Effects of forest management intensity on the performance of mahogany in Bolivia

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SUMMARY

Big-leaf mahogany (*Swietenia macrophylla*) is the leading commercial timber species of Central and South America but the species is threatened by unsustainable logging which does not provide for its regeneration. The dramatic decline of mahogany populations in the last decades has made successful regeneration of the species indispensable to sustain future yields. Therefore appropriate forest management is required.

In this study the impact of management intensity on the regeneration of mahogany was determined under four management types varying in intensity. Data was gathered in the Long Term Silvicultural Research Plots within the La Chonta Forestry Concession in Bolivia. Parameters measured were tree height, diameter at breast height, crown position, crown form, stem quality, liana load and soil type. For 58 reproductive trees seedling dispersal was measured. Additionally, in a small scale nursery experiment the effects of light availability (1% and 10%), humus (with and without humus) and the soil type (two superficial soil types) on seed germination and early seedling development were tested.

Light availability was the major factor determining growth of mahogany. Effects of stem quality, liana load and soil type were of minor importance in determining growth of mahogany. Under intensive management, growth was better and seedling dispersal range was wider. However, although more open forest environments might favour seed dispersal it does not guarantee successful regeneration because of increased competition, insect attacks or decreased moisture levels due to higher evaporation. Germination rate was significantly increased in soils containing organic humus, probably because of its high water holding capacity. The other factors tested for did not significantly influence germination or the rate of germination.

Thus forest management can significantly affect population structure and tree growth of mahogany but intensive management does not necessarily positively affect natural regeneration and performance of mahogany.

RESUMEN

Mara (*Swietenia macrophylla*) es la especies maderable mas importante en Central y Suramérica, pero también es una especies amenazada si el manejo forestal no garantiza su regeneración natural. La dismunición dramática de las poblaciones de mara durante las últimas décadas muestra la importancia de regeneración natural para sostener un eventual aprovechamiento en el futuro. Por lo tanto se requiere un manejo forestal apropiado.

En este estudio se evaluó el efecto de la intensidad de manejo forestal en la regeneración de mara. Datos fueron recolectados en las parcelas experimentales de largo plazo en la concessión forestal de La Chonta en Bolivia. Parámetros medidos fueron altura del árbol, diametro a la altura del pecho, posición de copa, forma de copa, calidad del fuste, infestación de bejucos y el tipo de suelo. Para 58

árboles semilleros se evaluó la dispersión de plantínes. Además, en un experimento en el invernadero se evaluó los efectos de la disponibilidad de la luz (1% y 10%), del humus (con humus y sin humus) y del suelo (dos tipos de suelo superficial) en la germinación de las semillas y el desarollo temprano de plantínes.

La disponibilidad de la luz era el factor principal que determinó el crecimiento de mara. Los efectos de la calidad del fuste, la infestación de bejucos y del tipo de suelo eran de menor importancia para el crecimiento. En el tratamiento intensivo el crecimiento era mejor y la dispersión de las plantínes era más amplia. Sín embargo, aunque los ambientes más abiertos del bosque pudieron favorecer la dispersión de las semillas este no garantiza la regeneración debido a más competencia, los ataques de los insectos o los niveles de la humedad disminuidos debido a una evaporación más alta. La germinación de semillas fue afectada significativamente por el humus, probablemente porque se aumentó el contenido de agua en este tratamiento. Los factores luz y suelo no eran de importancia en la germinación de semillas.

El manejo forestal afecta la estructura de la población y el crecimiento de mara pero el manejo intensivo no necessariamente afecta positivamente la regeneración natural.

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1. INTRODUCTION

1.1 Problem description[1]

Big-leaf mahogany (*Swietenia macrophylla* King)[2] is considered the leading commercial timber species of Central and South America. Nevertheless, the species is threatened by unsustainable logging which does not provide for its regeneration (Kometter et al. 2004, Snook et al. 2005). In the past, timber supplies were sustained through the unsustainable logging of primary forests in Central and South America. To date, the abundance of mahogany across much of its natural range has been severely decreased as a consequence of overexploitation and forest conversion (Gullison 1996; Snook et al. 2005). This has led to concern about the survival of many mahogany populations and the sustainability of its commercial trade in particular (Snook et al. 2005). Due to this concern, the species was included in appendix II of the Convention on International Trade of Endangered Species (CITES) in November 2002.

Mahogany is an emergent deciduous tree with a wide natural range spreading from Mexico southwards through Panama, Venezuela and along the western and southern rim of the Amazon basin to the Brazilian state of Pará. The species generally occurs at low densities (<1 adult tree ha^{-1}) in (semi)deciduous and evergreen rainforests, often clustered together in groups along watercourses or in highly disturbed transition zones between forest types. The species is found under widely ranging climatic, hydrologic, edaphic and competitive circumstances across its natural range (Grogan et al. 2002). So far mahogany is understood to regenerate in areas subjected to large scale catastrophic disturbances such as hurricanes, wildfire or flooding (Grogan et al. 2003; Gullison et al. 1996; Gullison et al. 2003; Snook et al. 2004; Frederickson et al. 2000; Lowe et al. 2003). Due to the ephemeral nature of these disturbances, mahogany trees tend to occur in essentially even-aged stands (Snook 2004). This strategy suggests that massive and prolonged canopy disturbances are required for successful regeneration. However, also small scale regeneration has been observed (Grogan et al. 2003). Brown et al. (2003) suggest that this is presumably accounted for by local variation in environmental factors such as soil fertility, light penetration and moisture availability. It is likely that such differences could explain the fact that mahogany population structure differs across its natural range.

Mahogany has often been exploited by selective logging, using a minimum cutting diameter of 50 or 70cm or sometimes 50cm (Gullison 1996, Grogan et al. 2002). Several researchers recognize that selective logging practices might cause a potential loss of sustainability due to changes in species

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[1] Paragraph 1.1 was written in conjunction with D. van der Staak.

[2] *Swietenia macrophylla* King will henceforth be referred to as 'mahogany'

composition. Yet, the effects of different forest management regimes are still poorly understood (Fredericksen and Licona 2000). Minimum cutting diameter extraction of all trees > 55cm in diameter depletes seed sources (Snook et al. 2005) and leaves a "shady, canopy-closed environment which is unfavourable for the establishment of mahogany seedlings" (Negreros-Castillo et al. 2003).
In addition logging has been correlated with a significant reduction in genetic diversity within the population (Gillies et al. 1999). Selective harvesting of mahogany trees is likely to decrease population size and to increase separation between populations. Gillies et al. (1999) suggest that this would raise the importance of long-distance pollination events. Yet, residual mahogany trees in selectively logged forests will suffer reduced outcrossing rates because an intact or disturbed forest canopy can restrict the recovery of genetic diversity in mahogany populations that have been exploited (Gillies et al. 1999).

The dramatic decline of mahogany populations in the last decades has made successful regeneration of the species indispensable to sustain future yields. Therefore appropriate forest management practices are required. Permanent sample plots in which different management regimes are applied are necessary to gain insight on how overexploited mahogany populations are recovering and on how environmental factors influence regeneration of this species. The Long Term Silvicultural Research Project (LTSRP) being carried out in different forest types of Bolivia by the Instituto Boliviano de Investigación Forestal (IBIF) provide such opportunity. This study is carried out in one of the study sites of IBIF, located within the FSC certified La Chonta forest concession. In this concession mahogany has been exploited for commercial production from 1974 until 1994. Since then it was excluded from the harvesting plans as it was already commercially extinct. This study thus basically looks at the recovery of an overexploited mahogany population.

1.2 Objective

This research tries to *determine the effect of four management regimes, varying in intensity, on the growth and development of mahogany populations*. This objective was unravelled to the following key questions:

- Does management intensity affect population structure and tree growth?
- Can these effects be attributed to light availability, stem quality, vine load and / or soil type?
- Is seedling dispersal altered under different management intensities?
- What is the role of soil type, organic humus and light availability in mahogany seed germination and early development?

1.3 General hypotheses

This study hypothesizes that intensive forest management regimes stimulate natural regeneration and performance of mahogany by increasing light penetration and reducing competing vegetation (figure 1a). Regeneration success is understood to be strongly light dependent (Grogan et al. 2003; Brown et al. 2003; Snook et al. 2005; Negreros-Castillo et al. 2003) and, as light availability will increase with management intensity (due to partial clearings or canopy openings), so will the survival of mahogany seedlings. In addition, mahogany seeds will probably be dispersed longer distances in more intensively managed (i.e. more open) forests.

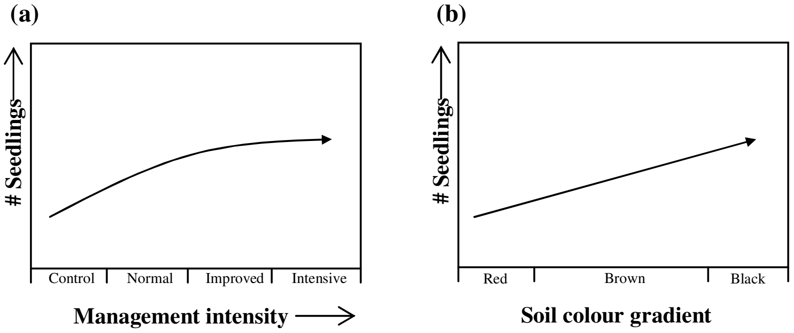

Figure 1 Hypotheses predicting the effect of management intensity (a) and soil type (b) on the regeneration of mahogany in the semi-deciduous tropical moist forests of Bolivia. The soil colour gradient is thought to represent a transition from low (red soils) to high (black) soil fertility.

