The effect of management regime on the population dynamics of *Swietenia macrophylla* in the humid lowland forest of La Chonta, Bolivia

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This study has been carried out together with C. Verwer (2006). The same data has been used for his research: "*the effects of forest management intensity on the performance of mahogany in Bolivia"*. The problem description has been written in conjunction with Verwer. This research combined with the research of Verwer can be used to gain a better insight on the effects of forest management regimes on the development of over exploited mahogany populations.

Summary

Big-leaved mahogany (*Swietenia macrophylla*) is the leading commercial timber species of Central and South-America. Unsustainable logging has lead to concerns about the commercial viability of the species. The dramatic decline in mahogany populations in the last decades has led to unsuccessful regeneration of the species to sustain future yields. The species has been included in appendix II of the Convention on International Trade of Endangered Species (CITES) in November 2002. Mahogany is required to be harvested legally and in a matter that is not detrimental to their role in their natural ecosystems, however, no guidelines are provided for doing so.

In this study the impact of four different management regimes (varying in intensity) on the population dynamics of mahogany have been investigated. Data was gathered in the Long Term Silvicultural Research Project plots within the La Chonta Forestry Concession; Bolivia in a period of 5 years. The mahogany populations have been over harvested, resulting in an almost absence of trees with a diameter > 70 cm. Parameters measured were survival, diameter increment and fecundity. Seedlings and their dispersal were measured for a number of parent trees.

For each of the treatments a structured population matrix was developed based on measured survival, growth and fecundity data. All treatments except treatment control show an increase in population over a period of 200 years. Increase of population coincides with the intensification of management regime.

Harvesting of mahogany was tested using different cutting cycles, different intensities and a threshold value. Sustainable harvesting is possible if silivicultural treatments are applied. Highest yields can be obtained using a low intensity and a long cutting cycle. The longer period between harvesting the more yield can be obtained sustainable. Forest management can affect population dynamics of mahogany positively and can result in sustainable harvesting with profitable yields.

Keywords: *Swietenia macrophylla*; population dynamics; sustainable forest management; Tropical forest ecology; survival; growth; harvesting; La Chonta; Bolivia

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.

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[1] Paragraph 1.1 was written in conjunction with C. Verwer.

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

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 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).

1.2 Research context

The addition of mahogany Appendix II of CITES has led to concerns about the way foresters should manage it. No guidelines have been established to ensure that the species is harvested in a non detrimental way as required by CITES. It was simple not done because it was not needed until then (Grogan, 2004). 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.

To gain insight in the dynamics of a mahogany population, differently managed populations could be studied within a forest. Forest plots in which different silvicultural management regimes are applied provide a great opportunity to determine and predict changes in population structure and dynamics. The Long Term Silvicultural Research Project plots within the La Chonta forest concession in Bolivia are a unique example of such forest plots (Pariona et al. 2003; Jackson et al. 2002; Bongers 2004). These plots were established by the Bolivian Sustainable Forest Management Project BOLFOR in 2000 and are currently monitored by the Instituto Boliviano de Investigacion Forestal (IBIF). For our research we will make use of these plots to examine the effects of different forest management regimes on the development of mahogany populations and the potential effects of harvesting on these populations.

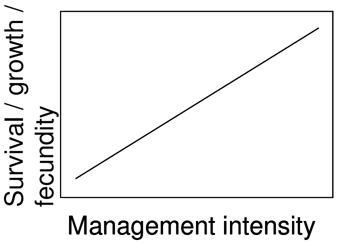
1.3 Objectives

The general objective of this research is:

To determine the effect of four management regimes, varying in silvicultural treatments and harvesting, on the population dynamics of mahogany.

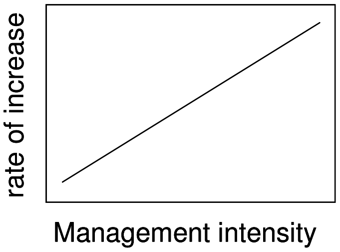
- In what way do survival, growth, and fecundity contribute to the population dynamics of mahogany?
- Do the management regimes have an affect on the population dynamics of mahogany?
- Are matrix models tools that can be applied to develop sustainable harvest systems for mahogany?

1.4 Hypotheses



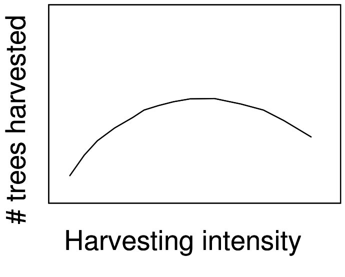
A

A number of silvicultural treatments are designed to improve the survival, growth and fecundity of a population. It is hypothesized (A) that an increase in management intensity will have a positive effect on the survival, growth and fecundity of the population.



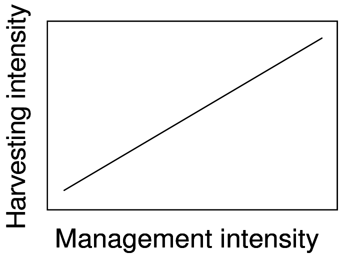
B

Hypothesis B indicates that with an increase in management intensity there will be a higher rate of increase of population. With a higher survival rate, growth rate and fecundity populations will have a higher rate of increase.



C

Harvesting of trees can be done using different intensities which result in different amounts of harvested trees in a given time period. We predict that harvesting of too few trees will result in under-exploitation and too much harvesting in over-exploitation of the stand through time. Hypothesis C predicts that there is an optimum harvesting intensity in which the highest amount of trees can be harvested.



D

When there is an optimum in amount of trees harvested using different intensities it can be derived that different management regimes show different optima in harvesting intensity. It is hypothesized (D) that an increase in management intensity will ensure a higher sustainable harvesting intensity.

2. Methods

2.1 Study site

This study was carried out in the Long-Term Silvicultural Research Project (LTSRP) plots in the forest concession Agroindustria Forestal La Chonta Ltda., located in the Guarayos province department of Santa Cruz, Bolivia (15°47' S, 62°55' W). The area lays around 250 m 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. The forest has been characterized as a transitional forest between wet Amazonian forests and tropical dry forests (Jackson et al. 2002) and has been classified by the Holdridge system as a semi-deciduous humid tropical forest (Holdridge, 1997). In the concession 178 treespecies with a DBH >10cm have been identified (diversity is 96 species per ha). The most common species are *Pseuldomedia laevis*, *Ampelocera ruizii*, *Hirtella triandra*, two species of *Ocotea* and *Terminalia oblonga.* The density of trees with a DBH >10cm is 367 per ha and basal area is 19.6 m2 per ha (IBIF).

In the past forestry in this concession largely consisted of selective logging and mahogany was harvested at relatively low volumes (< $1m^3$ ha^{-1}) (Fredericksen 2002). At the moment two tree species are not harvested in La Chonta; Spanish cedar (*Cedrela odorata* L.) and mahogany. This is done so that the species may recuperate from past high-grading (Pariona et al. 2003).

The plots were established to simultaneously compare different silvicultural systems (see Appendix 1). This was done to be able to evaluate which treatment supplies the best combination for obtaining sustainable yield, conserving biodiversity and increasing the economical benefits (IBIF). These plots have also provided an opportunity to investigate the ecological impacts of different silvicultural systems on biodiversity, forest dynamics and the ecosystem processes on a large scale. By including control plots a comparison can also be made with carbon fixation and the effect of area protection.

There are 12 LTRSP plots established in La Chonta equally divided over 3 blocks. Each block contains four 27 ha plots that received one of 4 different silvicultural treatments. The treatments are control, normal, improved and intensive. Each of the treatments comprises a number of silvicultural treatments (Table 1).

Table 1; Silvicultural treatments in the LTRSP plots of La Chonta (Bongers 2004). X indicates that the silvicultural treatment has been carried out; XX indicates an intensification of the treatment.

Treatments	**Control**	**Normal**	**Improved**	**Intensive**
▪ Forest inventories	X	X	X	X
▪ Cutting of lianas on harvestable, commercial trees	X	X	X	X
▪ Planning of logging roads		X	X	X
▪ Species specific minimum cutting diameters		X	X	X
▪ Retaining 20% of trees above minimum cutting diameter		X	X	X
▪ Directional felling		X	X	X
▪ Marking Future Crop Trees (FCT) with a DBH > 10 cm			X	XX
▪ Cutting lianas on FCT's			X	XX
▪ Liberating part of the FCT's, by poison girdling surrounding non-commercial trees			X	XX
▪ Girdling non-commercial tree-species with a DBH>40 cm (expect for trees important for wildlife)				X
▪ Soil scarification				X

Due to over-exploitation of mahogany in La Chonta, during the period 1974-1994, there has been no harvesting of mahogany in the plots. All mahogany trees found in the plots have been marked as FCT and have received silvicultural treatments in accordance to the treatments in which they are located.

