of the most diverse ecosystems on this planet (Gentry 1995, Wilson 1995, Arets 2005). Large differences in tree species diversity are found in tropical forests between continents and regions (Gentry 1988, ter Steege 2000, Arets 2005). Due to the high (tree) species diversity found in the humid tropics most research on tropical forest has been focussed on regions with wet forests, consequently considerably less attention has been given to drier deciduous tropical forests (Parker *et al.*1993).

Bolivia contains one of the largest tropical dry deciduous forests, which is known as the Chiquitano dry forest. In comparison with other deciduous forests in countries like Brazil, Paraguay and Argentina, the Chiquitano dry forest is still rather intact and undisturbed (Parker et *al.* 1993, Fredericksen & Mostacedo 2000a). Although the Chiquitano forest is historically well conserved recent deforestation has dramatically increased due to infrastructural development, low land prizes and a shift to an export oriented economy (Pacheco 1998, Markesteijn 2004).

Recently more research attention has been given to the ecology of dry forests because this forest is one of the least understood tropical forest type (Fredericksen & Mostacedo 2000a). There is a growing interest from the Bolivian government and international development groups in the development and implementation of sustainable management in these forests (Heuberger & Fredericksen 2002). Sustainable forest management can make a substantial contribution to the conservation of the dry tropical forest by generating a stable economic income, which would avoid that the forest will be converted to other land-uses, while maintaining a large part of the biological integrity and biodiversity of the forest. It is difficult to find the right balance in this trade-off decision (Pinard *et al.*1999, Heuberger & Fredricksen 2002). Ecological research can assist in developing management guidelines for sustainable forest management.

1.1 Regeneration after logging

Vital to any sustainable forest management system is the regeneration of commercial tree species (Mostacedo & Fredericksen 1999, Fredericksen *et al.* 2000b). Conventional selective logging has been shown to reduce the regeneration of commercially interesting species (Pinard *et al.* 1996, Fredericksen & Mostacedo 2000a, Jackson & Fredericksen 2002). One way to secure or increase natural regeneration of commercial trees within the residual forest is by adjusting silvicultural treatments (Pinard *et al.* 1999, Rheenen & Boot 2004). Silvicultural methods like extra soil disturbance, clearing of gaps from competitive vegetation and enrichment planting are used to improve the regeneration of tree species in the forest. Changing the intensity and combination of silvicultural treatments will result in differences in the seedling composition and growth rates of tree seedlings. The differences among treatments depends also on environmental conditions during harvest, harvesting intensity, felling methods used, and the care with which harvesting is carried out (Ewel & Conde 1980, Pinard *et al.* 1999).

In logged forests with large logging gaps tree species that regenerate well in high light and are fast growing will have a much higher abundance compared to slower growing shade tolerant species (Pinard *et al.* 1999). In contrast shade tolerant species that have a slow reaction to high light conditions with the ability to germinate and persist in shade will be favoured in small logging gaps (Pinard *et al.* 1999, Poorter & Aerts 2003, Whitmore 1996, Brokaw and Busing 2000). The shade tolerance of tree species, however, may differ during their life cycle (Zagt 1997). Various traits determine in what sequence of environments species will perform better compared to other species.

In highly disturbed forests tree seedlings experience more competition from fast growing herbs and pioneer trees, which can greatly decrease the regeneration success of commercial seedlings (Fredericksen & Mostacedo 2000a). Additionally lianas establishment have a negative influence on growth and survival of seedlings (Putz 1984, Pérez *et al.* 2004). Some studies suggest that liana distribution is less on trees with certain architectural characteristics, like high tree flexibility and long leaves (Putz 1894, Alvira *et al.* 2004). Another study found little evidence for a difference in liana infestation among tree species and suggested that liana distribution was clumped (Pérez et al. 2004). This would mean that infestation depends more on whether a tree is located near a cluster of lianas than its specific architectural characteristics. When lianas are cut before logging there will be a significant less lianas found after logging compared to gaps were no lianas were cut (Alvira *et al.* 2004)

1.2 Difference in regeneration between species

Due to the enormous variability in forest conditions, species composition and ecology among specific forest types, research is necessary to determine the appropriate combination of silvicultural practices to improve regeneration of a commercial tree species (Pinard *et al.*1999, Kennard *et al.* 2002). Several previous studies conclude that an increase in disturbance provide the right micro conditions for certain commercial species to regenerate (Fredericksen & Mostacedo 2000a, Kennard *et al.* 2002, Jackson & Fredericksen 2002). Although seedlings of certain species established and grew better with soil and canopy disturbance other species decreased in density. When high-intensity burns created high soil temperatures it was found that the densities of viable seeds were reduced and shade intolerant species were favoured over shade tolerant species (Kennard *et al.* 2002, Kennard *et al.* 2004). Kennard suggests a mixture of logging intensities to favour the different regeneration strategies of species in tropical dry forests.

This study considered the regeneration of a broad range of tree species in a tropical dry forest in Bolivia. Saplings of 24 tree species were measured in one control treatment and three logging treatments with different harvest intensities and silvicultural treatments. The main objectives are 1) to find the ecological characteristics of the selected tree species on shade tolerance, habitat preference, growth response and mortality, and 2) to determine the response of these species to different logging treatments.

2. Method

2.1 Study site

The study site is located in the INPA forest private property of the INPA Parket Company. The property has an area of 30,000 ha, and it is located 40 km to the east of the town of Concepcíon (16°6'S, 61°42'W), in the province Nuflo Chávez, department of Santa Cruz in Bolivia. The average temperature is 24.3 ºC, however Southern winds that occur during the dry season can make the temperature drop to 8 ºC. There is an average annual rainfall of 1100mm with a strong dry season (< 100 mm m-1) for 4 to 6 months (from May until October) (Killeen 1991, www.ibifbolivia.org.bo 2005). In this period 95% of the tree species lose their leaves. The topography is variable from flat to light slopes, with an altitude above sea level between 200-240m. The soils are described as well-drained reddish brown, sandy clay loams and are generally poor in nutrients (www.ibifbolivia.org.bo 2005). Most soil pits on the interfluves encounter bedrock within 70 cm of the soil surface. There are no permanent waterways in the property.

The forest has been classified as a dry deciduous forest (Gentry 1995). In this area 115 tree species have been identified with a diameter > 10cm. The average forest height is about 18m with emergent trees up to 25m. In each hectare there is a density of 420 trees with a diameter > 10 cm and a basal area of 18,3m^2 per hectare. The forest canopy is very open and therefore, the understorey is denser when compared to tropical forests with a higher rainfall. Lianas are very abundant in this type of forest, so that 60% of the trees with a diameter > 10 cm have some degree of liana infestation. Part of the forest floor is densely covered with a terrestrial bromelia (*Pseudoananas sagenarius*). In drier upland forest parts this species is able to compete effectively for soil moisture (Fredericksen & Mostacedo 2000a).

About 90% of the area of INPA forest is designated for logging, while the remaining area is designated as protected area or area for other uses (Pariona & Fredericksen 2003). The cutting cycle of the area is 25 years. The company uses reduced impact logging techniques, such as seed tree retention, use of a minimum DBH (Diameter at Breast Height: 1.3 m from the ground) for cutting (40 cm for most of the species) and census of commercial trees before logging. From the 115 tree species that are found in the forest, 17 are considered of commercial interest but at the moment only 9 are being harvested from the forest (www.ibifbolivia.org.bo 2005). The forest management of the company has been FSC certified since 1999.