The model in figure 1a suggests a certain optimum for the regeneration under intensive management. If management intensity (i.e. harvested volume) will increase further than shown in this graph, it is likely that the regeneration of mahogany is less successful as it suffers an increased felling damage. This might hamper mahogany regeneration either by direct damage to the seedlings or by altering the site for instance through compaction of the soil or through the induction of erosion on steep slopes resulting in the removal of nutrients from the top soil.

We expect that germination, growth and survival of mahogany is best on nutrient rich black soils (figure 1b). The presence of calcium and magnesium is essential in early mahogany seedling performance (Grogan et. al 2003). Naturally these highly mobile nutrients often accumulate in soils at low elevations such as in stream valleys or landscape depressions but they also occur in the Amazonian anthropogenic soils. These soils are characterized by their high organic matter content and elevated nutrient levels, in particular phosphorus, calcium, potassium and sodium (Woods et al. 2000, Glaser et al. 2001, McCann et al. 2001). Results found by Paz Rivera (2003) suggest that anthropogenic black soils can be found all over the La Chonta forest concession, indicating the existence of former livelihoods within the forest area. She reported that the presence of long-lived and generally poorly regenerating tree species such as mahogany may reflect this former cultivation. On the basis of this we predict the soil type an important determinant in successful regeneration of mahogany in the La Chonta concession.

Although it is not clear whether soil type may influence the germination of mahogany seeds as well, evidence suggests that soil moisture is the main factor triggering seed germination (Brown et al. 2003; Gerhardt 1996). Based on the water holding capacities of organic humus, we therefore hypothesise that germination will be better on highly humic soils.

2. METHODS

In order to assess the effect of management intensity on the development of mahogany a large scale field inventory has been performed. Effects of soil type, light intensity and organic humus on seed germination and early seedling development were additionally tested for in a nursery experiment.

2.1 Field inventory

2.1.1 Study site

This study focuses on the mahogany population being monitored since 2002 in the LTSRP plots in the La Chonta forest concession (see appendix I). This 100.000ha concession forms part of the Guarayos Forest Reserve in the department of Santa Cruz, Bolivia (15°47’ S, 62°55’ W). The area is situated around 250m above sea level and has a mean annual temperature of 25.3°C. Annual precipitation averages 1517mm with a five month dry season from June through October. Soils have been reported relatively infertile (oxisols, inceptisols and ultisols), with about 15% of the area being covered by anthropogenic soils (Pariona et al. 2003). Forests in this region are characterised as transitional forests between wet Amazonian forests and tropical dry forests (Jackson et al. 2002) and have been classified as a semi-deciduous humid tropical forest (Holdridge 1947). The forest has an average stem density of 367 stems ha^{-1} covering a basal area of 19.3 m^2 ha^{-1} and the average canopy height is 25m (all data for trees >10 cm DBH; IBIF, *unpublished data*). In the past forestry in this concession largely consisted of selective logging and mahogany was harvested at relatively low volumes (< 1m3 ha-1) (Fredericksen and Pariona 2002). These logging practices resulted in the current scarcity among larger size classes. Together with Spanish Cedar (Cedrela odorata L.), mahogany is currently not being harvested at La Chonta so that the species may recuperate from past high-grading (Pariona et al. 2003).

2.1.2 Experimental design

Within this concession IBIF is monitoring a total of 12 LTSRP plots covering 324 ha divided over three blocks[1]. Each block has been established in different annual timber compartments so that the natural range of basal area of timber species is included in the experiment. Each block contains four 27 ha treatment plots (450*600m), each of them receiving one of four treatments (figure 2 in appendix II). The treatments vary in harvesting intensity and application of silvicultural treatments (Table 1), ranging from an unharvested plot[2] to an intensively managed plot. All of these treatments are considered ‘sustainable forest management’. In all plots the inventoried trees have been labelled with a unique number and are recorded in a x y coordinate format.

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[1] The project was originally set up as a nested design with the blocks as replicates

[2] Until the 1990s mahogany has been harvested all over the concession and thus also in the ‘unharvested’ control.

Table 1 Management practices applied in the different treatments of the LTSRP plots at the La Chonta forest concession (after: Bongers 2004)

Treatments	**Control**	**Normal**	**Improved**	**Intensive**
▪ Forest inventories	●	●	●	●
▪ Cutting of lianas on harvestable, commercial trees	●	●	●	●
▪ Planning of logging roads		●	●	●
▪ Species specific minimum cutting diameters		●	●	●
▪ Harvesting of 80% of trees above cutting diameter		●	●	●
▪ Directional felling		●	●	●
▪ Marking Future Crop Trees (FCT) with a DBH > 10 cm			●	●
▪ Cutting lianas on FCTs			●	●
▪ Liberation of FCTs from surrounding non-commercial trees using poison-girdling			●	●
▪ Additional marking of lesser commercial species				●
▪ Cutting lianas on marked lesser commercial trees				●
▪ Liberating of FCTs marked lesser commercial trees by poison-girdling				●
▪ Cutting and poisoning of liana resprouts				●
▪ Girdling all non-commercial tree-species with a DBH>40 cm (except for trees important for wildlife)				●
▪ Soil scarification, removal of competing vegetation				●

In the LTSRP plots all mahogany trees > 1 cm in diameter at 1.3 m from the soil (DBH) have been inventoried in March-April 2002 (Ohlson-Kiehn 2003), July-August 2003 (Bongers 2004), and March – May 2006 (this study[1]). During the inventories all individuals were tagged and the following measurements were performed when applicable: diameter at breast height (DBH), height[2], crown position index (CPI)[3], crown form (CF), stem quality (SQ), and vine load (LIA). In 2006 the colour of the top soil layer (samples of top 10cm of the soil) was additionally evaluated using the Munsell color chart classification (Munsell Color 2000). Additional soil samples were taken at every 50m on the inventory trails in all plots of block I to determine the variation in soil colour independent of tree growth. In the 2003 and 2006 census newly recruited plants were as well recorded and tagged. It was also noted which plants had died between inventories.

Seedlings (<1.3m height) were recorded around 58 randomly selected parent trees most of them with a DBH>30cm. All seedlings located within a two meter circle around the base of each of these trees were tagged and measured. From the edge of that circle six strata comprising 60° arcs were defined and 48-meter long transects were placed within each stratum (Ohlson-Kiehn 2003). All seedlings within one meter of each transect were recorded. For each seedling height, percentage overstory cover,

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[1] Fieldwork for this study was carried out by D. van der. Staak and C. Verwer

[2] Tree height of trees >2m height was estimated using cross-triangulation or, when impossible, rougher estimates. Tree height of trees <2m was measured exactly with a height measuring tape.

[3] Categories of CPI, CF, SQ and LIA are given in appendix III

slope, slope position and distance to the parent tree were determined[1]. Diameter was measured only when trees were higher or equaled 1.3 meter height.

2.2 Nursery experiment

To determine the role of soil type and the presence / absence of organic humus on the seed germination of mahogany a short term nursery experiment was set up in greenhouses at the office of IBIF in Santa Cruz city, Bolivia (17°45' South, 63°14' West). In this experiment the germination and early seedling growth was followed on two different soil types (dark reddish grey soil (in the Munsell colour chart: 2.5yr 4/1) and a dark brown soil (in the Munsell colour chart: 7.5yr 3/3), two organic humus treatments (with and without a 3-4cm humus layer) and two light levels (1% and 10% illumination). The nursery experiment comprised of 16 trays each containing 24 mahogany seeds (48 seeds per treatment) (figure 3 in appendix II). To compare seed viability of different fruiting years this experiment was carried out for seeds of the most recent fruiting period (September 2005) and for seeds from the previous fruiting period (September 2004). Seeds did not obtain special conservation treatment. Germination success was determined as the percentage of germinated seeds. The seedling length (cm from soil surface to apex) and the number of leaves were measured for each of the seedlings. Measurements were done weekly, lasting 9 weeks since the beginning of the experiment. Seeds were considered to have germinated as soon as the embryo inside visibly had penetrated through the seed coat. Leaves were recorded as such when the leaf primordium was ≥ 0.5cm in length.

2.3 Statistical analysis

Data of all three inventories were joined into one datafile and statistical analysis was done using the statistical software program SPSS 12.0.1. Within the statistical analyses the field inventory and the nursery experiment are distinguished.

2.3.1 Field inventory

Population structure

To visualize the population structure of mahogany in the research plots, the density of individuals (# trees/ha) was calculated per diameter class. The width of diameter classes was determined as the square root of the average number of trees in the least represented treatments (Control, Improved and Intensive) which resulted in DBH classes of 15cm. This class width limited the number of not

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[1] The percentage overstory cover, slope and slope position were only recorded in 2002 and 2003, distance to the parent tree only in 2006.

represented size classes. Within the smallest size class (0-15cm DBH) seedlings (<0.5m height) and saplings (0.5-1.3m height) are distinguished.

To discover whether population structure differed significantly between 2002 and 2006 the cumulative frequency distribution of DBH in both years was compared using a two-independent sample Kolmogorov-Smirnov Test (KS). This test was performed for the total population regardless of treatments and blocks, and for each treatment, block and plot separately. In order to detect differences in diameter distributions among treatments and blocks within the same year, similar analyses were done for all treatments and blocks in 2002 and 2006.