2.2 Data gathering

Data on mahogany was gathered over three different periods by four different researchers:

- May 2002 (Kirsten Olshen-Kiehn)
- July – August 2003 (Laurent Bongers)
- March – May 2006 (Daniel van der Staak, Caspar Verwer)

During these measurements all mahogany-trees > 1.00 m in height were searched, identified, labeled and measured for height and / or diameter at 1.30 m from the soil (DBH). The exact location of each individual tree was determined (in m) using the grid system of the plot so that future re-measuring could be carried out. For different research purposes the crown position, the crown form, the liana infestation, the stem quality and the color of the soil in which the tree was growing, were determined using methods as described by Verwer (2006).

Plants < 1.00 m in height were searched around 58 randomly selected trees using the following method: All plants located within a 2 m circle around the base of the tree and along six transects were measured and tagged. The transects were 2 m wide and 48 m long, originated at the edge of the 2 m circle around the base of the tree, and were located each 60° of the circle (Ohlson-Kiehn 2003). For each of the plants found, the same measurements as mentioned above were preformed. Additionally, the distance from the plant to the adult tree was determined.

New found individuals in 2003 and 2006 were given a number and x and y coordinates were determined to allow possible re-measuring. For all trees it was determined whether a given individual was alive (1) or dead (0). Trees that were not found at the determined x and y coordinates were assumed to be dead (2). It is possible that a number of trees have been measured as different individuals during the different censuses. This has led to possible under or overestimations of the number of plants found for each adult tree or each plot. Due to method of data-gathering in 2002 and 2003 this was inevitable. In 2006 all plants have been labeled with aluminum tags instead of plastic ones to guarantee this from not happening again.

2.3 Structured population matrix

Matrix population models are instruments that are widely used to analyse plant and animal demography as they apply a standardised model and yield output. With them it is possible to give a clear biological / ecological interpretation (Zuidema & Zagt. 2000, Caswell, 1989). In their normal, standardized, form matrix models use the following equation:

$$A^*n_t = n_{t+1} \tag{1}$$

Each entry in the matrix represents the transition probability, or mean contribution, of an individual in a category to another category in one time step t (in our case a year). By multiplying the matrix A by a vector (n) representing the number of individuals in each category at time t one obtains a new vector in which each entry represents the number of individuals per category at time t+1 (n_{t+1}).The elements of a matrix represent the different probabilities of event occurring over the given period (Figure 1).

$$\boxed{\begin{matrix}
P1 & 0 & 0 & F1 & F2 & F3 & F4 & F5 & F6 & F7 \\
G1 & P2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & G2 & P3 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & G3 & P4 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & G4 & P5 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & G5 & P6 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & G6 & P7 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & G7 & P8 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & G8 & P9 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & G9 & P10
\end{matrix}}$$

Figure 1: Transition matrix. Element *P* represents the probability of surviving and remaining in a stage (stasis elements). Element *G* represents the probability of surviving and growing to a stage with larger individuals. Elements *F* are not probabilities but actual values of the number of offspring produced per individual tree. 0 indicates that nothing happens in this part of the matrix.

The number of categories is extremely important for the outcome of a matrix as it affects the relative contribution of the stasis elements to the population growth (Zuidema & Zagt. 2000). For this research we have chosen to use the most used classification of the population. 84% of the matrix studies investigated by Zuidema & Zagt (2000) have used a classification that is based on biological intervals with simple category limits. These intervals are based on DBH; therefore we used classes of 10 cm width. We have chosen to develop the matrix until 90 cm, with intervals of 10 cm, and above 90 one category which represents all trees > 90 cm DBH. This was done because the trees will be dominant in the canopy and their survival is relatively high.

A number of mathematical properties of matrix A correspond to the different demographic characteristics a certain population represents (Caswell, 1989);

- Dominant eigenvalue (λ): the finite rate of population increase/ decrease
- Right eigenvector (w): stable size distribution
- Left eigenvector (v): size specific reproductive values

The sensitivity to changes of λ in entries of a_{ij} in a matrix can be assessed in two different ways. Firstly the sensitivity of s_{ij} of matrix element a_{ij} considers the absolute change in λ due to an absolute change in a_{ij} and secondly, the elasticity analysis considers the relative changes in λ due to a proportional change in a_{ij} (Caswell 1989, Zuidema and Zagt, 2000).

Population matrices can be used to compare demography of different species or that of different populations of the same species (Zuidema and Zagt, 2000). In this sense a matrix is a very suitable tool to analyze the demography of mahogany growing in the different management regimes in La Chonta.

For this research four different matrices were developed. Each matrix represents the population dynamics of one of the different management regimes that were applied.

3. Analysis

Statistical analysis was done using the statistical software packages SPSS 12.0 / 13.0 and Poptools for Microsoft Excel.

3.1 Field data

To define whether population structure differs significantly among management regimes, the frequency distribution of DBH was compared among all treatments using a two-independent sample Kolmogorov-Smirnov Test. A similar analysis was done to detect differences in diameter distributions between the three blocks and hence to test whether blocks represent suitable replicates.

To construct the matrix it is necessary to calculate the parameters *P*, *G* and *F* (see Figure 1). These parameters are calculated by obtaining different probabilities of survival, growth and fecundity based on the data gathered in the field.

3.2 Survival

The survival of trees in the different size categories is based on the survival of individual trees within a DBH-class present in 2002. The survival was calculated using the following formula:

$$a - b = c^4 \tag{2}$$

Where a is the percentage of trees alive in each class in 2002; b the percentage of trees that are dead in 2006 and c is the survival over t years (in our case t = 4) in percentages. This had to be adjusted to the survival over one year. DBH-classes that did not have any mortality or that did not have any representatives in the field were given an assumed survival rate of 99.0 %.

The survival rate obtained using the above equation is then used to calculate the probabilities of *P* and *G* elements of the matrix. The exact data obtained of this formula is the sum of the *P* and *G* elements. To be able to distinguish between the elements, the probabilities to grow to stage with larger individuals needs to be calculated.

3.3 Growth

For construction of the matrix it is necessary to calculate the increment in diameter or in height. Because the matrix is based on diameter classes; the annual diameter increment (in cm) was calculated for trees above a >1.30 in height. Since this is not possible for seedlings (trees with a height < 1.30 m), we measured for this category the height increment (in m). The increment was calculated on a daily basis because of the different periods of data gathering over the years.

$$(DBH_{(X+1)} – DBH_{(X)}) / (date_{(x+1)} – date_{(x)}) * 365 \qquad (3)$$

To obtain the growth rate of diameter classes with few or no individuals (DBH classes > 60 cm), the growth data was fitted into the Hossfeld IV equation:

$$Y = a + b1*(DBH2002) + b2 (DBH2002^2) + c1*(Intensive) + c2*(Improved) + c3*(Normal) + c4*(Control) \qquad (4)$$

Where a, b1, b2, c1, c2, c3 and c4 are calculated using model expression for non-linear regression analysis. The values are then used to predict the diameter increment per year for the different diameters. The growth rates obtained are used to calculate the time an individual spends in a given diameter class, the Average Residence Time (ART) using equation 5 where β_x is the width of class x in cm and Y is the growth rate per year for each diameter class.

$$ART = \beta_x / Y \qquad (5)$$

The probability that a tree will transcend into the following diameter class is *G*-probability and is calculated using the following equation:

$$C_x / ART_x \qquad (6)$$

Where C is the survival rate of DBH class x divided by the ART of the same diameter class.

The probability that a tree will remain in the same DBH class, the *P*-probability is the difference between c (of equation 2) and the *G*-probability of the DBH-class.

3.4 Fecundity

The final important element of a matrix is the Fecundity (*F*). For this we return to the raw data. As mentioned before a number of adult trees were determined of which the amount of seedlings were measured. From the seedling data we can calculate the average number of seedlings produced by the adult trees per treatment. We assume that all trees are potentially seed bearing trees. It is possible that trees do not produce seeds every year and do not always start producing seeds once they reach a diameter of which seed production is possible. Additionally, trees do not produce the same amount of seedlings each year. Because the matrix model assumes the same fecundity over the years, the parameters have been optimized so that every tree, present in a given diameter class, produces the same amount of seedlings. The seedlings produced per year have a given survival rate, which is calculated using equation 2. So, the number of seedlings produced multiplied by the derived survival rate and the Average Residence Time of a seedling in the same stage, calculated using Equation 3 (using height) gives us the value for fecundity for the different diameter classes. For the diameter classes that are not represented in the plots the assumption is made that trees > 75 cm DBH produce 3.733 times as much seeds as trees < 75 cm. This is in correspondence to research done by Snook (2005).