2.2 Studied Species

Twenty-four tree species were selected for this study based on their actual or potential commercial value and based on their importance in the forest structure (Table 2.1). Nineteen of those 24 tree species were included since the start of this study in 2003. When the second measurement took place in 2005, five extra species were added to the species list because of their importance in forest ecology (Pinard *et al.* 1999, pers. comm. Poorter 2005). The identification of the species was done based on books (Killeen *et al.* 1998, Jardim *et al.* 2003, Mostacedo *et al.* 2003, Justiniano *et al.* 2004) and the expert opinion of local field assistants, Dr. Lourens Poorter and forest engineers of the IBIF project.

Table 2.1 The scientific name of the 24 tree species with the family name and the name that is locally used. Five species were added during the second measurement in 2005.

Tree species	**Family**	**Local Name**
Acosmium cardenasii	Fabaceae	tasaa
Albizia niopoides	Mimosaceae	cari cari
Anadenanthera colubrina	Mimosaceae	curupau
Aspidosperma cylindrocarpon	Apocynaceae	jichituriqui colorado
Aspidosperma subincanum	Apocynaceae	jichituriqui blanco
Aspidosperma tomentosum	Apocynaceae	jichituriqui amarillo
Astronium urundeuva	Anacardiaceae	cuchi
Capparis prisca	Capperidaceae	pacobillo *(added in ‘05)*
Cedrela fissilis	Meliaceae	cedro
Ceiba samauma	Bombacaceae	mapajo colorado
Ceiba speciosa	Bombacaceae	toborochi *(added in ‘05)*
Centrolobium microchaete	Fabaceae	tarara amarilla
Cesalpinia pluviosa	Caesalpiniaceae	momoqui
Cordia tetrandra	Boraginaceae	picana blanca *(added in ‘05)*
Gallesia integrifolia	Phytolaccaceae	ajo ajo *(added in ‘05)*
Guibourtia chodatiana	Caesalpiniaceae	sirari
Hymenaea courbaril	Caesalpiniaceae	paquio
Machaerium scleroxylon	Fabaceae	morado
Phyllostylon rhamnoides	Ulmaceae	cuta
Schinopsis brasiliensis	Anacardiaceae	soto
Simira rubescesns	Rubiaceae	gabetillo *(added in ‘05)*
Sweetia fructicosa	Fabaceae	mani
Tabebuia impetiginosa	Bignoniaceae	tajibo negro
Zeyheria tuberculosa	Bignoniaceae	cabeza de mono

2.3 Data collection

This study was carried out in the experimental plots of the Long-term Silvicultural Research Project that IBIF is carrying out in three different tropical forest types in Bolivia. Plots of block 1 were established and harvested in 2002, while plots of block 2 were established and harvested in 2003. Each block consists of four 20 ha plots. Each plot receives one of four treatments (Table 2.2). In each of the plots four 420 m long transects were established in 2003. A nested design was used within transects to sample plant size categories (Fig. 2.1). Transects were divided in 20 m long segments to facilitate data collection.

Table 2.2 Activities that were carried out in the four treatments.

Treatments	Control	Normal	Improved	Intensive
Reduced impact logging		X	X	X
Seed tree retention		X	X	X
Logging intensity		X	X	XX
Marking of future crop trees (FCT)			X	XX
Cutting lianas on FCT			X	XX
FCT Liberation by girdling			X	XX
Extra soil disturbance by skidder				X
Stand refinement				X

Seedlings < 0.3m in height were measured in two 1 x 2 m subplots within each segment. One subplot was located at the beginning of the segment on the left side of the central transect line, while the other subplot was located 10m from the starting point of the segment at the right side. Saplings 0.3 – 1.5m in height were measured within 1 m on each side of the central line of the transect. Juveniles from 1.50m in height - 20cm in DBH were measured within 2m on either side of the central line (Fig. 2.1). The area per transect in which seedlings were measure was 84m^2, for saplings 840m^2 and for juveniles 1680m^2. Height was measured as a straight line between the base of the plant and highest leaf in the position in which the plant was found.

In 2003 all saplings of the nineteen species found along transects were identified, tagged and measured in height and diameter. In 2005 the height and diameter of all tagged plants was measured again. Saplings that were previously not encountered were tagged and measured for the first time. When a tag from 2003 was found but the plant was not found, the plant was considered dead. When both the tag from 2003 and the plant could not be found it was considered disappeared.

For each encountered plant of the species list the light environment was characterized by a visual estimation of a modified version of the Dawkins Crown Illumination Index (CII) (Dawkins & Field 1978, Clark & Clark 1992, Poorter & Arets 2003) (Table 2.3). For each plant two independent observers estimated the CII. These independent measurements were highly symmetric (Kappa = 0.627, Appr. T =28.148, p< 0.001, n=6850).

Two other variables were collected for each individual plant that was encountered. Firstly the surrounding habitat of a given plant was recorded. Four different habitat categories were used to define the habitat (Table 2.4). The gaps were defined as was proposed by Popma 1988 who also includes the edges of the gap which are already vertically covered by canopy (Popma 1988, van der Meer 1998) This is an extension of the gap which was defined by Brokaw (1984) as “A hole in the forest extending through all level down to an average height of 2m above ground. Secondly each for each individual plant it was recorded whether or not lianas were growing on it.

Additionally at the beginning of each segment the canopy openness was measured, independently of a plant, using a densiometer. At the same location and height, two independent observers visually estimated the CII. The canopy openness and the CII were highly correlated to each other (Spearman correlation, r= 0.751, p<0.001, n=685). The different CI categories were identified as homogeneous subsets when compared with the average canopy openness as measured with a densiometer. Moreover an independent habitat observation was done at the beginning of each segment.

Table 2.3 Crown Illumination Index categories with their definition.

Dawkins code	Definition	canopy openness (%)
1	The canopy shows no opening; no direct light.	9.3
1.5	The canopy shows some openings; low amount of lateral light.	15.1
2	The canopy shows several openings; medium amount of lateral light.	20.4
2.5	The canopy shows many openings; high amount of lateral light.	26.2
3	The canopy shows openings in such a way the individual receives vertical light; part of the crown receives direct overhead light.	32.1
4	The canopy is very open above the individual; the whole crown receives direct overhead light.	37,44
5	The individual is above the canopy; the individual receives all lateral as well as all vertical light; crown completely exposed.	no data