Median DBH was compared among treatments for all blocks in 2002 and in 2006 with the non-parametric Kruskall-Wallis H test[1] (KW).

To express the relation between diameter and height for the mahogany population in the research plots the asymptotic regression equation of Thomas (1996) was used: $H_{max}*(1-e^{-\alpha*DBH^\wedge\beta})$, in which H_{max} is the maximum tree height and α and β are estimated parameters, initially set to 0.5 in this study. This equation was used only to describe the general pattern, regardless of treatments and blocks. It is based on maximum height of the trees and makes therefore ecological sense than linear regressions. Nevertheless, linear regressions were also done for the same variables on plot level to detect deviations from the general trend among treatments and blocks.

Growth

To figure out whether diameter growth is influenced by silvicultural treatments, diameter increment of trees > 1.3m height was compared among treatments. Diameter growth was calculated using the linear regression of the diameter increment (ΔDBH) between 2002-2003, 2003-2006 and 2002-2006. For each tree the slope of the linear regression represents the average daily growth rate. This is multiplied by 365 to obtain the annual growth rate. To increase reliability only trees that survived throughout the four year period were included in growth calculations. Differences in growth rates between size classes were subsequently calculated using linear regressions between diameter and diameter increment.

Tree characteristics

In order to discover to what extent variation in secondary growth can be attributed to individual tree characteristics, correlations between diameter growth (dependent) and CPI, CF, SQ and LIA (independents) are tested with the Spearman Correlation method. Clearly, interactions between these tree characteristics and DBH are important to include in the analysis. To account for these confounding effects the predicted diameter growth of mahogany was calculated in a series of

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[1] DBH data was not normally distributed and proper transformation was not possible. Therefore non-parametric tests were performed for this variable.

Univariate analyses (ANCOVA) where the independent variables were inserted as factors and DBH as covariate.

Effects of soil type

Soil types found during the field inventory were compared between blocks with a Chi-square Test. To detect potential soil preference in the mahogany population, the soil types measured via grid sampling in block I were compared with those that were sampled at each individual in the same block. These sample groups were statistically compared using the non-parametric Kolmogorov-Smirnoff Z test.

Seedling transects

Seedling abundance was compared between 2002, 2003 and 2006 for all treatments separately. The amount of seedlings was compared between parent trees in order to detect the extent of local variation in recruitment. Subsequently, the fecundity of parent trees was estimated for all years using logistic regression of the recruitment data (0=recruitment absent; 1=recruitment present) and inserting DBH as independent variable. This way the fruiting probability (%) for a range of DBH values was calculated.

Seedling growth has been used to indicate between treatment differences. Seedling annual growth rates were calculated similarly as the annual diameter growth rates (using linear regressions), but they are based on height increment (ΔH) instead of ΔDBH.

Additionally, to indicate the effect of management intensity on seedling dispersal, for each treatment the number of mahogany seedlings around the parent tree was correlated with the distance from its parent tree. Dispersal distances are compared <u>between</u> all treatments in a Kolmogorov-Smirnov Z test.

2.3.2 Nursery experiment

To detect differences in germination among all the factors tested for in the nursery experiment (light intensity, soil colour and humus layer), germination success was calculated for those factors separately with non-parametric Mann-Whitney tests. Furthermore time after which germination occurred was analysed for each treatment and their interactions with the Cox Regression Analysis in which the independent factors are inserted as covariates.

Correlations between the independent variables of the nursery experiment (soil colour, light intensity and humus layer) and the dependent variables (germination rate, seedling length, height increment and the number of leaves on each of the seedlings) as well as interactions between them are determined with linear regression analyses.

3. RESULTS

3.1 Field inventory

3.1.1 Population structure

During the initial inventory in 2002 1441 mahogany trees were recorded of which the majority (78%) were seedlings and saplings (< 1.3m in height). In 2003 605 living mahoganies were found (52% <1.3m height) and 57 of the trees tagged in 2002 were recorded dead. In 2006 only 504 living trees (42% <1.3m height) and 148 dead trees were found. The amount of individuals recorded differed considerably not only among years but also among treatments and blocks. Most mahogany in block I was found in the intensive plot (n=259) whereas in block III most individuals occurred in the normal plot (n=437). In block II numbers did not differ much between treatments except in the improved plot where hardly any (n=6) trees were found. Tree density in the total population averaged 4.4 ha^{-1} in 2002 and 1.6 ha^{-1} in 2006. Nevertheless this large difference was completely due to the huge amount of seedlings found in 2002. Densities of larger size classes (≥1.3m height) were slightly higher in 2006 as compared to 2002 and averaged about 0.1 ha^{-1}. Overall population structure differed significantly between 2002 and 2006 (KS: Z=8.695, p<0.001) but the densities among trees >1.3m height were not significantly different (KS: Z=0.668, p=0.763) (figure 2). Analogous results were found when

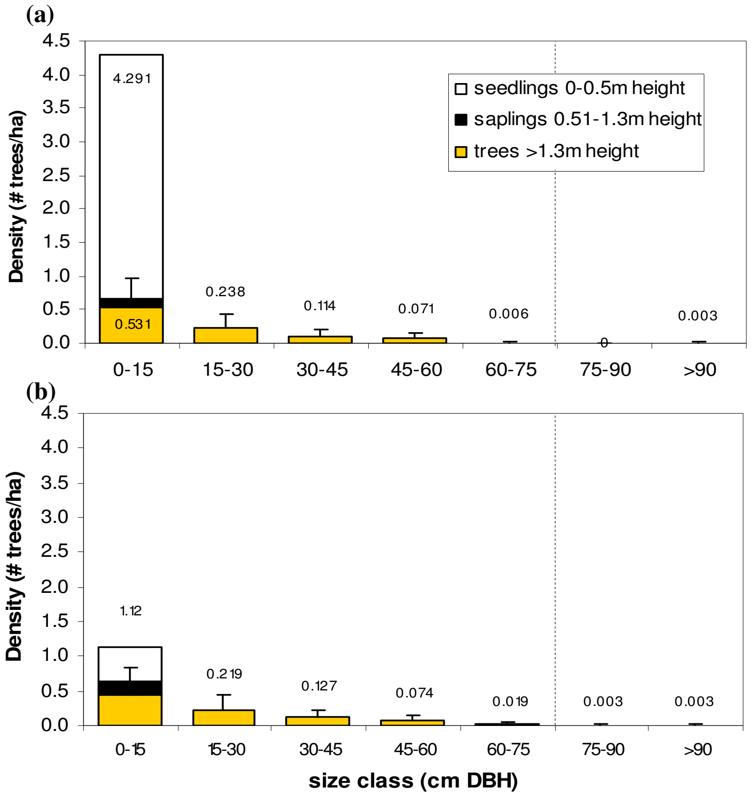

Figure 2 Tree density of mahogany per size class in the LTFRP plots at La Chonta. Data represents all individuals recorded in 2002 (a) and in 2006 (b). Error bars show the standard deviation calculated per plot for the trees >1.3m height. Vertical dashed lines show the minimum cutting diameter for mahogany.

comparing the densities per treatment (KS: $Z \geq 1.838$ and ≤ 6.039, $p > 0.05$ when including all individuals and $Z \geq 0.273$ and ≤ 0.669, $p > 0.05$ when including only trees ≥1.3m height) (figure 4 in appendix IV). In both 2002 and 2006 mahogany density generally decreased with increasing size class, but in 2006 densities of seedlings were much lower compared to 2002. Nevertheless, in both years differences occurred between treatments and between plots (figures 5 and 6 in appendix IV). In the normal treatment most of the size classes increased in the period 2002-2006 (table 2). In the improved plot of block II density of the smallest size class did not exceed 0.037 ha^{-1} in 2002 and in 2006 trees in the smallest size classes were not found at all. Trees with a DBH above the minimum cutting diameter (70cm DBH) were only present in the normal plot of block III. In block III the DBH of trees ≥1.3m height seemed equally distributed among all treatments, except in the control treatment where the smallest size class was very poorly represented. Differences in DBH distributions between the blocks were significant only between block I and III (KS: $Z=1.724$, $p=0.005$). Between the other blocks differences in the distribution were non-significant (between I and II: $Z=0.67$, $p=0.76$ and between II and III: $Z=1.255$, $p=0.086$).

Table 2 Change in mahogany density (# individuals ha^{-1}) per treatment for each size class in the period 2002-2006. Within the smallest DBH class seedlings (0-0.5m height) and saplings (0.51-1.3m height) were distinguished. Positive values (shaded) indicate an increase in tree density.

DBH(cm)	H(m)	Control	Normal	Improved	Intensive
0-15	0-0.5	-1.235	-5.383	-2.062	-3.951
	0.51-1.3	-0.049	0.111	0.210	0.025
	≥1.3	-0.062	-0.173	-0.062	-0.049
15-30		0.012	0.025	-0.025	-0.086
30-45		-0.062	0.037	0.012	0.062
45-60		0.025	0.025	-0.037	0.000
60-75		0.000	-0.012	0.049	0.012
75-90		0.000	0.012	0.000	0.000
>90		0.000	0.000	0.000	0.000

In 2002 median DBH differed significantly among treatments (KW: $X^2=9.655$, $p=0.022$) and was almost significant in 2006 (KW: $X^2=7.772$, $p=0.051$). It appeared that median DBH was only significantly different among treatments in block II (KW: $X^2=11.908$, $p>0.05$ in 2002 and $X^2=10.476$, $p>0.05$ in 2006) but not in blocks I and III (KW: $X^2 \leq 6.948$, $p>0.05$).