With the different probabilities of elements *P* and *G* and values of element *F* the finite rate of increase or decrease of the population (λ) can be determined and the elasticity and sensitivity calculated.

3.5 Harvesting

We used different matrix models to simulate harvesting of trees with different cutting cycles, different intensities (for one cutting cycle) and for a threshold value at which 80% of the harvestable trees is removed. Harvesting of trees will only be conducted on trees with a DBH > 70 cm. This is in correspondence with the current minimum cutting diameter being used for mahogany in Bolivia.

The effect of harvesting is provided by running the matrix a number of times with the actual data. The following cutting cycles were used: no harvesting, every 5, 10, 20, 30 and every 60 years for a period of 200 years. From these frequencies the amount of trees > 70 cm DBH that were harvested was also calculated.

Since not all trees are always harvested it is very important to know how many trees can actually be harvested when a strictly regulated harvesting system is introduced. In this system the amount of harvested trees is a fixed percentage of which the total amount of trees with a DBH > 70 cm. In this way it can be determined what effect of harvesting will be on the population dynamics. Furthermore it can be shown how much yield, as measured in number of trees, will be obtained over a period of 200 years. For this simulation the cutting cycle of 30 years will be used.

Since it is not always worthwhile harvest at a fixed time the third simulation, harvesting with a threshold will be carried out. We assume that the harvesting will occur the moment that there are 0.15 trees of > 70 cm DBH present per ha in the system. At this moment 80 %, as is mentioned in the silvicultural treatments of the management regimes (Table 1), of the trees will be harvested. In this way it can be shown how many times there is a possibility of harvesting for the different treatments for a period of 200 years.

4. Results

4.1 Data distribution

The data clearly indicates that trees > 50 cm DBH are almost absent in the area (Table 2; Figure 2). It is also shown that there is a dramatic decrease in amount of trees with no diameter (trees with height < 1.30 m, trees < 0 in Table 2) during the measuring years.

Table 2; Average amount of trees present for each diameter class per treatment measured in 2002, 2003 and 2006 per ha.

Size categories	Control			Normal			Improved			Intensive		
DBH (cm)	2002	2003	2006	2002	2003	2006	2002	2003	2006	2002	2003	2006
< 0	5.136	2.185	0.296	7.457	2.556	1.247	1.864	0.185	1.000	4.531	2.537	0.296
0 - 10	0.222	0.210	0.160	0.901	0.654	0.605	0.185	0.173	0.136	0.383	0.333	0.160
10 - 20	0.099	0.099	0.099	0.407	0.383	0.420	0.123	0.123	0.086	0.309	0.210	0.185
20 - 30	0.136	0.148	0.148	0.173	0.136	0.235	0.086	0.086	0.086	0.136	0.136	0.123
30 - 40	0.111	0.086	0.062	0.099	0.111	0.111	0.049	0.037	0.074	0.111	0.160	0.136
40 - 50	0.074	0.074	0.049	0.099	0.086	0.086	0.025	0.012	0.012	0.025	0.025	0.062
50 - 60	0.012	0.025	0.049	0.025	0.062	0.074	0.074	0.074	0.049	0.037	0.037	0.025
60 - 70	0.000	0.000	0.000	0.012	0.012	0.012	0.000	0.012	0.049	0.000	0.000	0.025
70 - 80	0.000	0.000	0.000	0.012	0.012	0.012	0.000	0.000	0.000	0.000	0.000	0.000
80 - 90	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
> 90	0.000	0.000	0.000	0.012	0.012	0.012	0.000	0.000	0.000	0.000	0.000	0.000

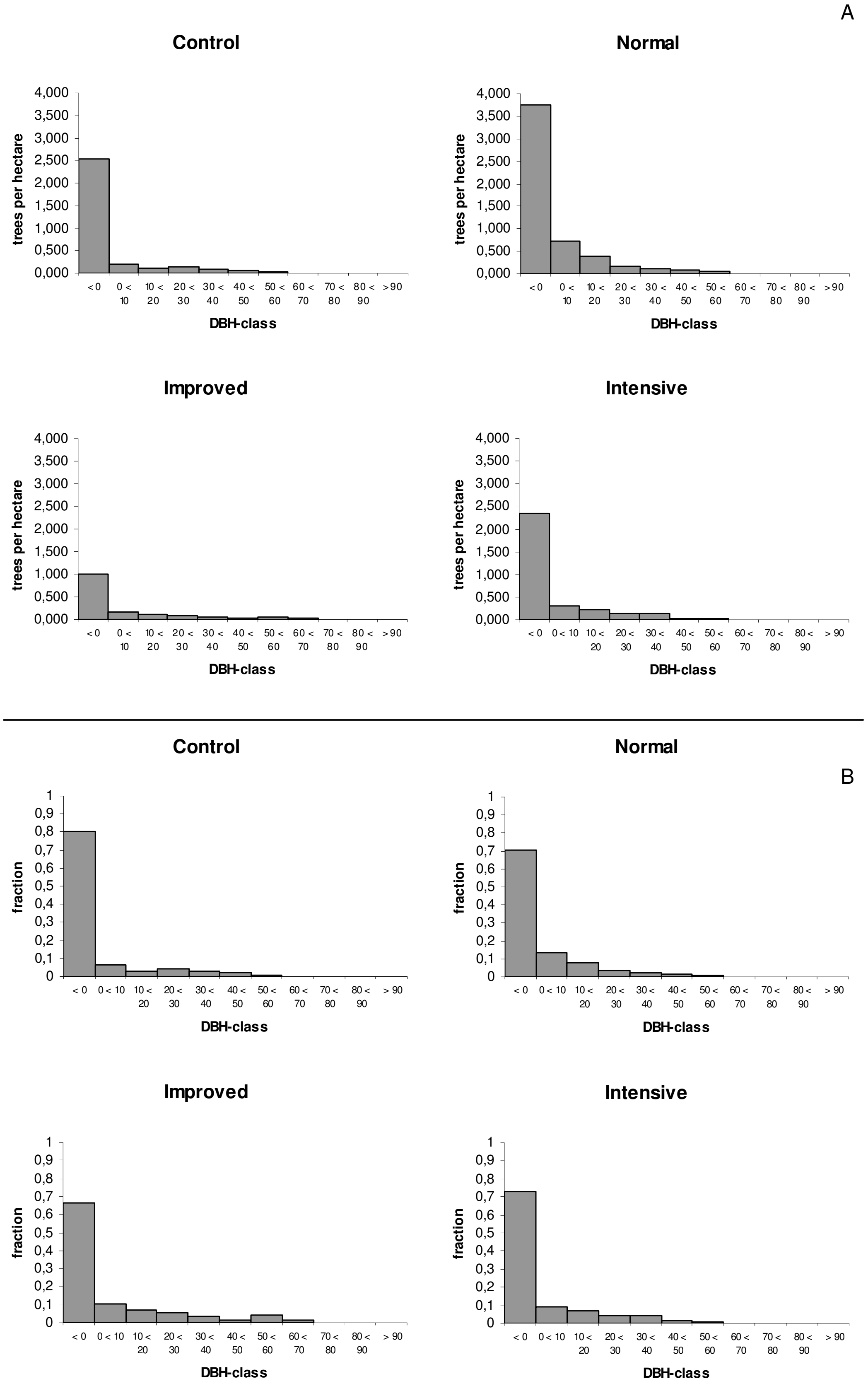


Figure 2; Diameter distribution of the different treatments in absolute numbers (A) and in fractions (B), averaged over time (2002-2006).

The size distribution does not differ significantly among blocks (Kruskal-Wallis: X^2=3.956; df=2; p>0.05) and among treatments (Kruskal-Wallis: X^2=6.641; df=3; p>0.05). This indicates that the presence of diameter classes is similar in all plots. For the remaining research a mean population structure will be used for the modelling.