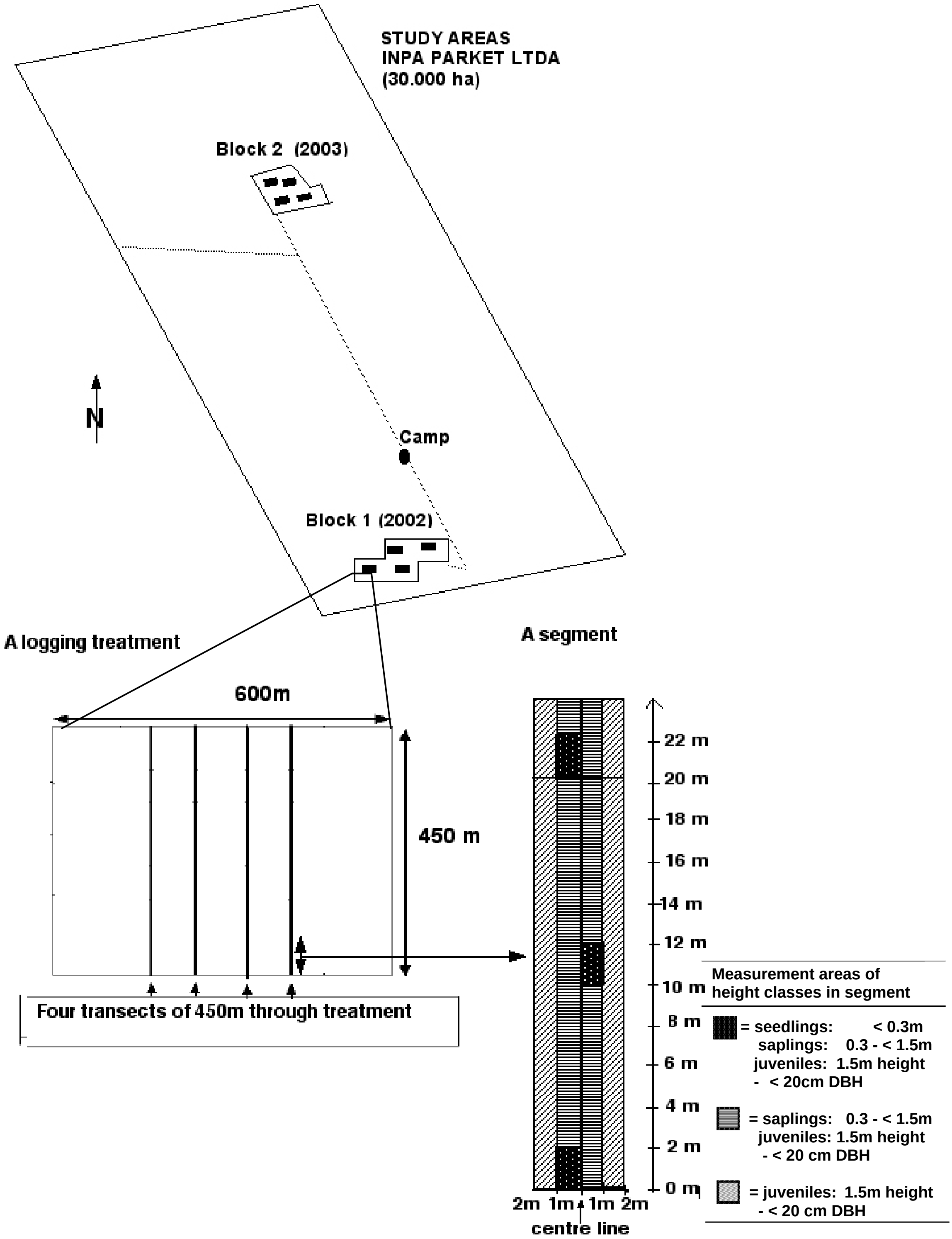

Figure 2.1 The design of the experiment. There are two blocks with each four treatment plots. Each plot is 600m by 450m and has four transects which were installed in 2003. Each transect is divided by segments of 20m which have a nested design for three different size classes.

Table 2.4 Habitat categories used to characterize the forest surrounding of each individual plants encountered along the transects.

Habitat	Definition
undisturbed	Canopy > 10m and no holes in the canopy until at least the next tree trunk with crown > 10m
skidder trails	Soil compacted by skidder during logging operations. The border of this habitat category is at the first tree trunk with crown > 10m in height. Canopy height is not taken into account
logging gaps	Clearing caused by a tree felling and with canopy < 10m in height. The border of this habitat category is at the first tree trunk with crown > 10m height.
natural gaps	Clearing caused by natural tree fall or breakage of large branch, canopy < 10 m in height. The border of this habitat category is at the first tree trunk with crown > 10m height.

2.4 Analysis

To test whether there were differences in habitat composition among the different treatments a Chi-square test with Boneferroni multiple comparisons was preformed on the independent habitat observations in all treatments together and among only the logging treatments. To test this statistically, a 2-way ANOVA was preformed in the form of a block design. The names of the four logging treatments were intensive, improved, normal and the control treatment. The difference in canopy openness among treatments and habitats was tested with a 2-way ANOVA in a block design.

In this report only plants up to 3 meter were included in the analysis. The shade tolerance of a species was characterized by the percentage of plants that a species was found in the low light i.e., CII = 1 and CII = 1.5. To increase the sample size, the occurrence in shade conditions for species is calculated by taking together the measurements for all four treatments. This is justified by the Pearson correlation between the shade tolerance values in the control treatment and the logging treatments ($r = 0.934$, $n = 11$, $p < 0.001$). To predict the CII as a function of tree height for different species, height-light trajectories (HLT) were analysed with a multinomial logistic regression (Poorter *et al.* 2005). A nominal regression was calculated for liana presence depending on the height for all species.

To assess the habitat preferences of different tree species for the four different habitat types, a Chi-square Goodness-of-fit test was preformed for plants up to 3m. The expected values were represented by the independently observed habitat composition of the three logging treatments taken together. This habitat composition was independently observed at the beginning of each segment.

Growth, survival and density determine to a large extent the success of a species in responding to logging. For every species a median growth rate was calculated per treatment and for all treatments together. The difference in mean growth between CII = 2 and CII = 1 for a species was correlated (Spearman) to the occurrence in shade conditions of a species. To quantify whether the occurrence in shade conditions of species says something about growth rate response higher light environment. There are 14 species that are included in the analysis on increased growth under higher light condition. The other 8 species of the 22 that were looked in this study were excluded from this part because for less than 4 individual's growth was measured in one of the two CII's.

The mortality analysis all 19 species were looked in 2003. Additionally a mortality rate has been calculated separately for seedlings (<0.3m) and saplings (0.3 -1.5m) when at least 10 individuals were found in that size class. The density per hectare was separately computed for the logging treatments and the control treatments, per species and size class. All statistical tests were preformed in the Mac OS X Version of SPSS 11.0.4.

3 Results

In the first section of this chapter the forest is characterized in terms of habitat and canopy openness. In the second section the species characteristics relating shade tolerance and liana presence are presented. In the last section the response of species to logging are given which includes the relation between shade tolerance and disturbance, growth and survival and habitat preference of a species. This study focuses on differences among treatments without consideration of the blocks. When significant and large differences between blocks were found, they are mentioned.

3.1 Forest characteristics

The habitat composition the difference among treatments was assessed. The habitat categories were 1) undisturbed, 2) skidder trails, 3) logging gaps and 4) natural gaps. Treatments differed in their habitat composition (Chi^2 16.919 = 78.505, p < 0.001, Fig. 3.1). The control treatment had significantly more undisturbed habitat (65.9%) and natural gaps (24.1%) than the logging treatments. The three logging treatments had more skidder trails and logging gaps. When the tree logging treatments were tested separately from the control treatment no significant difference was found (Chi2 12.592 = 9.941, p = 0.127) (Fig. 3.1). The mean distribution of habitats that was found in the three logging treatments was undisturbed 46%; skidder trails 11.5%, logging gaps 18.6% and natural gaps 23.9%. Between blocks there was no difference in habitat composition (p = 0.993).