In both 2002 and 2006 the distribution of size classes differed significantly between some of the treatments (table 3a). Nevertheless, these differences were dissimilar between years. All differences were caused merely by the smallest size classes (i.e. seedlings and saplings <1.3m height). Excluding these smallest individuals from the analysis eliminated the significant differences (table 3b).

Table 3 Differences in the distribution of DBH classes between the silvicultural treatments in the LTFRP plots at La Chonta in both 2002 and 2006. Results of the Kolmogorov-Smirnoff test (Z = test statistic; p= significance level) are given for the whole population: a) including seedlings and saplings (<1.3m height) and b) excluding seedlings and saplings (thus only for trees ≥1.3m height). Marked numbers are statistically significant at the 0.05 level.

		2002		**2006**	
	Kolmogorov-Smirnoff:	**Z**	**p**	**Z**	**p**
a. all trees	Intensive – Improved	0.662	0.774	3.260	0.000
	Intensive – Normal	0.386	0.998	1.493	0.023
	Intensive – Control	1.835	0.002	0.770	0.593
	Improved – Normal	0.673	0.756	2.278	0.000
	Improved – Control	1.100	0.178	2.189	0.000
	Normal – Control	1.653	0.008	0.758	0.613
b. trees ≥1.3m height	Intensive – Improved	0.603	0.860	1.056	0.214
	Intensive – Normal	0.119	1.000	0.720	0.678
	Intensive – Control	0.862	0.448	0.237	1.000
	Improved – Normal	0.673	0.756	0.666	0.767
	Improved – Control	0.210	1.000	1.204	0.110
	Normal – Control	0.948	0.330	0.758	0.613

Diameter – height relation

Linear regression between DBH and height measured in 2006 yielded a significant relation between the two variables (F=1.066.58, P<0.001, R^2=0.78). The asymptotic equation of Thomas explains 86,5% of the variation (figure 7 in appendix IV) with a maximum height estimated at 31.8m. All plots separately confirm the general trend in this figure (figure 8 in appendix IV). In some of the plots a clear asymptotic relationship between DBH and height can be seen, thus levelling off to a certain maximum height. In general this pattern was remarkably similar between all treatments in block III, but the relationship was only hardly visible in the control and improved plots of blocks I and II.

3.1.2 Survival

Survival of trees through the four year period was very limited among seedlings and saplings but increased rapidly in larger size classes (table 3.2). Most individuals in the smallest size class (n=1092) that were alive in 2002 were reported dead or missing in 2006. 253 individuals newly recruited in 2006. Mortality over the four year period reached from 60 to 100% among seedlings and saplings and was on average 6% for larger trees. Table 4 presents the survival and new recruitment (including newly found individuals) over the four year period.

Table 4 Survival (*S*: % of total in 2002) and new recruitment (*R*: % of total in 2006) of mahogany trees within each size class per treatment as observed in the LTFRP plots at La Chonta in the period 2002-2006. Individuals that changed between sizes in this period are not indicated.

		Control		Normal		Improved		Intensive	
DBH(cm)	**H(m)**	***S***	***R***	***S***	***R***	***S***	***R***	***S***	***R***
	0-0.5	0.00	100.00	2.15	76.32	1.41	93.94	0.28	76.47
0-15	0.51-1.3	0.00	87.50	9.62	59.09	0.00	93.33	6.67	75.00
		45.83	0.00	46.07	0.00	50.00	0.00	47.83	3.70
15-30		84.62	0.00	65.63	0.00	54.55	0.00	42.86	0.00
30-45		58.33	9.09	77.78	0.00	33.33	25.00	80.00	0.00
45-60	≥1.3	75.00	0.00	100.00	0.00	42.86	0.00	75.00	0.00
60-75		-	-	50.00	0.00	-	-	-	-
75-90		-	-	-	-	-	-	-	-
>90		-	-	100.00	-	-	-	-	-

3.1.3 Growth

The average diameter growth rate for the mahogany population measured was 0.8 cm yr^{-1} but there was huge variation among size classes. Growth rates significantly increased with increasing DBH (Linear Regression: $R^2=0.263$, F=74.85, p<0.001) (figure 9 in appendix IV). Differences in growth rates among treatments were significantly influenced by DBH (ANCOVA: F: 99.832, p<0.001). In block I diameter growth rates obviously increased with increasing management intensity but in the other two blocks this clear pattern was not observed (figure 3). Mahogany in the intensively managed plot of block II had higher growth rates than the control plot but in block III diameter growth rates barely differed between treatments.

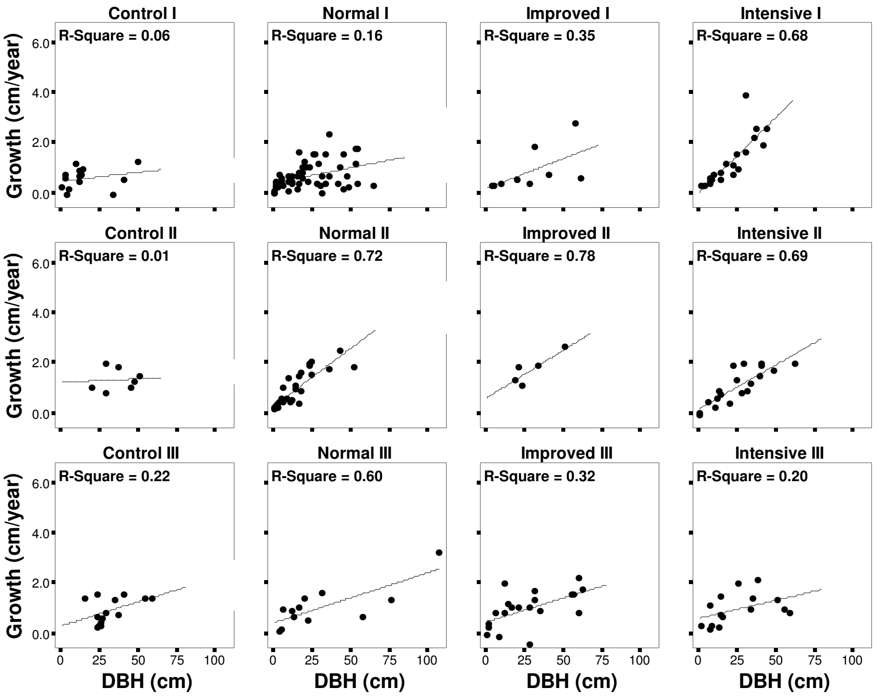

Figure 3 Diameter-growth relations of mahogany for each of the LTFRP plots at La Chonta. Linear regression lines are projected in each scatterplot.

3.1.4 Tree characteristics

Twenty-one percent of the mahogany trees inventoried in 2006 were classified as emergent or dominant but the majority (59.6%) occurred in the understory and was classified as "shaded". CPI increased with increasing DBH (figure 10 in appendix V). Strong correlations between CPI and DBH were found in all years of measuring (Spearman's rho: $p<0.001$, with correlation coefficient = -0.274, -0.691 and -0.8 for 2002, 2003 and 2006 respectively). Correlations between CF and DBH were less pronounced (Spearman's rho: $p<0.05$ in 2002 and 2003 and $p=0.217$ in 2006, correlation coefficients were -0.187, -0.173 and 0.073 for the three years respectively). Results for LIA and SQ do not indicate an obvious trend. Small liana loads generally occurred among trees smaller than 20cm DBH. Trees with lianas on both trunk and crown were generally thicker than the rest whereas heavily infested trees had similar diameters as the first two categories. Stem quality of the trees did not differ significantly but our findings suggest that a good stem quality was more common among thicker trees and worst qualities were generally found among the smaller DBH classes.Most of mahogany trees recorded at La Chonta had perfectly shaped crowns (75.9%) and a good stem quality (82.5%).