4.2 Survival

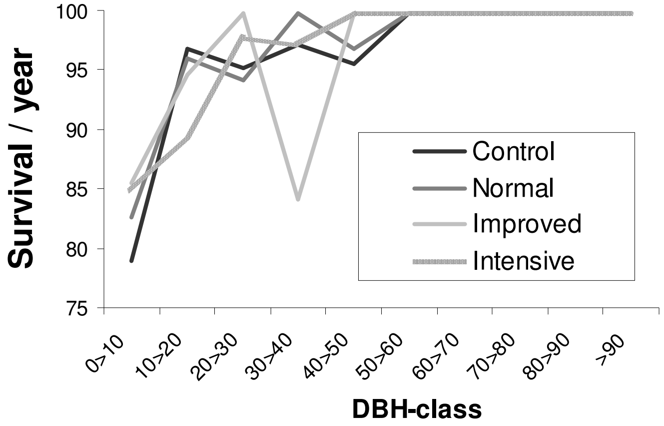


Figure 3; Survival of trees with a diameter above 1.30 m from the soil per year for each management treatment.

Survival of the different treatments seems to follow the same trend. Survival increases as diameter increases (Figure 3). For diameter classes with no mortality over the four years the mortality was assumed as 1 % per year.

4.3 Growth

Diameter increment rate is shown for the different treatments (figure 4). This is significantly different (ANOVA (F: 14.326 P <0.001)). Although they follow the same trend, it is clear to see that trees in treatment intensive have a higher diameter increment than the other treatments. There seems to be an optimum in diameter increment for trees with a diameter of 50 – 80 cm.

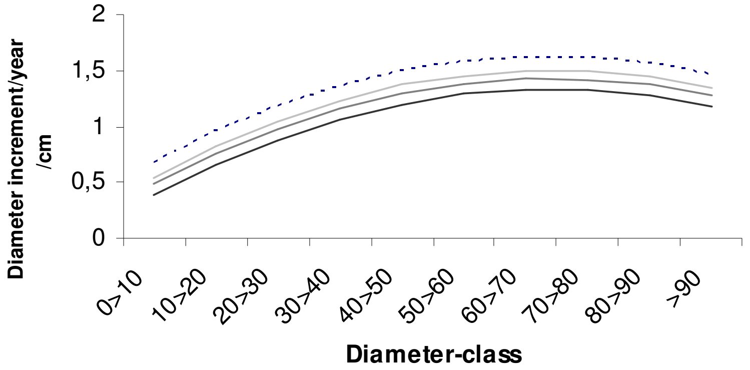


Figure 4; Predicted diameter increment of mahogany per year for each diameter class using the Hossfeld Equation IV.

The amount of adult trees designated as adult trees is not uniformly distributed among treatments (Table 3). There are less adult trees present in treatment Improved than in the other treatments. The fraction of adult trees that do not produce any seedlings is for this treatment also the highest (54%). A distinction can be made between the amounts of seedlings produced by adult trees within the different treatments. It seems that trees in treatment control and treatment normal produce approximately the same amount of seedlings per year. The same trend can be seen for treatment improved and treatment intensive. However this is not significantly.

Furthermore table 3 illustrates that the chance that a seedling will reach a diameter is different for each treatment.

	Control	Normal	Improved	Intensive
Amount of adult trees	17	16	11	16
Amount of non-producing adult trees	6	1	6	4
Amount of seedlings produced per tree	6,35	7,54	14,36	14,38
Survival of seedlings per year (%)	73,57	47,28	50[1]	63,28
ART until height = 1.30 m	17	14	14	14
Survival of seedlings until height = 1.30 m (%)	1.2079	1.3361	1.3151	1.294

Table 3; Data necessary to calculate the fecundity of the different DBH-classes. Survival of seedlings is the probability that a seedling will survive until it is 1.30 m high and, therefore, has a diameter above 1.30 m from the soil.

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[1] The data has shown a complication for the seedling survival per year of seedlings in treatment improved. All seedlings that were alive in 2002 and 2003 were dead in the second census. This means that survival rate should be 0 %. A survival chance of 0% ensures the death of the population. To be able to use the data for treatment improved we have assumed a survival of 50 % per year and an ART of 14 years.

The amount of adult trees designated as mother trees is not the same in the different treatments (Table 3). There are less adult trees present in treatment improved than in any other treatment. The fraction of adult trees that do not produce any seedlings is for this treatment also the highest (54%). A distinction can be made between the amounts of seedlings produced by adult trees within the different treatments. It seems that trees in treatment control and treatment normal produce approximately the same amount of seedlings per tree. The same trend can be seen for treatment improved and treatment intensive. Furthermore table 3 illustrates that the chance that a seedling will reach a diameter ,at 1.30 m from the soil, is different for each treatment.

4.5 Matrix construction and output

For the vector data of the matri we have used the average amount of trees in each DBH-class of theyears 2002, 2003 and 2006. This data will be used as the vector data for the matrix. The Average Residence Time is directly calculated from the growth (diameter increment) and provides the distinction which needs to be made between the *P* and *G*-probabilities.

With the data provided from Table 4 the matrices for the different treatments can be constructed. The exact matrix and the corresponding sensitivity and elasticity analysis are given in Appendix 3. In all treatments the mahogany population increased (figure 5). The exact path the population is predicted to follow is given in figure 6.

Table 4; Matrix parameters for the different treatments. Trees/ha indicate the average number of trees present in each treatment (measured in 2002, 2003 and 2006). Growth is the average diameter increment (in cm) for trees present in each DBH-class per year. ART is the average time a tree will spend in each diameter class before it grows to the next class (in years). Survival is the probability that a tree will survive a year in a given DBH-class. *P* represents the probability that a tree will remain in a DBH class during the year, *G* the probability that it will transcend to the following DBH class. *F* is the contribution to the fecundity of a tree present in a given DBH-class per year.

	Control						
DBH-class	Trees/ha	Growth	ART	Survival	*P*	*G*	*F*
0>10	0,298	0.38	26	0.7897	0,7585	0,0312	0,0000
10>20	0,212	0.65	15	0.9672	0,8999	0,0672	0,0000
20>30	0,136	0.88	11	0.9511	0,8593	0,0918	0,0000
30>40	0,096	1.06	9	0.9710	0,8559	0,1151	0,0767
40>50	0,052	1.2	8	0.9554	0,8252	0,1303	0,0767
50>60	0,045	1.29	8	0.9975	0,8434	0,1466	0,0767
60>70	0,010	1.33	8	0.9975	0,8381	0,1519	0,0767
70>80	0,003	1.32	8	0.9975	0,8394	0,1506	0,1814
80>90	0,000	1.27	8	0.9975	0,8460	0,1440	0,2862
>90	0,003	1.17	-	0.9975	0,9900	-	0,2862

	Normal						
DBH-class	Trees/ha	Growth	ART	Survival	*P*	*G*	*F*
0>10	0,298125	0.48	21	0.8261	0,7845	0,0417	0,0000
10>20	0,211917	0.75	13	0.9598	0,8819	0,0778	0,0000
20>30	0,13575	0.98	10	0.9415	0,8392	0,1023	0,0000
30>40	0,095583	1.16	9	0.9975	0,8666	0,1309	0,1007
40>50	0,052417	1.30	8	0.9672	0,8226	0,1445	0,1007
50>60	0,04525	1.38	7	0.9975	0,8315	0,1585	0,1007
60>70	0,010167	1.43	7	0.9975	0,8248	0,1652	0,1007
70>80	0,003	1.42	7	0.9975	0,8262	0,1638	0,2384
80>90	0	1.37	7	0.9975	0,8328	0,1572	0,3760
>90	0,003	1.27	-	0.9975	0,9900	-	0,3760

	Improved						
DBH-class	Trees/ha	*Growth*	ART	Survival	*P*	*G*	*F*
0>10	0,29813	0.54	19	0.8546	0,8058	0,0488	0,0000
10>20	0,21192	0.82	12	0.9457	0,8613	0,0845	0,0000
20>30	0,13575	1.05	10	0.9975	0,8805	0,1170	0,0000
30>40	0,09558	1.23	8	0.8409	0,7230	0,1179	0,1888
40>50	0,05242	1.37	7	0.9975	0,8328	0,1572	0,1888
50>60	0,04525	1.45	7	0.9975	0,8221	0,1679	0,1888
60>70	0,01017	1.49	7	0.9975	0,8167	0,1733	0,1888
70>80	0,003	1.49	7	0.9975	0,8167	0,1733	0,4468
80>90	0	1.44	7	0.9975	0,8235	0,1665	0,7048
>90	0,003	1.34	-	0.9975	0,9900	-	0,7048