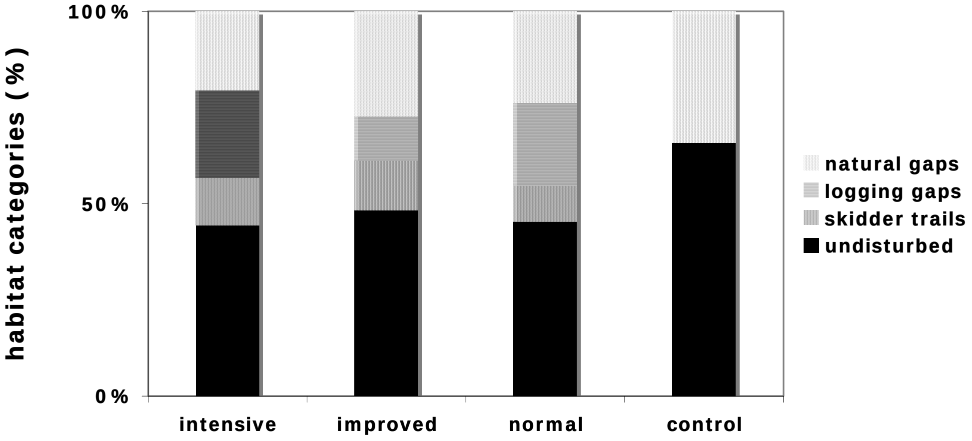

Figure 3.1 The habitat composition of the four treatments.

The differences of canopy openness were assessed among four habitat categories, the four treatments and two blocks. The canopy openness tended to be lower in the control treatment (mean = 12.6%) than in the logging treatments (all means+/- 16.3%), but this differences was not significant (2-way ANOVA, for treatment, $F_{3,}$ = 124.2, p =0.067).

The mean canopy openness for the habitat categories was undisturbed (13.4%), skidder trails (21.2%), logging gaps (19.3%), and natural gaps (15.2%). The ANOVA showed that there were three groups of canopy openness to be made from the four habitat categories (2 ANOVA, for habitat, $F_{3,}$ = 23.8, P < 0.001). In the Boneferroni post-hoc test, undisturbed and naturally gaps had a different canopy openness (p =0,027, 95% CI = 0.14; 3.62). Natural gaps and logging gaps habitat also differed (p < 0.001, 95% CI = 1.63; 6.44). but logging gaps and skidder trails weren't different in canopy openness (p = 0.67, 95% CI = -1.26; 5,05) (Fig. 3.2).

The mean canopy openness for block 1 (13.5%) was significantly lower than the canopy openness while for block 2 (17.4%) (2 ANOVA, for blocks, $F_{1,}$ = 54.8, p < 0.001). There was no interaction effect between the treatment and the habitat (2 ANOVA, interaction, F_7, = 0.9, p = 0.469).

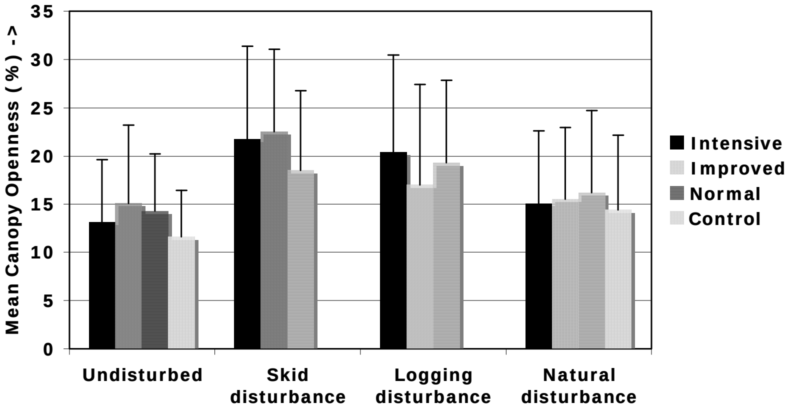

Figure 3.2 Mean canopy openness per habitat category and treatment. Data are mean + 1 SD.

3.2 Species characteristics

Shade tolerance of the study species was assessed by the percentage of plants of a given species growing in low light conditions (Crown Illumination Index (CII) 1 or 1.5). Species substantially differed in shade tolerance (Table 3.1). Only 3 of the 24 species included in the study had less than 40% of their individuals in shade conditions. All other species had more than 50% of their individuals up to 3m under shaded conditions. Although the range of CII values in which all species occur was similar, the distribution of individuals over CII categories differed among species (Kruskal-Wallis test, Chi2 = 606.0, do = 24, p < 0.001).

Table 3.1 Percentage of individuals (<3 m height) occurring in shade conditions (CII = 1 or CII = 1.5).

Species	Percentage in shade	n
Phyllostylon rhamnoides	94%	170
Gallesia integrifolia	92%	25
Acosmium cardenasii	88%	1905
Guibourtia chodatiana	88%	1072
Capparis prisca	84%	56
Aspidosperma subincanum	81%	233
Aspidosperma tomentosum	79%	172
Machaerium scleroxylon	78%	52
Schinopsis brasiliensis	77%	102
Anadenanthera colubrina	76%	740
Cesalpinia pluviosa	74%	557
Simira rubescesns	74%	34
Sweetia fructicosa	73%	446
Aspidosperma cylindrocarpon	72%	220
Hymenaea courbaril	72%	25
Ceiba samauma	69%	42
Zeyheria tuberculosa	67%	27
Astronium urundeuva	62%	53
Ceiba speciosa	62%	84
Cordia tetrandra	55%	101
Albizia niopoides	52%	23
Centrolobium microchaete	34%	166
Cedrela fissilis	32%	31
Tabebuia impetiginosa	24%	21

To evaluate to what extent light conditions change, as saplings grow taller, multinomial regressions between CII and height were constructed for the 24 study species. Regressions for 13 of the 24 species were significant, thus predicting significant changes in light conditions with sapling height. For these species, a general trend of increasing CII with increasing height was observed, although relations differed considerably among species. In some species (*Anadenanthera colubrine*; $r^2 = 0.219$) light level increases rapidly from below average to above average. Others (e.g. *G. chodatiana*; $r^2 = 0.071$) show only small increases in light level. (Annex 2, Tab. 8.1). For *C. speciosa* a lower CII was found with increasing height a.

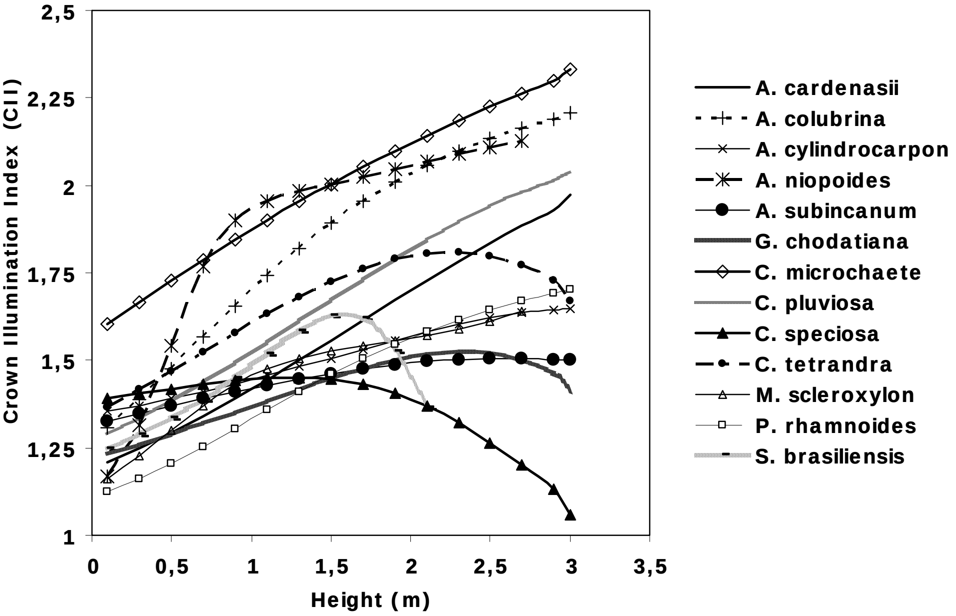

Figure 3.3 A multinomial regression for significant 13 tree species, which predicts the Crown Illumination Index of a species, based on their height up to 3 meter. All regressions shown were highly significant ($p<0.001$) and had R^2 values of 0.071-0.641.