Diameter growth was significantly lower in overtopped, understory and shadowed trees (average 0.48cm yr^{-1}) as compared to the growth of dominant and emergent trees which averaged 1.3cm yr^{-1} (figure 4). Univariate analysis revealed that treatment had significant effects on diameter growth but

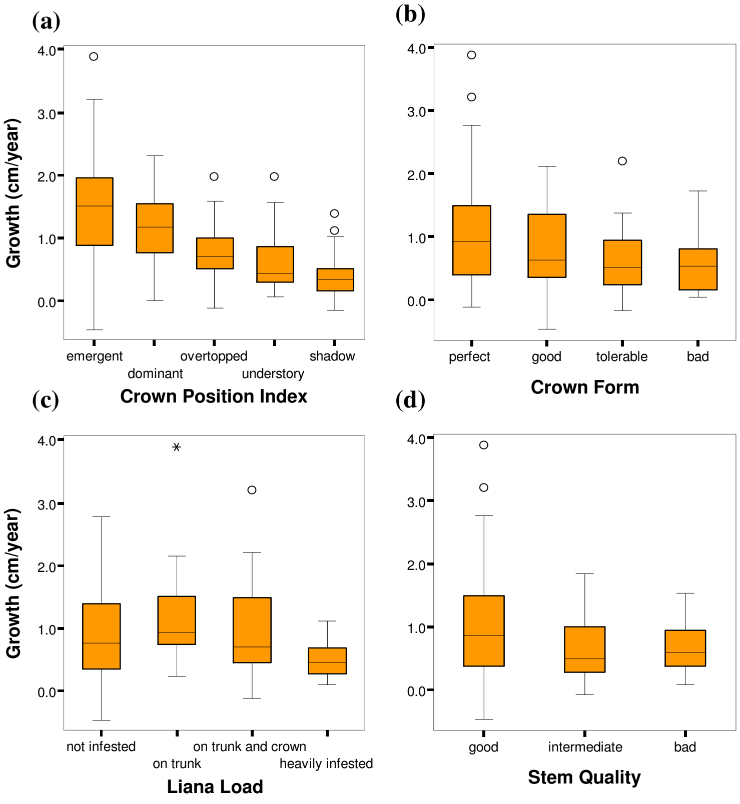

Figure 4 Relative growth rates (cm/year) for mahogany as a function of a) Crown Position Index, b) Crown Form, c) Liana load and d) Stem Quality. In this figure the total population as inventoried at La Chonta in 2006 is shown, thus regardless of the treatments and blocks. Circles represent extremes, asterisks represent outliers.

effect was strongly influenced by tree size (ANCOVA: F=2.834, p=0.039 for treatment and F=99.832, p<0.001 for DBH). CPI, CF, LIA showed highly significant effects on diameter growth (CPI: F=5.283, p<0.001; CF: F=6.739, p<0.001; LIA: F=4.501, p=0.004). SQ did not significantly influence diameter growth (SQ: F=0.1.864, p=0.158). When combining all these factors in the analysis it appears also that the interaction terms TREATMENT*LIA and CF*LIA had significant effects on diameter growth (F=3.213, p=0.016 and F=3.488, p=0.035 respectively).

Diameter growth was not evidently limited in mahogany trees that were infested with lianas. In heavily infested trees diameter increment averaged 0.7cm yr^{-1}. For trees that were not infested with lianas this was 0.9cm yr^{-1}. The vast majority of all mahogany trees (79%) were not liana-infested and only 4% of the trees were categorized as heavily infested (figure 11 in appendix V).

3.1.5 Effects of soil type

Twenty five different soil colours of the Munsell colour chart were recorded in the field. This number was reduced to twelve different colours by using the Munsell description of the soil colour rather than the colour code. Soil colour differed significantly between blocks (X^2 = 80.645, df=2, p<0.001). Nevertheless, in all plots the majority of trees (>65% of the individuals measured) were found in 'dark brown' soils. 'Brown' and 'very dark brown' soils were common as well. Grid sampling in block I showed that these soil types were also the most frequently occurring in the area (figure 5). The soil colours among tree inventory data did not differ significantly from grid inventory data (KS: Z=-0.672, p=0.757). Mahogany trees were rarely observed in black and red soils. Correlations between soil type and tree height, DBH and DBH increment were not found (Spearman's rho: Correlation Coefficient <0.064, p>>0.05) and diameter growth rates did not differ significantly among soil types (ANOVA: F=1.197, p=0.29).

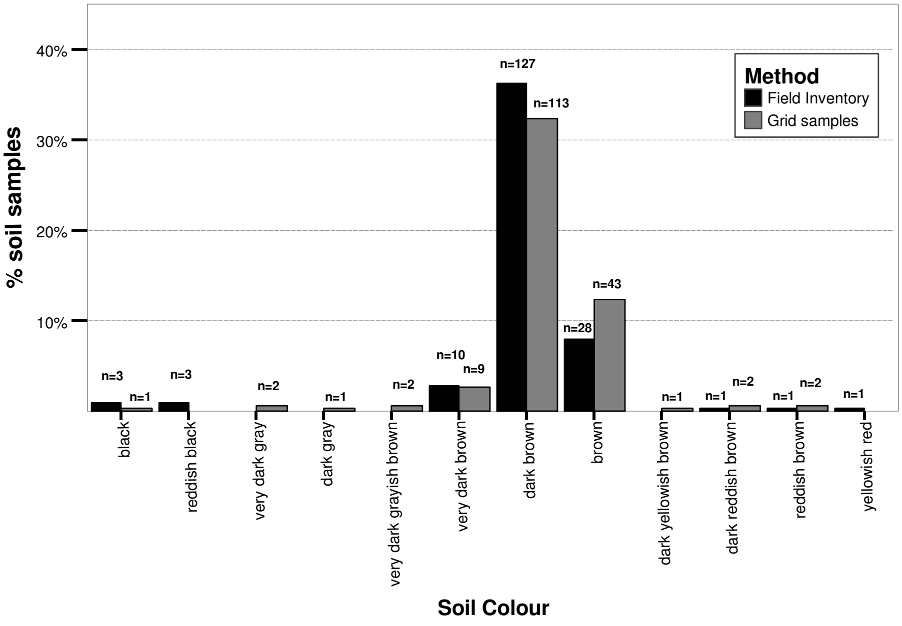

Figure 5 Percentage of mahogany trees found in each soil type in block I (black bars) and the percentage of soil types found during grid sampling of block I (gray bars).

3.1.6 Regeneration transects

The majority (82%) of the mahogany individuals measured within the regeneration transects in 2006 were between 20-60cm height whereas seedlings <10cm and >60cm were very poorly represented. The amount of seedlings differed considerably between years and treatments (table 5). On average most regeneration occurred in the normal treatment. However, the decline since 2002 was strong, especially in the intensive and normal plots. Furthermore, between 2002 and 2003 the number of seedlings in the improved treatment diminished greatly. More importantly however, the recruitment differed considerably between parent trees and for each parent tree recruitment also differed noticeably between years (figure 12 in appendix VI). Yet, the general pattern was that, in all years of measuring, the probability of fruiting significantly increased among larger size classes (Logistic Regression: -2Log Likelihood ≤66.531, $p<0.05$). Figure 6 shows the fruiting probability based on the 2006 inventory data.

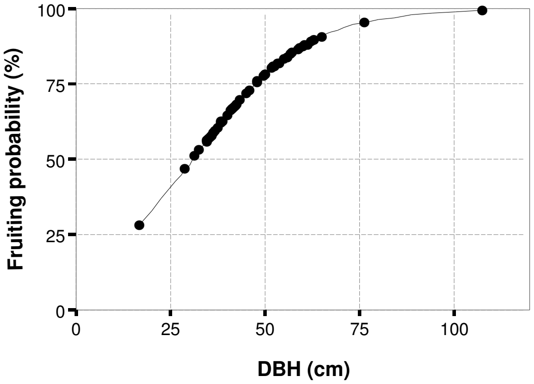

Figure 6 Probability of fruiting as a function of DBH for the parent trees in the mahogany transects within the LTFRP plots at La Chonta. Data were measured in 2006. The dots represent the predicted probability as calculated by a logistic regression model for each individual parent tree. Cut-off value used in the regression was 0.5.

Tabel 5 Numbers and relative abundance (% of total number of individuals found in the transects) of mahogany seedlings and saplings (<1.3m height) measured in the regeneration transects within the LTFRP plots at La Chonta. Results are given for the three years in which these transects were inventoried. The percentages do not add to 100 exactly because trees ≥1.3m height were also measured in the transects (not indicated in the table).

	Treatment			
Year	**Control**	**Normal**	**Improved**	**Intensive**
2002	117 (10.34%)	519 (45.85%)	119 (10.51%)	346 (30.56%)
2003	76 (21.1%)	114 (31.67%)	9 (2.5%)	124 (34.44%)
2006	25 (9.88%)	91 (35.97%)	79 (31.23%)	28 (11%)

Seedling dispersal

The number of mahogany seedlings diminished rapidly with distance from the parent tree (figure 7). Recruitment essentially occurred regularly in all directions measured (figure 13 in appendix VI), but variation within and between treatments and blocks was high.

Dispersal distance differed significantly between most of the treatments (KS: $Z \leq 3.623$, $p<0.05$), but differences between the normal and control plots were not significant (KS: $Z=1.218$, $p=0.103$).

In the control treatment the number of seedlings seemed to diminish very rapidly further from the parent tree whereas in the intensive treatment this number dropped only slowly. However, this pattern in the control treatment is caused by the large amount of seedlings of just one parent tree (#137) (figure 14 in appendix VI). Maximum dispersal distance was found in the intensive plots.

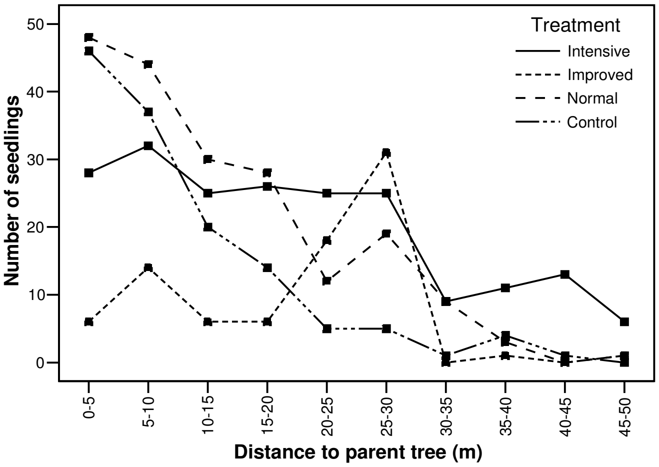

Figure 7 Seedling abundance for mahogany as a function of the distance to the parent tree (m). Results are given for all seedlings within the regeneration transects established in the LTFRP plots at La Chonta. Different lines indicate the silvicultural treatments.