	Intensive						
DBH-class	Trees/ha	Growth	ART	Survival	*P*	*G*	*F*
0>10	0,298125	0.67	15	0.8476	0,7867	0,0609	0,0000
10>20	0,211917	0.95	11	0.8944	0,8005	0,0939	0,0000
20>30	0,13575	1.18	8	0.9765	0,8458	0,1306	0,0000
30>40	0,095583	1.36	7	0.9710	0,8181	0,1528	0,1861
40>50	0,052417	1.49	7	0.9975	0,8167	0,1733	0,1861
50>60	0,04525	1.58	6	0.9975	0,8042	0,1858	0,1861
60>70	0,010167	1.62	6	0.9975	0,7986	0,1914	0,1861
70>80	0,003	1.61	6	0.9975	0,8000	0,1900	0,4405
80>90	0	1.56	6	0.9975	0,8070	0,1830	0,6949
>90	0,003	1.46	-	0.9975	0,9900	-	0,6949

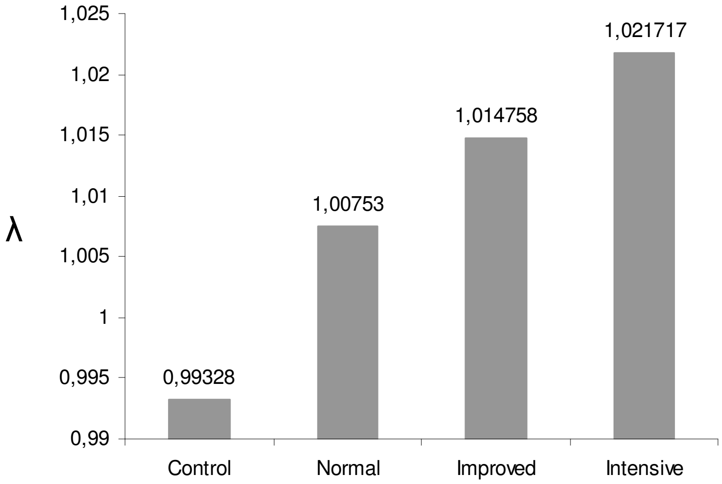


Figure 5; Rate of increase (λ) for each treatment. λ > 1.00 indicates that the population is growing.

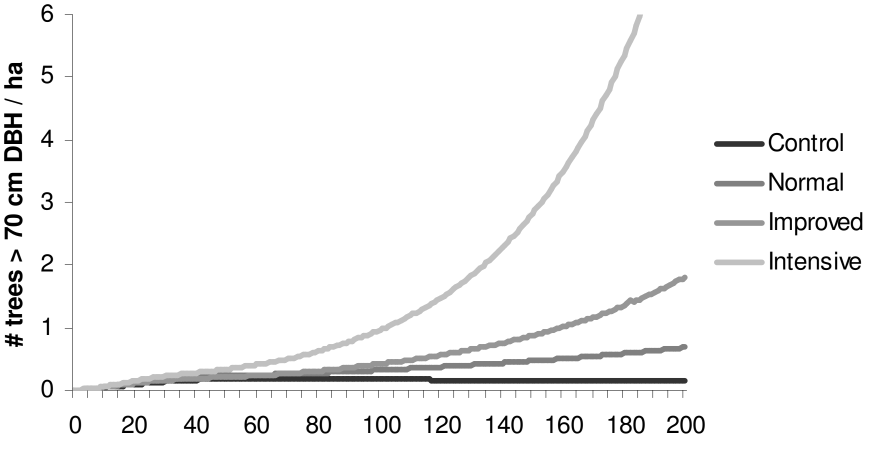
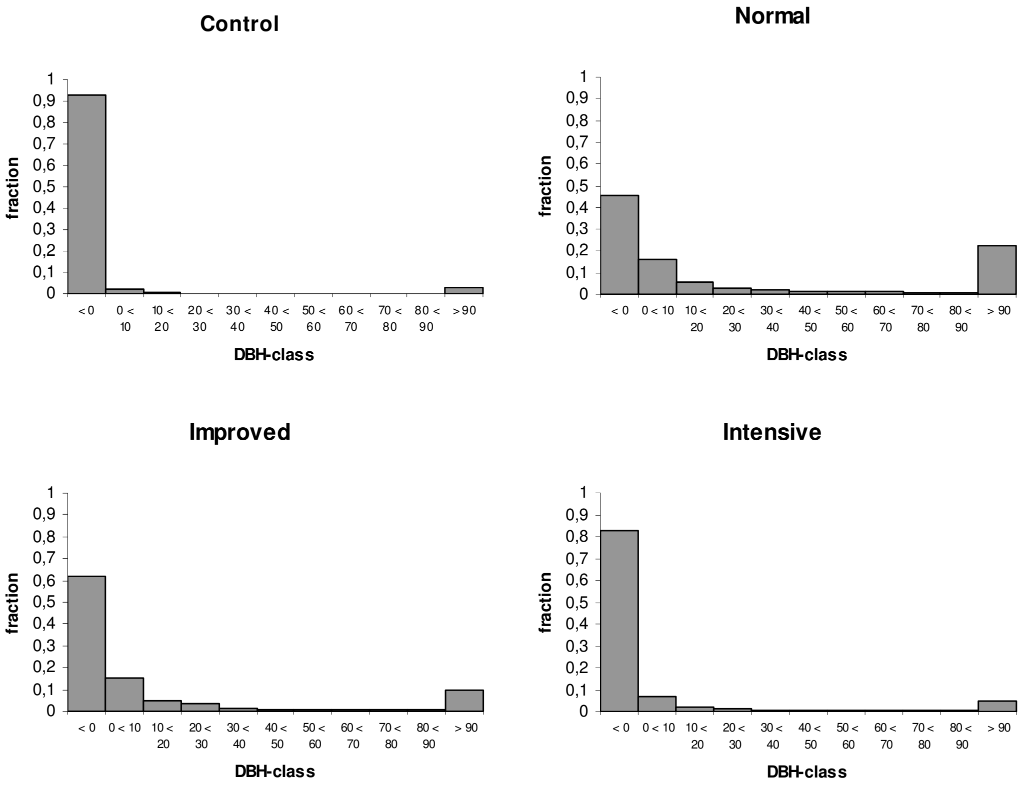


Figure 6; Population number of trees with a diameter > 70 cm per ha over the next 200 years for the different treatments.

The amount of trees with a diameter > 70 cm increases over time in all but one treatment (figure 5 & 6). Population increase rate shows that there is an increase in λ when management treatments are intensified. Without silvicultural treatments (control), rate of increase will be lower than 1.00 indicating a decreasing population.



Control

Normal

Improved

Intensive

Figure 7: predicted diameter distribution of mahogany (in fractions) for all four treatments without harvesting when a stable diameter distribution is reached.

Implementation of the different matrices will result in a stable diameter distribution (Figure 7). The different treatments reach a stable distribution after different periods of time (Control; 108 years, Normal; 123, Improved; 94, Intensive; 84). The actual shift towards a stable size distribution can be seen in Appendix 4. It can be seen that without harvesting, trees > 90 cm DBH will be present in the different treatments.

The highest effect of change in the *P*-elements can be reached with changes in the DBH class >90 cm. The *G*-probability seems to be consistently throughout the whole matrix for each of the treatments. The fecundity is unequivocally affected the most by changes in the highest diameter class.