Liana infestation strongly increased with sapling size: less than 10% of small individuals had lianas, while this was >70% for 3-m tall saplings. The liana presence for individuals below 3 meters with all species together was calculated with a binary logistic regression (constant = -2.719, B = 1.264, $p < 0.001$) (Fig. 3.4). On less than 10 % of the seedlings below 30 cm lianas were found while on 60 % of saplings of 3 meters lianas were found. When the Crown Illumination Index (CII) was included into the second step of the regression all Dawkins categories were significant except CII 2.5.

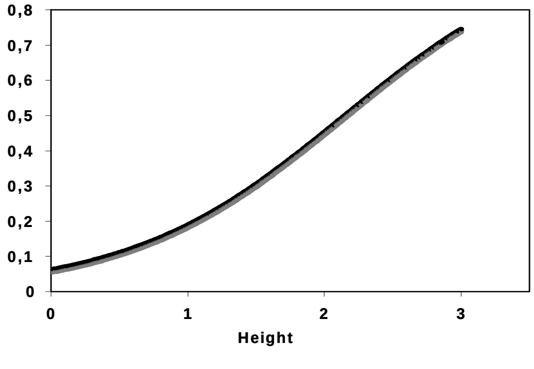

Figure 3.4 The relation between liana presence and plant height (n=6421)

3.3 Species response to logging

3.3.1 Species density

There are large differences in density between species per size class ranging from 0-16339 individuals per hectare for seedlings (<0.3m height) and from 0-865 individuals per hectare for saplings (0.31-<1.5m) (Appendix II, Table 8.3). There are species for which no individuals were found in the smallest size class while in higher size classes some individuals were found.

Sixteen of the 24 study species had a lower density in the logging treatments while density was higher for 6 species. Of the species with economic value, 6 had lower densities in logging treatments (including the highly valuable *Cedrela fissilis* and *Machaerium scleroxylon*), while 4 had a higher density in the logging treatments (including the highly valuable commercial species *Tabebuia impetiginosa*). These differences are not statically tested however a difference of 25% is observed between logging treatments and the control treatment can be considered as a reasonable certain difference.

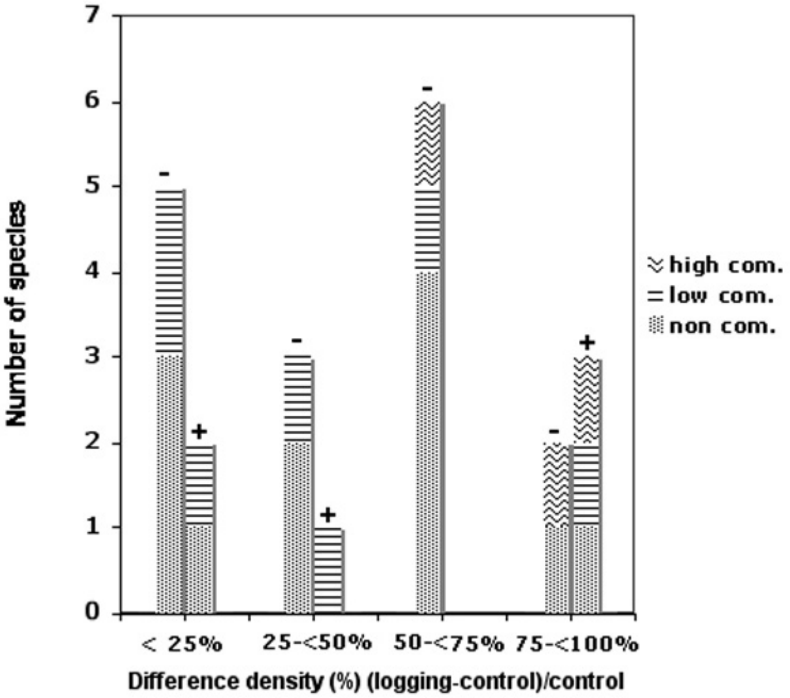

Figure 3.5 Number of species for which sapling densities differ between logged and control treatments. "-"= lower density is logging treatments and "+" = higher density in the logging treatments. The figure differentiates between high commercial timber value, low commercial timber value and non-commercial tree species.

3.3.2 Habitat preference

Habitat preference of tree species was assessed, with a Chi-square goodness-of-fit test. The expected values were based on the average distribution of habitats in the three logging treatments (these were not significantly different among treatments): undisturbed 46%, skidder trails 11.5%, logging gaps 18.6% and natural gaps 23.9%.

For nine of the 22 tested species sapling distribution over habitats was significantly different from the expected value based on the average distribution of habitats in the three logging treatments (Table 3.2). Some species had higher densities in logging gaps (*A. cardenasii, A. niopoides, A. colubrina, A. urundeuva, C. microchaete and T. impetiginosa*) while others occurred at lower densities in this habitat type (*A. cylindrocarpon, A. subincanum, A. tomentosum, G. chodatiana* and *P. rhamnoides*). Three species had higher densities in skidder trails (*A. colubrina, C. microchaete* and *T. impetiginosa)* while eight species occurred at lower densities in this habitat type (*A. cardenasii, A. niopoides, A. cylindrocarpon, A. subincanum, A. tomentosum, A. urundeuva, G. chodatiana* and *P. rhamnoides*) (Table 3.2). There was a difference among species in the intensity of habitat preference which indicated with the amount of symbols (+ and -) which indicates how much percentage “(Observed-Expected)^2/Expected” has contributed to the Chi^2 value.

Table 3.2 The habitat preference of 22 tree species tested with the Chi^2 Goodness-of-fit test. Plants up to 3 m were included in this analysis. “-“= a species is found less in a habitat category than expected, “+” = a species was found more often than expected. The amount of symbols indicates how much percentage (Observed-Expected)^2/Expected has contributed to the Chi^2 value. 1 +/- = < 20%, 2 +/- = 21-40%, 3 +/- = 41-60%, 4 +/- = 61-80%, 5 +/- = 81-100%.

Species	p	Chi^2	undisturb. habitat	skidder trails	logging gaps	natural gaps	n
A. cardenasii	0.000	19.915	+	-----	+	+	1417
A. niopoides	0.000	41.735	--	-	++++	-	23
A. colubrina	0.004	13.496	--	++++	+	-	566
A. cylindrocarpon	0.000	17.843	+++	--	--	-	194
A. subincanum	0.058	7.466	++	---	-	+	188
A. tomentosum	0.068	7.123	+	--	--	+	149
A. urundeuva	0.047	7.933	-	--	+	+++	43
C. fissilis	0.454	2.620					30
C. samauma	0.212	4.503					28
Ceiba speciosa	0.706	1.396					71
C. microchaete	0.000	52.912	-	++++	+	-	139
C. pluviosa	0.793	1.034					396
G. chodatiana	0.003	1.881	++	----	-	-	915
C. tetrandra	0.753	1.201					89
H. courbaril	0.581	1.959					20
M. scleroxylon	0.274	3.883					20
P. rhamnoides	0.002	15.357	+	-	---	+++	86
S. brasiliensis	0.167	5.059					90
S. rubescesns	0.992	0.101					34
S. fructicosa	0.801	1.001					369
T. impetiginosa	0.000	23.680	-	+++	+	-	21
Z. tuberculosa	0.617	1.792					26

3.3.3 Growth

For 22 tree species a median growth rate was calculated (Appendix II, Tab. 8.2). The median growth rates range from -12.8 cm to 26.4 cm in height per year. Within species there was a high variance in growth rate. The negative growth rates are caused by damage to the plants. At the 25 percentile all growth rates are negative while at the 75 percentile there are 12 species than are above 20cm/y in height.