Seedling growth

Height growth of seedlings and saplings over the four-year period averaged 5.38cm yr^{-1} and increased significantly with the height of the individuals as measured in 2006 (Linear Regression: $F=11.430$, $R^2=0.37$, $p=0.001$). The regression results are shown in appendix VI, figure 15.

3.2 Nursery experiment

Only seeds from 2005 germinated in the nursery experiment; consequently, results presented here are solely based on the germination of seeds from 2005. Seeds germinated significantly faster on soils containing an organic humus layer (Cox Regression: -2Log Likelihood=170.96, $X^2=6.798$, $p<0.05$). Light intensity, soil colour and interaction effects between the variables were non-significant in this analysis ($X^2 \leq 4.006$, $p>>0.05$). The survival curves for the main variables are projected in figure 8.

At the end of the experiment (i.e. nine weeks after the seeds were planted) germination was slightly higher in high light conditions but results were not significant (Mann-Whitney Test: $U=18144$, $Z=-0.672$ $p>>0.05$). Twice as much seeds germinated in grey soil (2.5yr 4/1) and slightly more seeds germinated on soils with an organic humus layer (figure 16 in appendix VII). Results were however neither significant (Mann-Whitney Test: $U=17760$, $Z=-1.569$, $p>0.05$ for soil type and $U=17952$, $Z=-1.121$, $p>0.05$ for humus layer).

Seedling development until the final week of the experiment did not differ significantly among treatments. In all treatments height growth as well as the number of leaves increased linearly with seedling height (Linear regression: F=16621.2, df=190, $p<0.001$ and F=1248.9, df=190, $p<0.001$ for height increment and #leaves respectively). However, this increment was much higher at low light levels compared to high light levels (figure 17 in appendix VII).

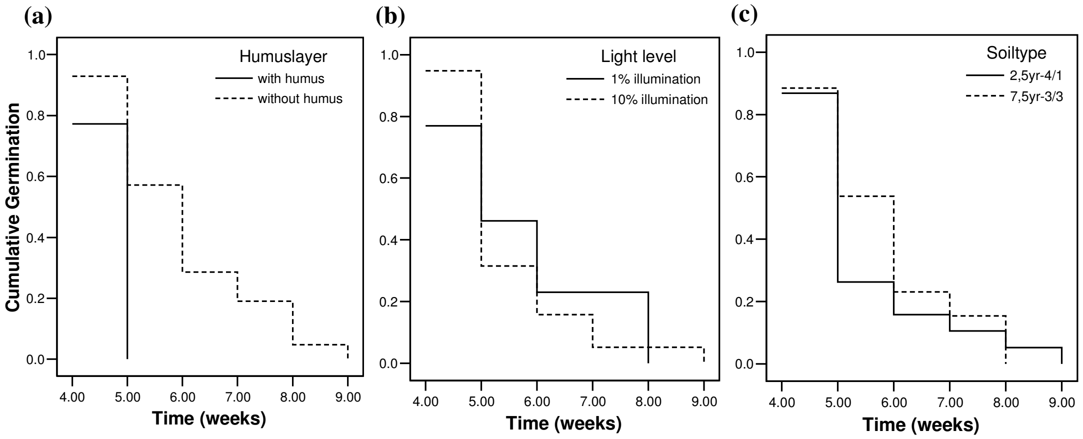

Figure 8 Survival function of germination (y-axis) of mahogany seeds during a nine week lasting germination experiment under different treatments: a) with and without humus, b) under high and low light availability and c) in grey (2,5yr-4/1) and brown (7,5yr-3/3) soil.

4. DISCUSSION

4.1 Population structure, growth and survival

The results presented in this study do not unequivocally confirm the hypothesis that intensifying forest management stimulates the recovery of mahogany populations. Natural regeneration and survival differed between management types but these differences were not always significant and the best regeneration did not occur in the most intensively managed forest plots. The growth of mahogany however, seems to respond positively on more intensive forest management.

Population structure

Seedling abundance in 2002 was exceptionally high compared to 2003 and 2006, especially in the control plot of block II and in the normal plot of block III. Recruitment was higher in 2002. This might be caused by the increased light availability after the recent logging operations in the plots. However, high seedling densities were also found in the unharvested control plots. It is therefore more likely that fruiting in the previous year (2001) was exceptionally high – a result that also supports the idea of great annual variability in mahogany fruiting (Grogan 2006). In all years of measuring most seedlings were recorded in the normal treatment. The majority of this recruitment stemmed from only few parent trees. The ample variation in tree density found among blocks and treatments illustrates the clumped distribution of mahogany within the research area. Although density variation was high among plots, the control and improved treatments harboured fewer individuals than normal and intensive treatments. In the control treatment low light availability presumably impedes the growth of mahogany seedlings and saplings. Low densities in the improved plots could alternatively be explained by increased interspecific competition and poor seed production in recent years.

Densities in the larger size classes did not differ greatly. Trees of reproductive size (>30cm DBH) had densities reaching from 0.1 to 1 ha^{-1} and densities of commercially sized mahogany trees (>70cm DBH) were low (0.01-0.1 ha^{-1}). In 2006 the least individuals were found in the improved plot of block II, all > 20cm DBH. Here, seedlings and saplings died as an effect of a recent forest fire (2004) which hit the improved and normal plots in this block. Two years later, during the 2006 inventory, this area was colonized by gap invaders shaping an environment highly inappropriate for mahogany regeneration (i.e. competitive exclusion of mahogany seedlings mainly due to low light availability). This observation seems anomalous according to the catastrophic disturbance paradigm (Snook 1993; Gullison et al. 1996) in which fire has been mentioned as one of the major disturbances required for successful mahogany regeneration (Gullison et al. 1996; Grogan et al. 2003). Seed rain was absent after the fire (pers. comm.) presumably because the reproductive trees in the plot were themselves recovering from the fire. It seems likely that photosynthate allocation was altered at the expense of reproductive capacity. Indeed, the potential seed trees had fire marks and were observed not to fruit at the sites that burnt recently.

Diameter distributions of the population differed between management types but these effects were only significant in blocks II and III. As an effect of previous logging operations almost all mahogany trees with a diameter > 70cm were absent. Generally all size classes below the cutting diameter were abundant in the research area, contradicting the idea that large scale disturbances have led to an even-aged mahogany population in this forest. The smallest DBH class was best represented in the normal and intensive plots. This suggests that regeneration is most successful under these treatments and hence does not support the hypothesis that mahogany regeneration increases with intensifying forest management. Contrary, the extremely low proportions of trees in the smallest DBH class in the control plots of blocks II and III suggest that the population is not successfully regenerating. Perhaps these plots recently suffered extremely low seed production/germination or high seedling mortality, effects that could both be induced by high environmental stress such as prolonged drought, herbivory or (felling) damage.

Between treatment differences in block III are hardly visible which suggests that treatment effects are negligible here. Possibly, logging effects on the mahogany population are not yet visible in this block as logging was done much later (January-October 2002) than in block one (January-May 2001) and two (June-September 2001) (Ohlson-Kiehn 2003). In addition, harvesting intensity depended on the density of harvestable trees present in each plot and for this reason differed between plots. In block II the number of harvested trees averaged 3.8 ha^{-1}, in block three 3 ha^{-1} and in block one this was only 1.8 ha^{-1}. Consequently, total gap area per treatment due to harvesting was highest in block II (on average 8.6% compared to 4.3% in block I and 7.5% in block III). So obviously block II was most intensively harvested. Nevertheless, the number of recruited seedlings measured recently after the harvest (2002 inventory) was not particularly higher in block II. In fact seedling density varied strongly among plots due to the differing numbers of reproductive trees and on the varying fecundity of these trees. Thus, mahogany recruitment may vary considerably on a local scale, regardless of any forest management regime.

Growth

Although mahogany growth rates appear to be remarkably consistent across its natural range (Gullison 1996), at smaller scales growth rates strongly depend on site specific light levels and might consequently react strongly on artificial canopy openings and other management measures that increase penetrating light. Average diameter growth rates of mahogany tend to vary widely in natural forest, ranging from 0.38 - 1.49cm yr^{-1} in this study, depending on the tree size. Clearly, highest growth rates occurred in the largest DBH classes. In blocks I and II of this study diameter growth rates of mahogany increased with increasing management intensity. In block III however, growth rates were similar in all treatments, suggesting that, in this block forest management did not affect mahogany growth rates at all. This could support the idea that logging effects are not yet visible in the mahogany population of block III (especially not among larger DBH classes as logging did not influence light availability in those size classes) but it could also indicate that factors other than light are limiting growth in this block. For instance Grogan et al. (2003) described the importance of high soil fertility and water availability for mahogany to achieve high growth rates. Nevertheless, clustering of the results per treatment yields a high variation within each treatment. Growth differences are therefore likely to be caused by small scale variation in both the physical and biotic environment. To assess long term management effects on growth and performance of mahogany this research should prolong for a longer period.