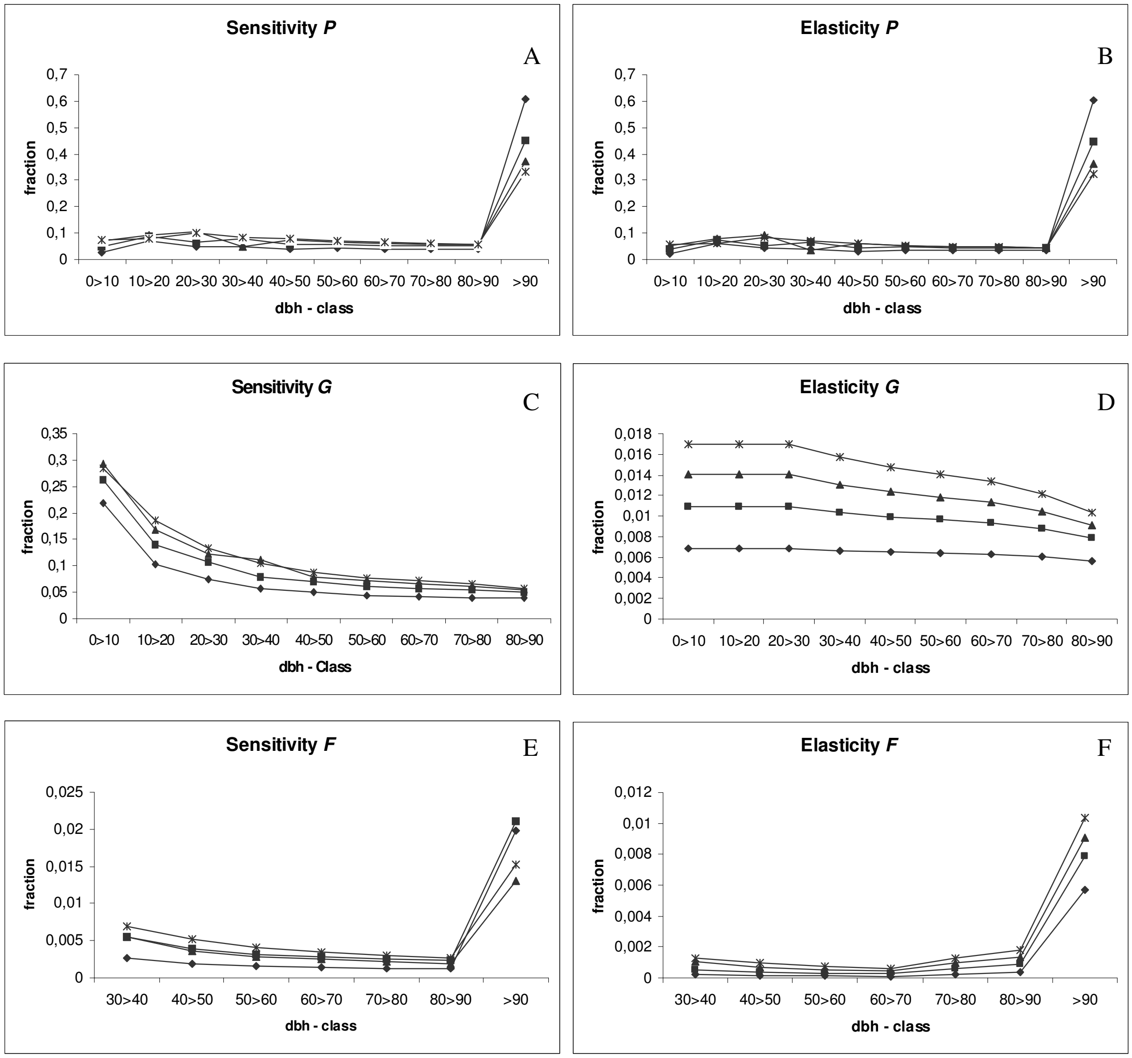


Figure 8 a-f: Sensitivity and elasticity analysis for the different elements *P,G and F* for the different treatments.

4.6. Harvesting

Different cutting cycles

If 100 % of the trees with a DBH > 70 cm are harvested, all populations will decrease dramatically in size regardless of the cutting frequency and management treatments applied (Figure 9). In some cases the populations will not be able to recover at all, and will perish completely (for example using a cutting cycle of 5 or 10 years).

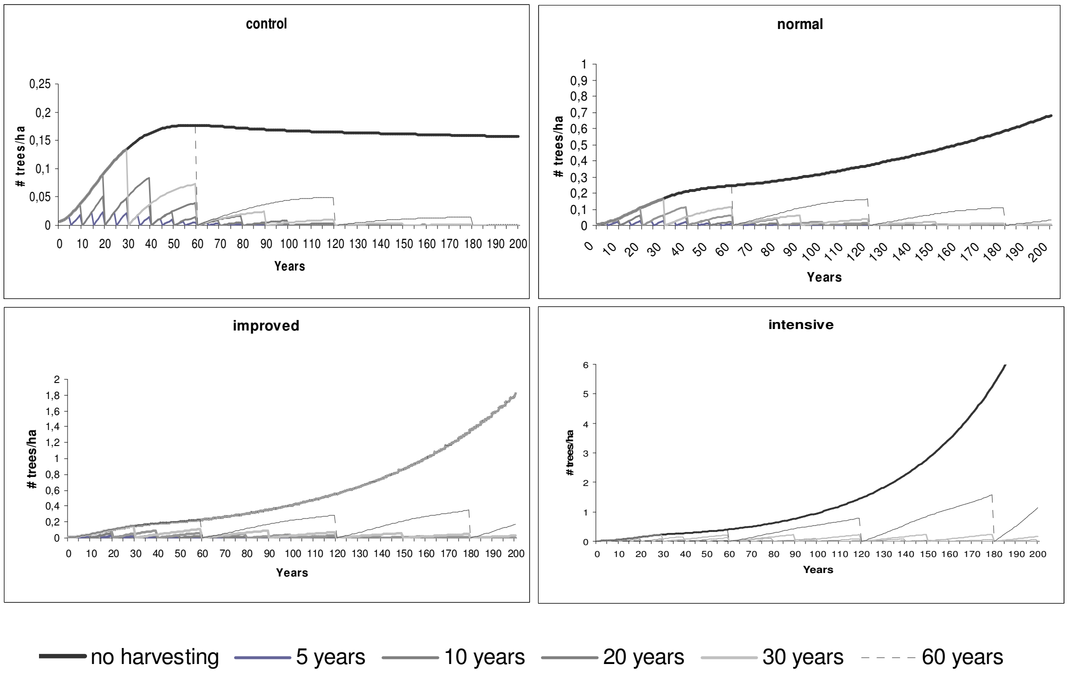


Figure 9; Harvesting of 100% of the trees (> 70 cm DBH) using cutting cycles of different intervals. Y-axis has different scales.

Different harvesting intensities

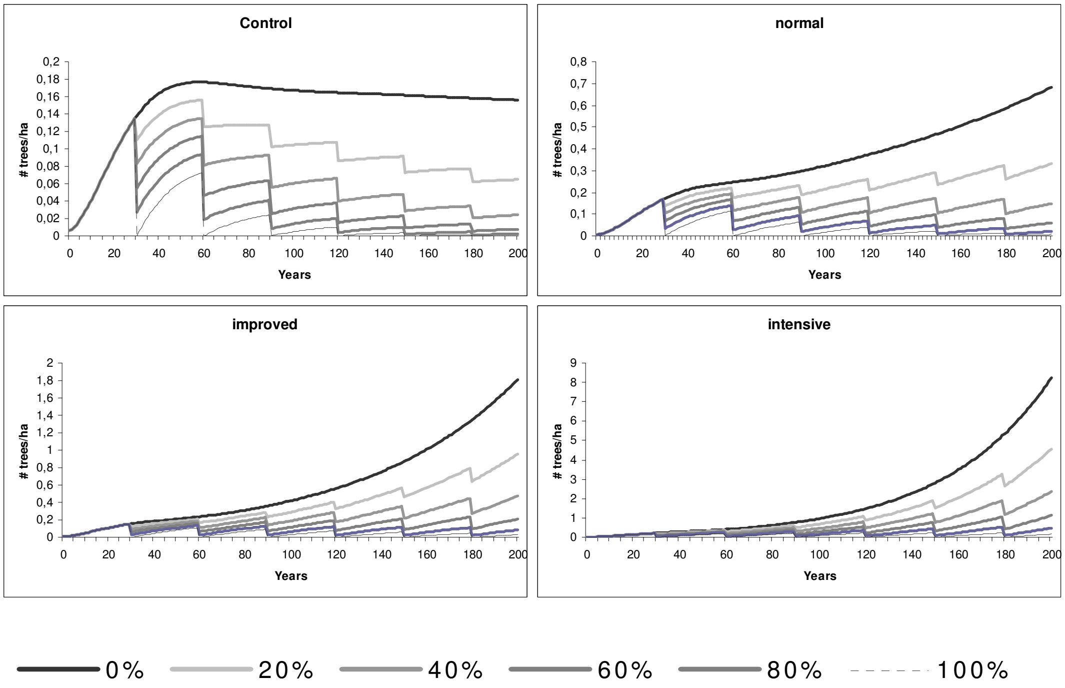


Figure 10: Harvesting of trees using different intensities with a cutting cycle of 30 years for the different treatments. Y-axis has different scales

With each different harvesting intensity, diminishment of the population can be observed in treatment control. However, if silvicultural treatments are applied harvesting under an intensity of 20% is possible in the other three treatments. Treatment control shows an increasing population until 20 % intensity. Treatment improved shows an increasing population with an intensity of 40 % and the population will still grow with a cutting intensity of 60% in treatment intensive.