A difference in growth rate among treatments was only found with *P. rhamnoides* (2-way ANOVA, for treatment, $F_{3,} = 28.1$, $p < 0.001$) and *A. cylindrocarpon* (2-way ANOVA, for treatment, $F_3 = 2.860$, $p = 0.041$). The post hoc test showed that *P. rhamnoides* had a higher growth rate in the intensive treatment compared to the other treatments and *A. cylindrocarpon* had a lower growth rate in the control treatment compared to the logging treatments. A difference in growth rate among habitat types was found with *A. cardenasii, A. niopoides, A. urundeuva,* C. *fissilis, C. pluviosa*, *S. fructicosa.* Generally the growth rates are higher in the habitats disturbed by skidder or logging (Table 3.3).

Table 3.3 Mean growth rates (cm/y) for six tree species among four habitat categories. Only species with significant growth difference between habitats were included. Waarom laat je medianen zien, terwijl je een normale ANOVA hebt gedaan?

	undisturbed (cm/y)	skidder (cm/y)	logging (cm/y)	natural (cm/y)	F	p	n
A. cardenasii	-0.6	6.9	2.8	2.0	3.419	0.017	745
A. niopoides	55.6	67.0	17.6	-5.6	4.383	0.018	26
A. urundeuva	16.1	96.1	61.2	9.2	6.840	0.002	27
C. fissilis	11.7		51.2	-44.1	23.135	0.041	6
C. samauma	15.0	54.1	12.3	4.3	3.742	0.019	24
S. fructicosa	-4.2	12.7	9.1	7.0	6.683	0.000	168

Table 3.4 Median growth rates of 13 tree species for CII 1 en 2 and a Mann-Whitney-U test showed whether these values were significantly different. Only those species with at least 4 individuals per CII class were included.

	CII 1 (cm/y)	n	CII 2 (cm/y)	n	increased growth MWU (p)
A. cardenasii	0.0	394	3.9	71	0.000
A. niopoides	4.3	5	24.1	7	0.685
A. colubrina	1.3	35	23.0	26	0.001
A. cylindrocarpon	1.3	33	17.2	24	0.020
A. subincanum	0.6	10	8.0	4	0.258
A. tomentosum	0.3	46	5.8	25	0.002
C. samauma	1.1	6	37.8	5	0.465
C. pluviosa	0.5	54	15.0	39	0.000
G. chodatiana	-1.3	304	-1.6	66	0.511
C. tetrandra	-1.9	13	29.8	11	0.002
P. rhamnoides	0.8	24	12.8	5	0.049
S. rubescesns	0.5	16	9.9	6	0.055
S. fructicosa	0.0	60	7.0	27	0.012

Additionally growth rates were compared between CII = 1 and CII = 2 with a Mann-Whitney-U test. In higher light conditions (CII 2) all species, except *Guibourtia chodatiana*, grew faster. At CII =1 the lowest growth rate was -1.9cm by *C. tetrandra* and the highest growth rate was 4.3cm by *A. niopoides.* At CII=2 the lowest growth rate was -1.6cm by *G. chodatiana* and the highest growth rate was 36.9cm by *C. samauma* (Table 3.4). Eight of the 13 species were found to have a different growth rate between CII = 1 and CII = 2 with the Mann Whitney test.

The difference in the growth in height between CII 1 and CII 2 is a good indication of how much a species reacts to an increase in light. The growth rate difference between CII 2 and CII 1 was negatively related to shade tolerance (Spearman correlation, r = -0.697, n = 13, p = 0.008)

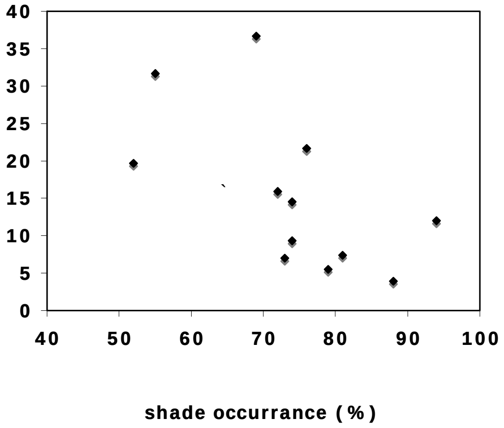

Figure 3.4 Relation between occurrence in shade conditions and growth rate difference at CII 1 and 2. Only those species that were measured at least 4 times per CII have been included.

3.3.3 Mortality

The mortality rate for saplings was very different between tree species. A species like *Simira rubenscens* had a low mortality of 2.6% between 2003 and 2005 while a *Anadenanthera colubrina* had a mortality rate of 14.1% (Tab. 3.5). Among occurrence in shade conditions and mortality no significant spearman correlation was found out (r = -0.311, n = 10, P = 0,382) (fig. 3.5). A low mortality was found with *Aspidosperma colorado* of only 1.6% with 72% of its individuals in shade conditions (Appendix II, Table 8.4). A high mortality was found with C. tetrandra of 19.1% with only 55% of these individuals found in low light conditions. This shows that this group of species no proven relation exists between low light conditions and a certain mortality rate.

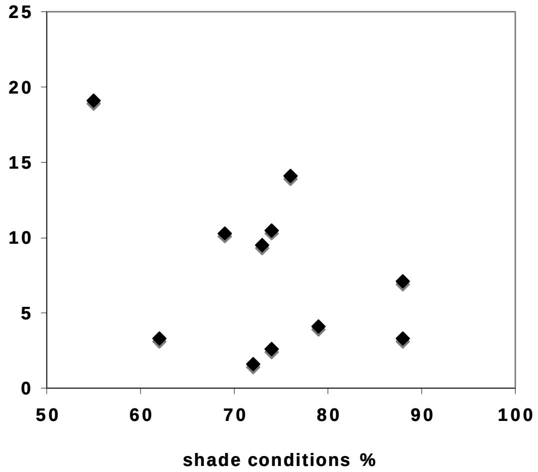

Figure 3.5 Relation between percentage occurrence in shade conditions and mortality (r = -0.311, n= 10, p = 0.382). Only species with >25 individuals in 2003 were included.

4 Discussion

The two objectives of this study were: (1) to find the ecological seedling characteristics of the selected species on shade tolerance, habitat preference, growth response, mortality and density; and, (2) to determine the response of these species to the effect of logging treatments.

4.1 Change in forest structure

As expected, logging changed the distribution of habitats in the study area by adding new habitats (logging gaps and skidder trails). However, it was remarkable that that no differences in habitat composition were found among the strongly different logging treatments. Apparently, the differences between logging treatment in intensity and silvicultural treatment were not sufficiently large to lead a shift in habitat composition.

There was a significant difference in canopy openness among the four habitat types that were distinguished. Skidder trails and logging gaps had higher canopy openness than the natural gaps and undisturbed habitat. Although skidder trails and logging gaps were not significantly different in canopy openness these habitat types are different in the amount of soil compaction. The difference in canopy between the undisturbed habitat and natural gaps shows that as expected natural processes in the forest have resulted in many different light environments.

Another unexpected result is that canopy openness did not differ between control and logging treatments, nor among logging treatments. This contradicts the assumption of many studies that logging leads to higher canopy openness (Frederickson & Mostacedo 2000a, Kennard *et al.* 2002). Figure 3.1 shows clearly that the standard deviations for canopy openness are very high for the different treatment groups within the habitats. This high variation is caused by the great range of light environments that are found in the forest, even were logging has taken place. The higher canopy openness in block 2 might have been caused due to a year difference in logging between block 1 and 2, due to earlier anthropogenic influences before this experiment or a difference in environmental factors (pers. comm. Mostacedo 2005). The difference between the blocks has not further been included in the analysis because that was not the goal of this study and the range of values in both blocks was overlapping.

When no differences are found in habitat composition and canopy openness possibly there was not enough difference in disturbance between the treatments. Due to high the high variance in light conditions there probably not enough measurements (168) to find differences in canopy openness among treatments. With more habitat observations differences can probably be found among logging treatments. The results of this study show that it is more useful compare among habitat types and determine per habitat type light and growth effects. This will give a better insight in biological relations. The comparison of treatments is very difficult due to the high variance in environmental conditions within one treatment, which causes also high variance in response for one species. It is very important that very clear definitions of habitats categories are made which should be extensively discussed among those who collect the data.

4.2 Different life strategies among tree species

The percentage that a species occurs in low light conditions can be considered as a good measure for shade tolerance (Poorter and Arets 2003). A wide range of percentages from 24% to 88% was found between tree species. This suggests that the tree community of tropical dry forest has very diverse life strategies as has been found for wetter areas. The diversity in ecological characteristic for tree species is common in several studies in which more species are included (Pinard *et al.* 1999, Mostacedo & Fredericksen 1999, Fredericksen & Mostacedo 2000a, 2000b, Rose 2000). However some considerations have to be taken into account when looking at this percentage of shade occurrence, which is made up by adding the percentages of the two lowest values of the Crown Illumination Index (CII) of a species. Firstly the CII is a nominal scale with seven categories which causes that the exact differences between the categories are arbitrary. This puts a constraint on the types of analysis that can be done with this important variable of light. Several authors argue that the CII is just as legitimate as other light measurement techniques and are often more practical in the field (Clark and Clark 1992, Poorter & Arets 2003).

The results of this study show that the CII can be used to find significant differences between species.

A second consideration is that tree species did not have a similar height distribution. When relatively higher numbers of small individuals (<30cm) are found it is more likely that a higher percentage of that species is found in low light conditions. The height-light trajectory (Poorter *et al.* 2005) circumvents this problem as it explicitly includes size. The analysis for 13 of our study species suggests that species exist in different light environment at different heights (fig. 3.3) (Lieberman *et al.* 1995, Poorter & Arets 2003). The third consideration is when species were found in low numbers (<25 indiv.) the shade tolerance value and the height-light trajectory can be influenced by a few odd values and therefore a significant effect is harder to find.

Another indication for life strategy differentiation is obtained by considering the growth response of seedlings to increased light. The significant negative relation between the occurrence in shade conditions and increased growth between CII 1 and 2 for tree species shows that shade tolerant species have a slower growth reaction to an increase in light (Rose 2000, Poorter & Arets 2003). Species for which low shade occurrence values were found will probably have to grow faster to prevent high levels of shading from neighbouring highlight species. Species which were found more often in shade conditions probably do not have to compete as much because they are more capable to survive in more shaded conditions.

Table 4.1 A comparison among classifications of shade tolerance made by three authors (Markesteijn 2004, Pinard *et al.* 1999, Mostacedo & Fredricksen 1999) and the percentage of plants in shade conditions that was collected during this study. LD = Light demanding, IS = Intermediate Shade tolerant and ST = Shade tolerant.

Species	Percentages plants in shade conditions	Markestijn	Pinard	Mostacedo
T. impetiginosa	24%	LD	LD	LD
C. fissilis	32%		LD	LD
C. microchaete	34%	LD	LD	LD
A. niopoides	52%			
C. tetrandra	55%			
A. urundeuva	62%	LD		LD
Ceiba speciosa	62%	LD	LD	
Z. tuberculosa	67%		LD	
C. samauma	69%		LD	
A. cylindrocarpon	72%	IS	IS	
H. courbaril	72%		LD	IS
S. fructicosa	73%	IS		
C. pluviosa	74%	LD		IS
S. rubescesns	74%	ST	ST	
A. colubrina	76%		LD	IS
S. brasiliensis	77%		LD	LD
M. scleroxylon	78%		ST	IS
A. tomentosum	79%	IS		
A. subincanum	81%			
C. prisca	84%	ST	ST	IS
A. cardenasii	88%	IS		
G. chodatiana	88%	IS		ST
G. integrifolia	92%	IS	ST	
P. rhamnoides	94%	IS	ST	IS

Several classifications were made on shade tolerance for the species that are found in the dry tropical Bolivian forest. A comparison was made among light strategy categories of other authors gave to tree species and the percentages of shade occurrence of a species that this study found. This comparison showed that for species with low shade percentages there is a general consensus that these are light demanding species (Tab 4.1) (Markesteijn 2004, Pinard *et al.* 1999, Mostacedo & Fredericksen 1999). However these authors often classify differently species with higher shade percentages. For example, Markesteijn and Mostacedo classify a species like *Capparis prisca* with a shade percentage of 94% as intermediate shade tolerant while Pinard considers it shade tolerant. Another example is *S. brasiliensis* other authors classify it as light demanding while a 77% seedlings were found in shade conditions. Possibly this is because Pinard and Mostacedo are considering mature trees while the presented percentage is from plants up to 3 meters.

Zagt (1997) wrote before that different life strategies are found when different life faces are studied. An approach, which includes seedlings as well as mature trees, will say more about the light strategy of a plant. This type of approach can possibly results in precise model, which describes light strategies for a species from germination until it is a mature tree. This model should not only included light response and growth rate but also population dynamic and a range of scenarios that can happen to a tree during its lifetime.

4.3 Growth, mortality and lianas

The reason for negative growth rates that was found for several species is damage that is caused to the individual plants. A plant can be damaged by several factors like branches fall, lianas and mortality. The growth rates show that plants have different strategies to react to higher light. This is proven in the correlation.

In the mortality analysis 10 species were included. This is because mortality percentage is based on plants that were higher than 15 cm but lower than 3m in 2003. Only plants that were higher than 15 cm in 2003 are included in the mortality percentage because some species had high numbers of these small seedlings while other did not. A higher number of small seedlings could possibly affect the outcome of the percentage because these seedlings have a much higher mortality rate. Besides only those species were included in the mortality analysis with at least 25 individuals between 15cm and 3m were found in 2003.

A significant regression found been height and liana occurrence (fig. 3.4) when all species were put in one group. Other authors that have often looked at lianas did not specifically look at the relation between seedling-height and liana occurrence (Alvira *et al.* 2004, Pérez *et al.* 2004). These authors generally recognize the detrimental effect of lianas have on the growth of commercial tree species and the increase of lianas after disturbance. The increase of lianas after logging can result in a much lower wood yield in the following cutting cycle (Clark and Clark 1992, Putz 1984, Pinard *et al.* 1996, Kennard *et al.* 1998, Pinard *et al.* 1999, Perez *et al.*2000).

4.4 Habitat preferences and density

According to the niche theory each species is specialized in its own combination of environmental factors and thus included in different functional groups (Swaine an Whitmore 1988, Poorter and Arets 2003). Species are usually included in functional groups on the basis of shade tolerance however there are few authors that have looked at species preference for habitat types in dry forest types (Pinard *et al.* 1996, Fredericksen and Mostacedo 2000a). Some species are specialized in habitats where disturbance occurs and the ground is compressed, while another species might be more suitable for a disturbed habitat were no ground is compressed. From the 22 species of which habitat preferences were assessed, 9 species did have a significantly different distribution over habitat types than expected from average composition of the three logging treatments together. The significance of these 9 species means that they occurred much more or a lot less of any of the four habitat categories. The other 13 species did not have a different composition. The null hypothesis is that species have a random distribution of seedlings and therefore occur in the same habitat composition as expected. A data consideration is that some species that are found in low numbers no significant difference can be found with the chi-square test.

The valuable timber tree species like *Anadenanthera columbrina* and *Centrolobium microchaete* occur significantly more on skidder trails (Tab. 3.2). When more of this habitat is created these species probably will have a better regeneration. Fredericksen (2000) also finds that more soil scarification will increase the growth and density of the above mentioned species (Appendix I, Tab. 8.1). Other valuable timber tree species like *Astronium urundeuva* and *Guibourtia chodatiana* have lower density than expected in skidder trails. It is remarkable that Fredericksen (2000) found that *G. chodatiana* has a higher abundance in logging gaps and areas disturbed by skidders. Extra soil compaction like proposed in some management practices would most likely reduce the regeneration of those three species (Mostacedo an Fredericksen 1999, Fredericksen and Mostacedo 2000a, Kennard *et al.* 2002). Other authors argue that more soil disturbance by skidders causes much damage to the residual stand of the forest (Jackson and Fredericksen 2002). The very abundant but not commercial *Acosmium cardenasii* has less regeneration on skidder trails than expected while a bit more in logging gaps. The reduced regeneration of *A. cardenasii* can be seen as a positive effect of skidders so other tree species can have a change to colonize this habitat.

A previous study by Rheenen (2004) found a lower morality and a high growth rate in the log landings and logging gaps for the four studied species of which was also looked in this study (*Hymenaea courbaril*). Skidder trails were found to be less suitable sites for regeneration (Rheenen *et al.* 2004). The suggestion made by Rheenen that logging gaps and log landing can play an important role in the regeneration of commercial tree species is too one sided. This is probably due to the fact that only four species were studied while with more species more differences are found in reaction to habitats.

The density of seedlings, saplings and mature trees of a tree species is primarily influenced by the amount of seeding trees, dispersal capacity, seed predation and mortality. These factors mainly cause that *Acosmium cardenasii* has a high density while a commercial species like *Cedrela fissilis* has a very low density. However the density of a tree species can be greatly influenced due to logging activities. A famous example of over harvesting is *Swietenia marcophiylla* (mahogany) where severe depletion has led to a scarcity of regeneration (Mostacedo and Fredericksen 1999). In the Chiquitania region the extremely harvesting of *Astronium urundeuva* for the missionary churches has led to a comparable depletion (pers. Comm. Mostacedo & Poorter 2005).

There are six species that occur less than expected in skidder trails while only 3 species occur more than expected (Fig. 4.1). There are 3 species that occur less in logging gaps while only one occurs more in this type of habitat. It can be concluded that the change in forest structure that is caused by logging also results in a change in seedling composition.

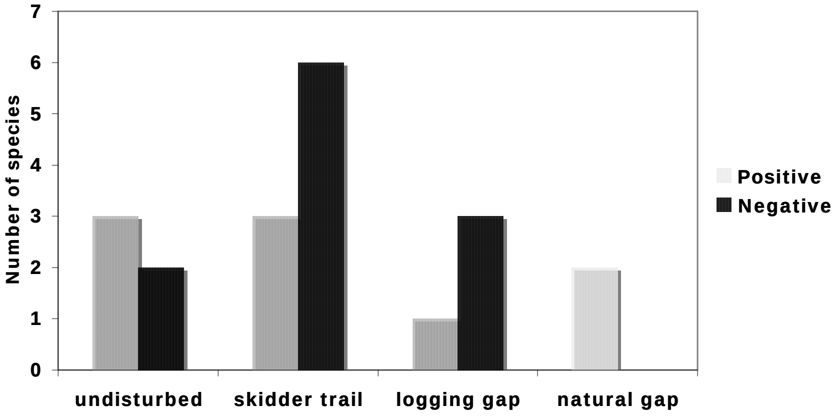

Figure 4.1 The number of species that occurs more (positive) or less (negative) than expected in a habitat category. The nine species that had a significant habitat preference are included in the figure. A positive or negative preference for a habitat type is counted when it contributed more than 20% to the (residue)^2/expected of the Chi-square.

5. Conclusions and recommendations

5.1 Conclusions

The first objective of this study was to ecologically characterize tree species in a dry Bolivian forest based on seedling performance. From the results that were presented it can be concluded that tree species saplings are very different in several ecological characteristics. This can be concluded because:

- Firstly, the individuals of the examined tree species, up to 3m, occur in shade conditions that range from 24% until 94%.
- Secondly, for thirteen tree species a unique height light trajectory was found and a correlation that proves the relation between shade tolerance and increased growth at higher light.
- Thirdly between tree species very different height growth rates and mortality rates were found.
- Lastly more lianas are found on tree saplings with an increasing height.

The second objective of this study was to determine the response of seedlings of tree species to logging. From the results that were presented and the conclusions of the first objective it is clear that species responded differently to the effects that are caused by logging. However it can be concluded that the regeneration for many of the examined tree species is negatively affected by logging activities. This can be concluded because:

- Firstly, while five species respond positive and two species respond negative to natural habitats. There are four species that respond positively and nine that responded negatively to habitats that were influenced by logging. Four of those nine species, which responded negatively to logging, have a commercial timber value.
- Secondly, there are 11 tree species that have a lower density of more than 25% in the logging treatments compared to the control treatment. Two of those species have a commercial timber value and two have a high commercial timber value. Many species have a higher density in the control treatment There are four tree species with a higher density of more than 25% in logging treatments of which two are with commercial value and one is with high commercial value.

5.2 Recommendations

It is widely understood that to make a FSC logging concession economical beneficial a balance has to be found between logging a certain amount of mature trees and preserving enough to ensure a harvest of comparable quantity in the following cutting cycle. From results and collected figures that are presented are presented in table 8.1 the following recommendations follow:
1. A diversification in use of the area that is assigned for logging each year (+/- 1000 ha/y). Which means that some parts more tree can be logged and more skid trails be made. This part with this treatment would favour species like *Anadenanthera colubrina, Centrolobium microchate and Tabebuia impetiginosaí*. However another part of the area that is yearly assigned for logging should contain more seeding trees of commercial species and should be disturbed less to allow for the regeneration of commercial species like *Guibourtia chodatiana, Astronium urundeuva and Cedrela fissilis*.
2. No more logging of the species *Astronium urundeuva* and *Aspidosperma cylindrocarpon* because their density of saplings per hectare is below 100 individuals and they occur less in habitats that are caused by logging.
3. No more logging of the species *Tabebuia impetiginosa* because its density is below 10 individuals per hectare.

For a more precise idea, however, on the regeneration of the tree species in a dry Bolivian forest future research is needed. Firstly more hard conclusions can be drawn on height growth, mortality, germination and densities when plants in the transects are measured again around march 2007. All individual plants that have been included in the analysis of this research have been tagged. Secondly an analysis should be made to asses the relation between the location specific density of seedlings and saplings and of the presents of seed trees. That analysis would give more precise figures on how successful seed trees are in the contributing to the seedling and sapling presnts of that species. An answer to the question how much seedling quantities are declining and what causes this would be one step closer.

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