Survival

Mortality of mahogany was highest among the smallest size classes as these are most vulnerable to environmental stress (drought, herbivory, insect attacks) and direct damage. Moreover, light is generally limiting in the forest understory. According to the results of this study light seems the major factor in the regeneration of the species. Regardless of the phenological state of the trees, growth and survival will be severely limited under low light conditions. In a shady environment seedling mortality was high and, as a consequence, successful recruitment basically occurred in more open forests. This study therefore suggests that increasing light levels may decrease seedling mortality. However seedling mortality can have several causes other than light shortage. It might as well reflect differences in precipitation, predation levels or nutrient status. A large proportion of the seedlings found had signs of insect predation, one of the major limiting factors growth and survival on abandoned slash and burn fields and in mahogany plantations (Snook et al. 2004; Negreros-Castillo et al. 2003). Effects of water and nutrient limitation were not identified in this study but are considered to be of major influence in seedling and sapling growth and survival (Gerhardt 1996).

4.2 Effects of tree characteristics, liana load and soil type

Tree characteristics

Light availability being the major determinant influencing mahogany growth and survival, was measured in the field by the CPI and the crown form. Both of these had significant effects on diameter growth of mahogany. In all treatments highest growth rates occurred among emergent and dominant trees. Overtopped and understory trees generally have smaller crowns and produce less photosynthates which they can invest in growth. Gullison (1996) has shown that mahogany trees allocate little of their photosynthates to reproduction, until they have grown to large size classes (i.e. >75cm DBH). Instead, they invest more in mechanical support (buttresses) and chemical defence (secondary compounds), which might, in the early life stages, go at the expense of growth. Although buttresses were scarcely observed on smaller trees, this study indeed identified slower growth among smaller size classes. The extreme variation in relative growth rates observed in this study may reflect the differences in photosynthate allocation especially among smaller individuals. These differences are possibly caused by the temporal as well as spatial highly varying levels of environmental stress, caused for instance by herbivory or drought.

Stem quality did not differ significantly among treatments and growth did not react on stem quality, but a positive correlation between stem quality and DBH was found for 2002 and 2003. Perhaps this indicates that a mahogany tree can improve its stem quality during its development.

Liana load

Although La Chonta is apparently among the most liana-infested forests in the world (Alvira et al. 2004), the majority of mahogany trees, particularly among smaller size classes, were not infested with lianas. Liana load did not increase significantly with tree diameter and the effect of liana load on diameter growth of mahogany was not obvious. Growth rates differed considerably among trees that had lianas only on the trunk, which is possibly caused by inconsistently cutting lianas in all treatments. Research of twelve commercial tree species at La Chonta revealed that both the proportion of liana-infested trees as well as the liana loads on these trees varied considerably among species (Alvira et al. 2004). Perhaps mahogany has a lower probability of being liana-infested due to species-specific characteristics that allow it to avoid or shed lianas (Putz, 1984b, 1995; Clark and Clark, 1990; Pinard and Putz, 1994; Campbell and Newbery, 1993; Carse et al., 2000. *In:* D. Alvira et al. 2004). Although most individuals measured in this research were fairly small (<20cm DBH) and not likely to become liana-infested, liana proliferation could still affect the mahogany population by impeding regeneration after small scale disturbances such as wildfire (Pinard et al. 1999). Indeed in the field some seedlings were overgrown by resprouting lianas. This resprouting might be enhanced in more frequently disturbed forests (Pinard and Putz, 1994; Pinard et al. 1999). Nevertheless, liana loads of mahogany were comparable between all treatments, likely because lianas were cut as a silvicultural treatment.

Soil type

Mahogany did not demonstrate a clear soil preference. Most frequent soil types in the research area corresponded with the soil types in which mahogany trees were found. Contrary to the hypothesis, most of the soils in the research area were classified as dark brown. Black and red soils only rarely occurred and indications of former livelihoods were not found in this study. However, we merely looked at the superficial soil layer (top 10cm) which forms only a limited part of the total soil profile. Other soil factors such as density (aeration, soil structure) and the presence or absence of a soil organic humus layer are likely to have a larger impact on tree performance as they influence water and oxygen availability in the rooting zone (see also Whitman et al. 1996). The importance of such factors should gain more attention in future research, not only because it is important for natural regeneration but also because it might reveal valuable information to increase growth and survival in mahogany plantations.

4.3 Seedling dispersal

Generally seedlings occurred randomly around the parent trees. Seedling density was highest directly beneath the crown and dropped rapidly with distance from the tree. Under a number of seed trees regeneration was strongly clustered together, probably because fruits opened only when already fallen onto the ground (pers.obs). Largest dispersal distances were observed in intensively managed forest, which could be explained by the hypothesis that dispersal is hindered by an extensive vegetation cover such as observed in the control plots. Lowe et al. (2003) stated that in open structured forests mahogany seeds can be dispersed long distances and seedlings are likely to establish as large clusters of mahogany trees. Nevertheless, uncertainty of the origin of seedlings exists in our method since the seedlings were not genetically compared with their presumed parent trees.

Although mahogany seeds are essentially wind dispersed (Gullison 1996) our results did not show a clear correlation of seedling density with prevailing wind direction. Perhaps germination was so low that seedling dispersal does not reflect seed dispersal. Seedlings were measured approximately one or two months after germination. It could thus be that germinated seeds died before they were observed. Recent seeds and/or seedlings could however also have suffered a very high mortality, caused by for example drought or predation. Janzen (1988) reported predation of mahogany seeds by some rodents but seed predation is still poorly documented for this species. Field observations in La Chonta suggested that fungi infestation as well as algae growth on seeds was common on wet soils. However, most of these observations were done on non-germinated seeds of the previous year. Still, mammals, invertebrates, and fungal pathogens may account for serious seed mortality (Grogan 2006).

4.4 Seed germination and early seedling development

The presence of a layer of organic humus appears to have significant effects on the germination of mahogany seeds. As germination has been found to be triggered by soil moisture (Brown et al. 2003) this could be explained by the higher water holding capacity of humus compared to bare soil. In addition, humus often contains important soil nutrients that are crucial for seedling growth. On the other hand humic soils contain organisms that might pray on mahogany seeds (fungi, small insects, larvae etc.). Moreover seeds other than mahogany that are present in the humus layer could potentially compete with mahogany. These effects were nevertheless trivial in this experiment.

In natural forest there is no mahogany seed bank in the soil because mahogany seeds are only a few months viable (Rodríguez y Pacheco and Barrio-Chavira, 1979; Parraguirre, 1994; Morris et al., 2000; In: Snook et al. 2004). This indicates that a suitable climate for germination should be present at the time seeds are shed. A late onset of germination could lead to desiccation of seedlings at the beginning of the dry season as their root system is not yet sufficiently developed (Gerhardt 1996).

The success of mahogany regeneration will strongly depend not only on the presence of suitable regeneration sites at the time seeds are released, but also on the quality and quantity of produced seeds. The results of this study indicated that seed production might vary strongly between years, probably in response to environmental factors ('resource matching strategy', elucidated by Snook et al. 2005). Yet, the major factors determining the fecundity of adult mahogany trees are not explicitly known and further research should provide more insight in this.

4.5 Synthesis

This study looked at the development of mahogany in a forest concession where mahogany was basically commercially depleted and seed sources were scarce. Low seed availability, as a consequence of selective mahogany logging in the past, restricts successful natural regeneration. Sustainable forest management is concerned with the question whether artificially opening up the canopy could stimulate natural regeneration of mahogany. In this study, highest seedling mortality was found in both control and intensive plots, suggesting that extensive regeneration can not be enhanced merely by intensifying forest management. Results from La Chonta indicate that canopy openings could drastically increase exploitation and interference competition by other, non-commercial species such as lianas, *Heliconia* sp., *Costus* sp., and ferns. Obviously this gap colonization by other highly competitive species significantly hampers successful post-disturbance regeneration and seedling growth of mahogany (Snook, Negreros-Castillo 2004).

Most mahogany regeneration in La Chonta does not occur under large canopy openings but rather in slightly lighter forest patches where strong competition is absent, which indicates an ecological optimum for the species' regeneration. Apparently coverage by different species occurring in forest clearings could have major advantages for the survival of mahogany seedlings as it helps 1) decreasing initial stress on seedlings by reducing evapotranspiration and temperature fluctuations (Grogan et al. 2003), 2) providing shelter against direct damage such as herbivory by larger mammals or damage caused by falling branches etc., 3) reducing the risk of soil erosion and consequently the loss of important macro and micro elements, and 4) offering physical or chemical protection ('shield') against insect attacks (Snook et al. 2004).

Nevertheless, relations indicated in this study may hold for Bolivian lowland moist forests, but may be different elsewhere in mahogany's natural range. Brown et al. (2003) suggested that mahogany population composition differed across a rainfall gradient from semi-deciduous forests to evergreen rain forests. In the latter light availability is far more limiting the regeneration of the species so that large scale catastrophic disturbances may be essential there for mahogany to sustain. In addition, large gaps are likely to form more suitable regeneration patches in evergreen rainforests because desiccation of seedlings will be less severe. Mahogany management should therefore take into account that the species may react differently across its range. Its requirements for large scale disturbances depend on both abiotic (e.g. light, moisture, nutrients) and biotic (e.g. seed predation, herbivory, competition) factors, that vary spatially and temporarily at different scales.

5. CONCLUSION

Sustainable forest management can alter population structure and tree performance of mahogany but intensifying forest management seems not to have an unequivocal impact on the development of mahogany populations. Growth of mahogany increased with increased management intensity but variation in growth was high, also in intensively managed forest. Induced growth can particularly be attributed to the availability of light. Other tree characteristics measured in this study (stem quality, liana load and soil type) only had negligible effects on diameter growth rates of mahogany.

Seed dispersal range seems to be wider in intensively managed forest, and thus also the chance of colonizing suitable patches for seedling growth seems to increase in forests under intensive management. More open forest environments might favour mahogany seed dispersal but do not guarantee successful regeneration. Mahogany seems able to persist in closed canopy environments of (semi-)deciduous forests that are periodically opened up by small-scale local disturbances. Therefore it appears that mahogany regeneration is not induced necessarily by large scale catastrophic disturbance events but that the necessity of disturbances for the persistence of mahogany particularly depends on the existing forest structure (i.e. light penetration). Although an intensive management regime may have positive effects on the growth of mahogany, intensifying forest management as such will not provide for successful mahogany regeneration. Mahogany regeneration seems particularly dependent on 1) the presence of appropriate regeneration sites and 2) the abundance and fecundity of parent trees. The presence of an organic humus layer at these sites may significantly trigger mahogany seed germination and prevent seedlings from desiccation. Superficial soil type and light level did not influence the germination of mahogany seeds in the greenhouse experiment of this study.

Seed production of reproductive trees may show considerably short term variations. Additionally, annual mortality among seedlings can reach extremely high levels. To sustain future yields it will therefore be especially important to 1) provide appropriate regeneration sites at the time seeds are released from their fruits; 2) mark and protect Future Crop Trees, in particular of reproductive (>30cm DBH) and commercial (>60cm DBH) size classes and 3) decrease mortality among small seedlings and saplings by avoiding felling damage and liberating them to decrease interspecific competition and the risk of insect attacks.

Sustainable forest management may help to recover overexploited mahogany populations in Central and South America, but the species is found to react differently across its natural range. Therefore, drastic silvicultural interventions such as proposed by some researchers are not necessary to sustain mahogany production in semi-deciduous forests. They may even form a threat to biodiversity and ecosystem functioning. Appropriate forest management should therefore take account of the full range of forest types in which mahogany occurs.

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APPENDIX I STUDY SITE

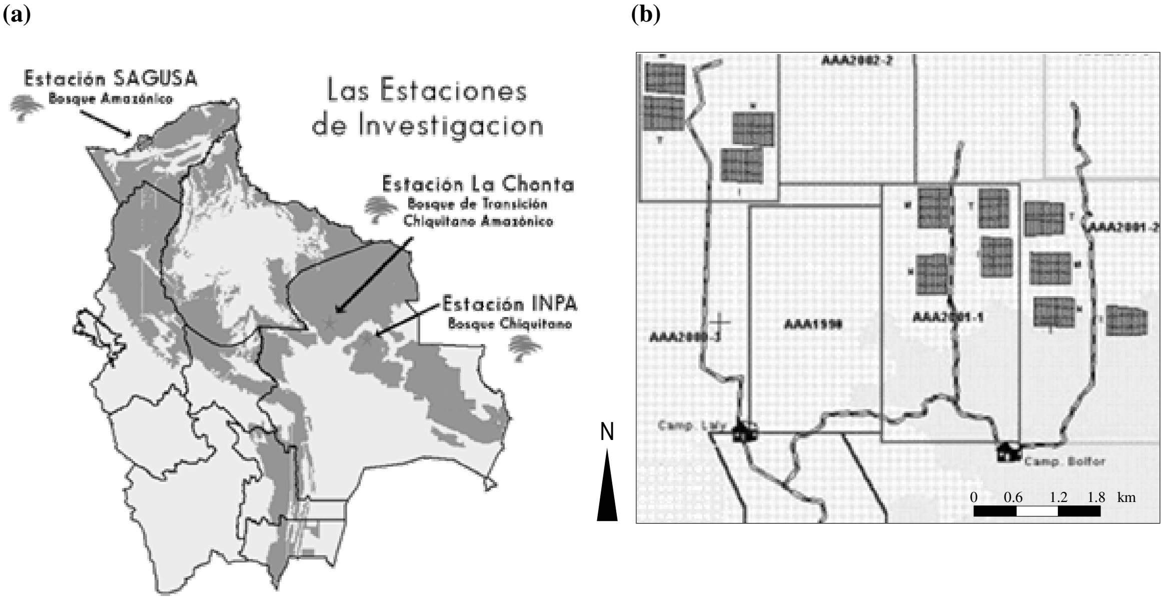

Figure 1 a) Overview of the IBIF research locations in Bolivia (source: www.IBIFBolivia.org); b) Part of the La Chonta forest concession in which the LTFRP plots are located (dark gray). From left to right the clusters of four plots constitute block III, block II and block I (four most right plots). Treatments are indicated in the figure (I= Intensive; M= Improved; N= Normal; T= Control).

APPENDIX II EXPERIMENTAL DESIGN

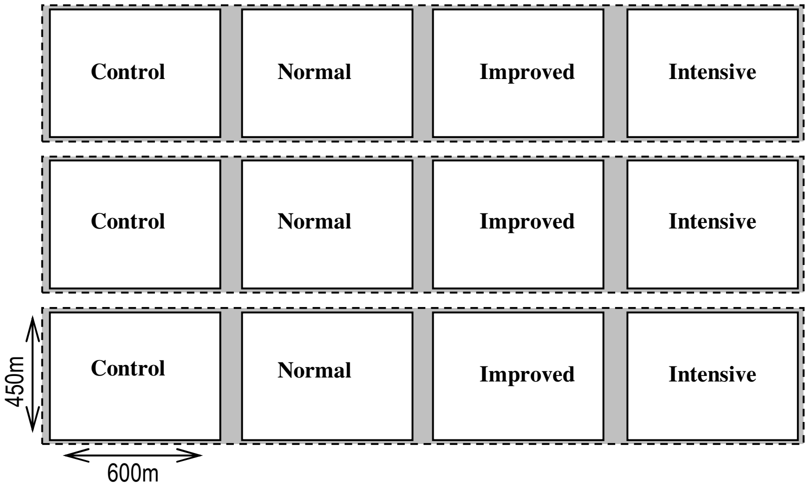

Figure 2 Simplified representation of the experimental design of the field experiment. Blocks are indicated by shaded areas and plots by solid lines. In each plot the treatment is indicated. All plots have approximately the same size (600m by 450m). The control plots are all surrounded by a 150m wide bufferzone (not indicated).

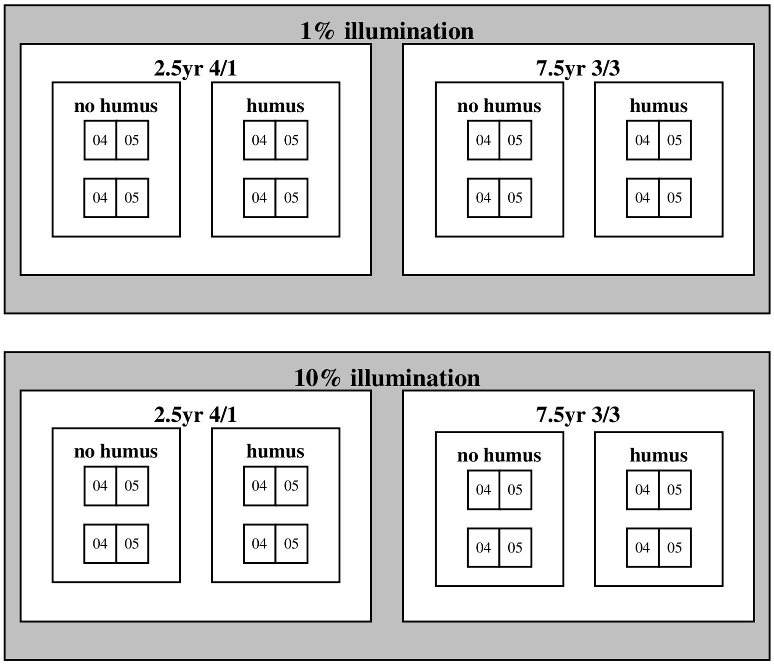

Figure 3 Experimental design of the nursery experiment. Split squares are the trays containing 24 seeds each: 12 from 2004 (04) and 12 from 2005 (05). The experiment was done under two different light levels (1% and 10% illumination) and on two contrasting soil types (dark reddish grey soil: 2.5yr 4/1 and a dark brown soil: 7.5yr 3/3). Furthermore the experiment was carried out on bare soils and on soils containing a 3-4cm humus layer.

APPENDIX III CLASSIFICATION OF CPI, CROWN FORM AND LIANA LOAD

Table 1 Dawkins Crown Position Classification (source: www.worldagroforestry.org)

Crown Position Index (CPI)	
1	No direct light
2	Only lateral light
3	Partly overtopped, less than 100% vertical light
4	Dominant in the canopy, 100% vertical light
5	Emergent, vertical and lateral light

Table 2 Dawkins Crown Form Classification (source: www.worldagroforestry.org)

Crown Form (CF)	
1	Perfect, regular and circular crown
2	Good, slightly irregular shaped
3	Tolerable, about half the size of a normal crown
4	Bad, less than half sized

Table 3 Vine load classification as it is used in the earlier inventories of the La Chonta forest (Bongers 2004)

Liana Load (LIA)	
1	Free of lianas
2	Lianas on trunk
3	Lianas on trunk and crown
4	Heavily infested