Harvesting based on a threshold

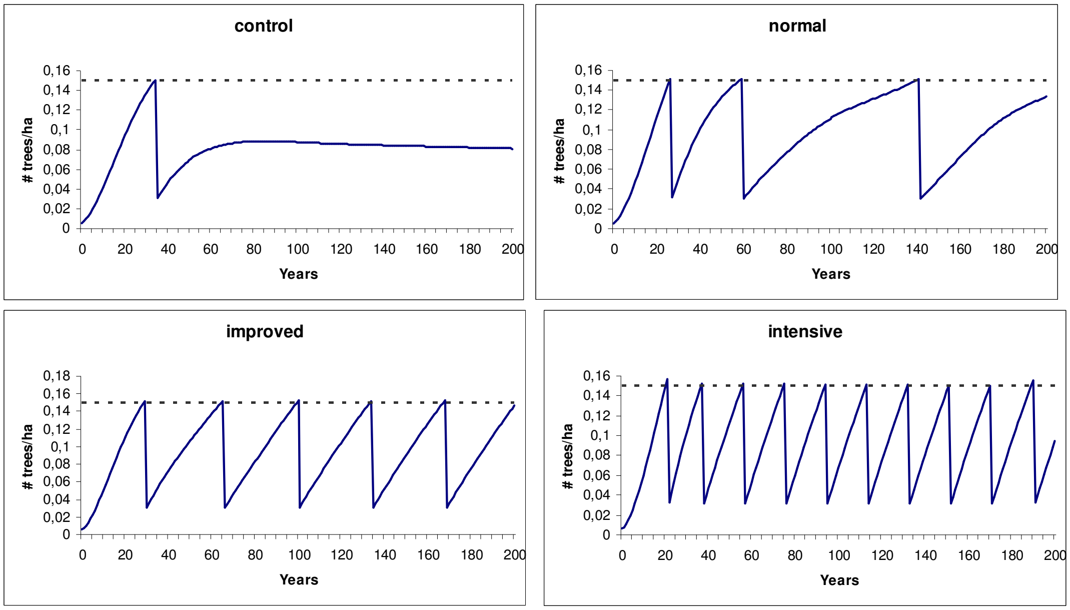


Figure 11: harvesting of 80 % of the trees with a diameter > 70 cm at a threshold of 0.15 trees/ha is obtained.

In the Bolivian regulations only 80 % of the harvestable trees are allowed to be cut (for mahogany: trees > 70 cm DBH). On average species that have more than 0.15 trees per ha present with a DBH larger than minimum cutting diameter are currently harvested. If these requirements are modelled there can only be harvested once in treatment control in 200 years. In treatment normal, there is a possibility to harvest 3 times and the time between harvesting increases. Treatments improved and intensive seem to be more consistent over the years and show an increasing amount of harvesting possibilities. Harvesting in treatments improved can occur almost every 30 – 35 years. While harvesting in treatment intensive it is possible to harvest every 20 years without depletion of the trees with a DBH > 70 cm.

Yield comparison

Final yield (# trees) has been calculated for different harvesting scenarios (i.e. based on frequency, intensity and threshold) for a model run of 200 years. It is possible to compare the yields of each method.

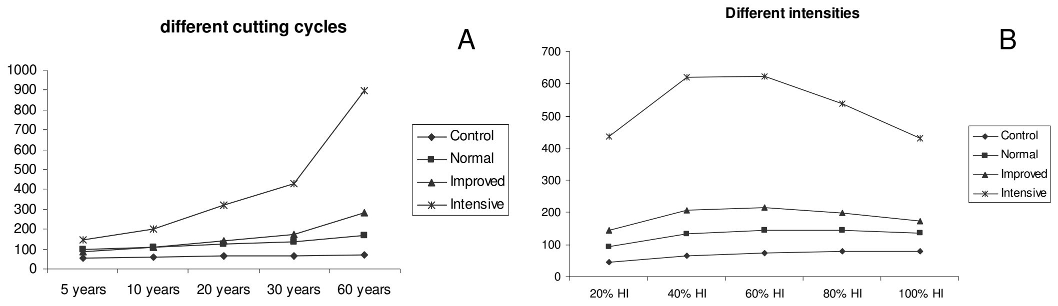


Figure 12: Obtained yield in 200 years for different cutting cycles (A) and different intensities (B) .Exact numbers of trees harvested are given in Appendix 5.

A decreasing cutting cycle results in a higher yield over 200 years (Figure 12a). As shown in figure 12a more trees will be obtained when cutting cycle is lower (more time between harvesting periods). Based on this information, harvesting fewer times will result in more harvested trees.

Harvesting more trees each harvesting period will not result in a higher total yield. Figure 12 B shows that there is an optimum in yield when harvesting occurs at a fixed intensity. Harvesting at a threshold tends to have a lower amount of trees harvested in 200 years (39 trees for treatment control; 117 for treatment normal; 234 for treatment improved and 390 for treatment intensive).

5. Discussion

To determine whether the management regimes affect the population dynamics of mahogany the survival, growth and fecundity have been calculated for each treatment. The silvicultural treatments applied in the LTRSP plots are designed to increase yields of the stands and to improve the survival, growth and fecundity of commercial tree species such as mahogany.

Population structure

In La Chonta there is an average of 367 trees per ha of a DBH >10 cm (IBIF). For mahogany an average density of 0.56 tree per ha of DBH >10 has been measured. Because the density is so low this research can only be used to explain a small part of the ecosystem.

In comparison with the 2003 and 2006, 2002 had a very high abundance of trees with a height < 1.30 m (Table 2, page 18). Most of these seedlings have died since 2002 (Table 3 survival rate seedlings). One of the possible reasons for high seedling is the re-closure of the canopy since the last harvesting. Most seedlings were found in treatment normal; this is possibly due to the presence of two trees with a high diameter (DBH > 75 cm). These trees have not been harvested at the time mahogany was exploited in the area. Since these trees were left in the area they have become a major source of seeds, and thus seedlings. Trees with a high diameter are the most important trees for the development of a stand (Figure 8, page 26).

Several researchers indicate the importance of large disturbances for the regeneration of mahogany in natural forests such as fire(Grogan et al. 2003; Gullison et al. 1996; Gullison et al. 2003; Snook et al. 2004; Frederickson et al. 2000; Lowe et al. 2003). This is however not shown in the population structure in La Chonta. The fire that occurred in 2004 and burned practically the Improved and control plots of Block II has not resulted in large regeneration of mahogany while adult trees were in the vicinity. In 2006 no regeneration of mahogany was found in this area, probably due to lack of seeds and large scale presence of gap-invaders (pers. obs.) The lack of seeds even when adult trees where present is possibly due to the fact that trees are allocating resources to recovery and growth rather than fruit production. The development of these plots needs to be further monitored to be able to provide more information about the regeneration of mahogany after fire.

The exploitation of mahogany occurred in the area until 1994. This exploitation has clearly affected the size distribution. There are almost no trees of a diameter > 70 cm found in all plots except in one treatment normal. This means that the size distribution has shifted towards the smallest sizes (Figure 2, page 19). This means that there are only 2 trees > 70 cm DBH present in an area of 324 ha (area covered by all plots). It is only after a number of years (Control; 108 years, Normal; 123, Improved; 94, Intensive; 84) that a more stable size distribution will be developed (Figure 7, page 25). The shift towards a stable size distribution seems to be partly linked with the λ of the different treatments. The higher the rate of increase, the faster the system will reach its stable size distribution

Survival

Survival of mahogany is lowest among the smallest size-class (trees with a height < 1.30 m). This trend is shown in all treatments; however, not all treatments show the same survival rate. It is hypothesized that increasing management intensity leads to an increase in survival. Figure 3 shows that this is completely not the case for trees with a DBH at 1.30 m from the soil. A large number of seedlings alive in 2002 have been found dead in the year 2003 and 2006 probably because light is the limiting factor for seedling survival (Verwer, 2006).

Survival of trees was not always possible to calculate properly. In a large number of diameter classes no mortality has been measured over the years. This is partly due to the fact that no dead individuals were found, but also to the fact that a large number of the diameter classes were absent in the research area. This is not a problem that is solely related to this research. Zuidema& Zagt (2000) calculated that 41% of the matrix studies on long-lived species had difficulties estimating survival rates due to absence or insufficient observations of mortality.

Growth

Despite the fact that diameter increment of mahogany seems to be very consistent across its natural range (Gullison 1996) small scale disturbances might indulge differences in diameter increment. Small disturbances, artificial as well as natural, can disturb light availability. Because light availability is the main limiting factor on height and diameter increment (Verwer 2006), locally different increment levels can be found. In this study average diameter increments ranged between 3.8 – 14.9 $\text{mm}\cdot\text{yr}^{-1}$. The upper bound is high in comparison with studies done elsewhere: Snook (1993) 2.0-10.9 $\text{mm}\cdot\text{yr}^{-1}$ and Gullison (1996) found 2.6-9.0 $\text{mm}\cdot\text{yr}^{-1}$. It seems that mahogany performs better in this study than elsewhere. The differences in mean diameter increment as shown in Figure 4 (page 21) can not be solely due to contribution of light availability. The differences in growth rates are significantly influenced by DBH (Verwer, 2006). Although DBH and light are the major contributors to the differences between treatments; Grogan et al. (2003) addresses the importance of soil fertility and water availability as important contributors for high growth rates. It is therefore likely that the distribution of growth rates can be influenced by small scale variation in abiotic and biotic factors.

Fecundity

Since fecundity is based on seed-production of trees and on the survival of seedlings, the seedlings of today will be the seed-producers of tomorrow. This fact will lead to the possibility that past events will affect the future. Sensitivity and elasticity-analyses (Figure 8, page 26) show the effect of reproductive capacity on λ, although the effect of changes can only be clearly seen in the last class (DBH > 90 cm), the effect of different levels is not clearly shown. In what way different amounts of seedlings affect the rate of increase of a stand is experimented. In the experiment fecundity levels are stabilized for all reproductive trees (DBH > 30 cm). The *P* and *G* elements are maintained so that a differentiation can be made between the treatments. The same trend in λ changes can be observed in all four treatments when fecundity increases (Figure 13, page 33). Fecundity has the highest effect on treatment intensive and there is hardly any difference between treatment normal and improved.

Furthermore it is clear that when fecundity increases the differences between treatments also becomes larger.

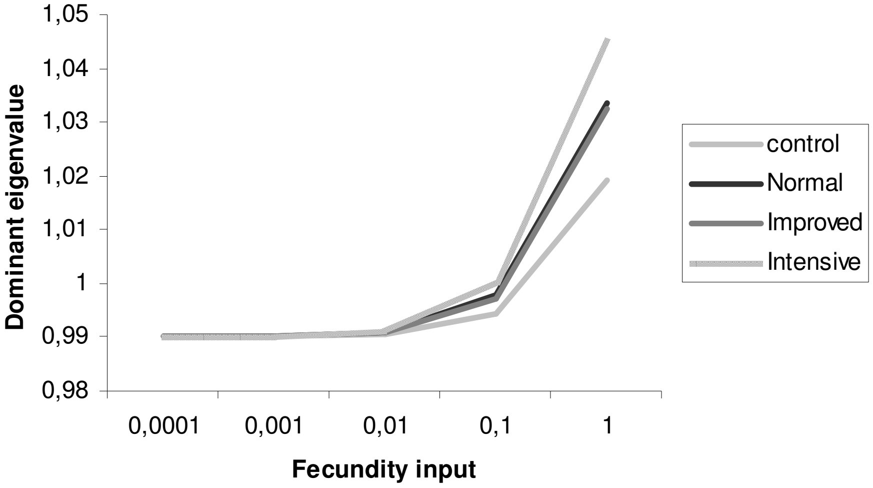


Figure 13: different fecundity-levels which will result in different outcomes of λ (rate of increase). A λ below 1 indicates that the population is decreasing, above 1 that the population is increasing. If λ is 1 the population is in a stasis.

This experiment shows that an increase in fecundity influences λ. The rate of increase is positively influenced with an increasing amount of seedlings that survive until they reach a height of 1.30 m. This means silvicultural treatments emphasized on the survival of seedlings are beneficial to the stand development and harvesting.

Matrix model

Implementation of a structured population matrix has shown that the set of silvicultural treatments of which a treatment is based (Table 1, page 12) has a positive effect on the development of a stand through time (Figure 6, page 24). The rate of increase (λ) is > 1.00 indicating that all treatments but control do result in a growing population. The rate of increase is highest for treatment intensive (1.0217) which indicates that an intensive treatment will result in a higher density of mahogany and consequently a higher yield.

It is, however, not a guarantee that the treatments do have the effect for which they were modelled. The λ indicates the development of a population until infinity. It therefore assumes that the elements will always be the same. In reality this is never the case. The final effect of the silvicultural treatments has not been possible to measure as well as the environmental changes.

For this model the forest has been regarded as a static element, in reality this is not the case. Changes in the forest will always have an affect on the mahogany population. For this study three measurements conducted in 5 years have assured that a number of disturbances have been taken into account in the model due to the calculations of the different elements of the matrices. A number of studies reviewed by Zuidema and Zagt (2000) have led them to the conclusion that looking solely at the values of λ is not sensible.

Harvesting

To investigate what the effect of harvesting is on the population dynamics of mahogany a number of simulations using different variables were run. Firstly, the effect of different cutting cycles of 100% harvesting of trees with a DBH > 70 cm. There is a tendency that a longer cutting cycle will have a positive effect on the amount of trees harvested. This simulation has been run because logging practices have typically resulted in mining operations at species levels (Grogan 2006). This method will lead to a sudden and severe reduction, often on a large spatial scale (Grogan, 2006). The outputs clearly indicate that a harvesting of 100% will lead to a perishing population regardless of treatment. The results suggest that when large intervals are used populations are able to recover.

When harvesting occurs at a fixed time interval, using different intensities there seems to be an optimum present for the amount of trees harvested (Figure 12b, page 30). This optimum can be derived form the fact that when harvesting occurs a population will still increase. This has been shown for all treatments except treatment control (Figure 10, page 28). When harvesting takes place at a low intensity and the growth of a population is ensured, it can be described as sustainable.

Fixed cutting cycles and intensities do derive complications when it is not sustainable. The model assumes that even when there are almost no trees left in the forest of harvestable size, there is still harvesting. Harvesting at a threshold value can be used as an alternative method. It is also a method that will ensure the survival of the population. It is shown that populations in which a harvesting intensity takes place of 80 % are not sustainable (Figure 12, page 30). However, when harvesting occurs at a threshold of 0.15 trees/ha populations will recover. However, possibilities to harvest can become scarcer when time passes (Figure 11, page 29).

When cutting cycle increases a critical level in which natural regeneration cannot compensate the loss will be reached. When this happens populations will perish and yields decline. The same trend can be seen with different harvesting intensities. As illustrated by

Figure 12b (page 30) an increase in intensity will result in a peak in obtained wood followed by a diminishing amount of yield. The intensity in which the highest amount of yield is sited can be derived from the dynamics of the population. When harvesting intensity is low enough to still ensure increasing of the population yield will increase every harvesting cycle. When harvesting intensity is too high the population will eventually perish. Figure 12b (page 30) illustrates that increasing intensity will reach an optimum. Harvesting schedules could be derived from this way of analysis harvesting intensities.

6 Conclusion

The main objective of this research is to determine whether the different management regimes have an effect on the population dynamics of *Swietenia macrophylla*. The data is very straightforward in answering this question. An increase in the application of management practices will lead to an increase in mahogany tree density. The population under management treatment intensive will result in having more trees than any other management treatment. With no management treatments based on stand improvement (treatment control) the population will decrease.

As shown in the results the more adult trees in a system the more seedlings there will be produced. It is also shown in the data that the amount of seedlings produced per tree increases with an increasing management regime. However it is only based on a limited amount of seed-providing trees. An increase in fecundity will have a positive effect on the population development of mahogany.

The way a population develops is determined by a few factors: input, the path a new input follows and output. In more an ecological terminology this is: seed-production, growth (height / diameter increment), survival and harvesting.

Diameter increment increases with an increasing intensity of management regime. One of the reasons more trees of the highest class are present in a system is that the time of reaching this class is shorter. Treatment intensive provides the best situation for diameter increment so the trees reach the highest class quicker. The faster trees grow the faster they reproduce. All these conclusions illustrate that it is vitally important to leave enough trees to provide for seed production and to improve seedling survival to maintain mahogany in the area.

Harvesting will always have an effect on the development of a stand. Clearly, no harvesting will result in the most trees present in a stand and in the most stable population. Simulations based on different methods suggest that cutting cycles should be as long as possible. Harvesting intensity has also an effect on the population dynamics of mahogany for the different management regimes. It is likely that with an increasing intensification of management regime, a higher number of trees that can be harvested sustainably. There seems to be an optimum in harvesting intensity; in all treatments it is shown that harvesting at a lower intensity, lower than 80%, a lower yield will be obtained in the end.

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Appendices

Appendix 1:	Map La Chonta
Appendix 2:	Absolute amount of trees measured for each treatment over different years.
Appendix 3:	Population matrices for each treatment with sensitivity and elasticity analyses.
Appendix 4:	Stable size distributions for each treatment
Appendix 5:	Amount of trees harvested using different cutting cycles and different intensities

Appendix 1 Map La Chonta

Map La Chonta: