Journal of Applied Ecology

Journal of Applied Ecology 2008, **45**, 1770–1779 doi: 10.1111/j.1365-2664.2008.01564.x

Silviculture enhances the recovery of overexploited mahogany *Swietenia macrophylla*

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Summary

1. Big leaf mahogany *Swietenia macrophylla* is the most valuable timber species in the tropics but its future as a commercial timber species is at risk. This study evaluates whether recovery of overexploited mahogany populations is enhanced by actively managing the species and its surrounding forest. We assessed the effect of four different management interventions that varied in their intensities of harvesting and silvicultural treatments. We tested the hypothesis that intensive forest management stimulates population growth rates.

2. Data were gathered over a 4-year period in the plots (326 ha) of the Long Term Silvicultural Research Program in Bolivia. Plants > 1·3 m tall were identified and monitored in the plots, while seedlings and saplings (< 1·3 m tall) were recorded and measured around 58 adult mahogany trees. Population growth rate was simulated using population matrices based on observed vital rates.

3. The application of silvicultural treatments only had an effect on seedling and sapling survival; survival being lowest in the unlogged forest and highest at intermediate levels of treatment application. Growth of larger trees tended to increase with management intensity, and was dependent on crown position and liana infestation. Removal of lianas and other competing trees had a positive effect on growth rates.

4. Model simulations suggested that the recovery of overexploited mahogany population is enhanced by the application of intermediate levels of silvicultural treatments. Recovery is dependent on the retention of large seed trees (> 70 cm diameter at 1·3 m height) that produce large numbers of seedlings. Harvesting simulations indicate that mahogany populations can only be sustainably harvested by increasing the cutting cycle length, reducing harvesting intensity and by maintaining optimal growing conditions.

5. *Synthesis and applications.* Mahogany is the most valuable timber species in the tropics, and its range has dramatically decreased mostly due to commercial harvesting. The results of simulation modelling based on field and experimental data suggest that overexploited populations are recovering and that sustainable harvesting will be possible in the future when cutting cycle length is increased, harvesting intensity is reduced and silvicultural treatments are applied regularly throughout the cutting cycle.

Key-words: Bolivia, forest management, population dynamics, silvicultural treatments, tropical forest, management simulations

Introduction

Big-leaf mahogany *Swietenia macrophylla* King, Meliaceae, is the most valuable timber species in the tropics (ITTO 2005) but its future as a commercial species is at risk. Mahogany populations have declined dramatically due to a variety of factors, primarily deforestation and overexploitation (i.e. harvesting at a rate and frequency that does not allow recovery of the population; Gullison *et al*. 1996; Snook 1996; Kometter *et al*. 2004; Grogan & Barreto 2005). Population declines have been so dramatic that mahogany is 'commercially extinct' in large parts of its wide geographical range (Gullison *et al*. 1996; Snook 1996; Snook, Cámara-Cabrales & Kelty 2005). Consequently, in 2002 mahogany was

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included in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). This Appendix specifies that, before being traded at the international market, mahogany must be harvested legally and at intensities that are non-detrimental to the survival of the species and to its role in the ecosystem (Grogan & Barreto 2005). An appropriate level of harvesting should be defined by the CITES Scientific Authority of each exporting country based on scientific information. However, at the end of 2007 this harvesting level had not been defined, although mahogany is probably the most studied timber species in the tropics. There is need for information to define management practices, such as silvicultural treatments, that will guarantee sustainable production from natural forests (Grogan & Barreto 2005, Grogan *et al*. 2008).

It has been argued that the regeneration requirements of mahogany coupled with the lack of seed trees remaining after logging are the main reasons for the decline in exploited populations (Lamb 1966; Gullison *et al*. 1996; Snook 1996; Mostacedo & Fredericksen 1999). Existing data suggest that mahogany regeneration varies along its distributional range, probably due to differences in the amount of light penetrating to the forest understorey in different forest types (Brown, Jennings & Clements 2003). Very little regeneration of mahogany is found in evergreen, late successional forest, where the species is believed to require catastrophic disturbances such as hurricanes, flooding events, and river migrations for mahogany establishment (Gullison *et al*. 1996; Snook 1996). By contrast, abundant regeneration is found in more seasonally dry forests (Lamb 1966; Gerhardt 1996; Günter 2001; Grogan, Ashton & Galvão 2003), where the species is able to regenerate after small-scale disturbances, such as canopy gap openings. Consequently, it has been argued that mahogany populations growing in semi-deciduous forests are more likely to be sustainably managed than populations growing in evergreen forests (Lamb 1966; Günter 2001; Grogan, Barreto & Verissimo 2002; Brown *et al*. 2003).

Bolivian mahogany has been commercially harvested since the 1950s and exported since the 1960s. It was the main timber species being harvested until mid-1990s (Bascopé 1992). Currently, mahogany has undergone commercial extinction in 79% of its range in Bolivia (Kometter *et al*. 2004). Much of the remaining mahogany is being harvested following best management practices defined in the technical norms of the forestry law (MDSP 1998), but illegal harvesting does occur. Due to the economic importance of mahogany, there is ample interest in determining if overexploited populations are recovering and will be harvestable again in the future. To test if silvicultural treatments contribute to such recovery, we used the Long-Term Silvicultural Research Program (LTSRP) plots established in a semi-deciduous moist tropical forest in Guarayos Province in Bolivia. The LTSRP plots allowed us to monitor an overexploited mahogany population over a large area (about 326 ha), and also to test the effect of silviculture on mahogany population growth, with the aim of providing insights into sustainable management practices for the species. Mahogany population growth rate was simulated using matrix models (Caswell 2001). Matrices allow the study of the effect of harvesting of forest products on population growth rates, and the assessment of both the harvesting effect on vital rates (i.e. survival, growth, reproduction) of the species and the sustainability of different harvesting scenarios (e.g. Bernal 1998; Zuidema & Boot 2002; Karsenty & Gourlet-Fleury 2006).

The objectives of this study were to: (i) determine whether mahogany populations are recuperating after intensive selective logging carried out for about 20 years at non-sustainable levels; (ii) identify the effects of silvicultural practices such as reduced competition and increased light levels on mahogany population dynamics; and (iii) model the future potential for sustainable mahogany harvesting. We tested the hypothesis that intensive application of silvicultural treatments stimulates the survival, growth and recruitment of mahogany; consequently, such treatments are expected to have a positive effect on population growth rate.

Methods

STUDY SPECIES

Mahogany is an emergent deciduous tree species that occurs in lowland forests from Mexico southwards through Panama, Venezuela, and along the western and southern rim of the Amazon basin to Bolivia and the Brazilian state of Pará. The species generally occurs at low densities (< 1 adult tree ha^{-1}) in (semi)deciduous and evergreen rainforests, often growing in groups along watercourses or in highly disturbed transition zones between forest types (Gullison *et al*. 1996; Brown *et al*. 2003). It is found under a wide range of climatic, hydrologic, edaphic, and competitive circumstances across its natural range (Grogan *et al*. 2002), and has been classified in different functional groups based on regeneration requirements under local forest conditions.

STUDY SITE

The study was conducted in the 100 000-ha forestry concession of Agroindustria Forestal La Chonta, 30 km east of Ascención de Guarayos, Bolivia (15°47′S, 62°55′W). This semi-deciduous tropical moist forest is transitional between (Chiquitano) dry forest and Amazonian forests (Dauber *et al*. 2000). Annual precipitation in the region is about 1580 mm, with 4 months receiving < 100 mm (May–September) and 1 month (July) during which potential evapotranspiration exceeds rainfall. About 30% of the canopy trees and many lianas are seasonally deciduous (Instituto Boliviano de Investigación Forestal, unpublished data). The area is situated on the south-western border of the Brazilian Shield; it has sandy-loam soils that are rich in nutrients and are characterized by a pH of around 7 [Paz-Rivera 2003; Instituto Boliviano de Investigación Forestal (IBIF), unpublished data]. For trees > 10 cm diameter at 1·3 m height (DBH), the forest has an average stem density of 367 stems ha^{-1}, basal area of 19·3 m^2 ha^{-1}, species richness of 59 tree species ha^{-1} (IBIF, unpublished data). There are about 160 tree species identified at La Chonta, 23 of which are considered to be merchantable. Average harvest volumes are about 6 m^3 ha^{-1}. The intended cutting cycle is currently 30 years and the company's management was certified by the Forest Stewardship Council (FSC) in 1998. Mahogany was the

Table 1. Treatments applied to the LTSRP plots in La Chonta forestry concession, Bolivia: C, control; N, normal; LS, light silviculture; and IS, intensive silviculture. •, management practice applied; ••, management practice applied with double intensity. Mahogany was not harvested during the application of these treatments; it had previously being logged at least once between 1974 and 1995

	Treatments			
Management practices	C	N	LS	IS
• Pre-harvest inventory of merchantable commercial trees, using specific minimum cutting diameters (50–70 cm DBH)	•	•	•	•
• Lianas cut on merchantable trees 6 months before logging		•	•	•
• Skid trail planning		•	•	•
• Retention of 20% merchantable commercial trees as seed trees		•	•	•
• Directional felling		•	•	•
• Merchantable trees harvested using species-specific minimum cutting diameters (50–70 cm in DBH)		•	•	••
• Pre-harvest marking of future crop trees (FCTs) ≥ 10 cm DBH			•	••
• Lianas cut on FCTs 2–5 months before logging			•	••
• Post-harvest liberation of FCTs from overtopping non-commercial trees by girdling			•	••
• Soil scarification in felling gaps during logging (1·1 gaps ha^{-1})				•
• Post-harvest girdling of non-commercial trees > 40 cm DBH (0·13 trees ha^{-1})				•

only species being logged in the concession for about 20 years (1974–1995) but currently is not being harvested because its density is lower than required by the technical norms (0·1 trees ha^{-1} with > 20 cm DBH; Ministerio de Desarrollo Sostenible y Planificación 1998). Fires are prevalent in the landscape matrix surrounding La Chonta; most are set annually during the dry season. In both 1995 and 2004, about 30% of the concession burned.

EXPERIMENTAL DESIGN

The study was carried out in the permanent plots of the LTSRP of the IBIF. There are 12 27-ha plots (326 ha in total) grouped in three blocks, each block established in different logging compartments. Each plot received one of four treatments (Table 1): (i) an unharvested control plot, hereafter referred to as 'control'; (ii) a plot logged following practices stipulated by the Bolivian forestry law, hereafter referred to as 'normal'; (iii) a plot harvested as in the normal treatment but with additional silvicultural treatments, hereafter referred to as 'light silviculture'; and (iv) a plot harvested as in the normal treatment but at double logging intensity and with application of more intensive silvicultural treatments, hereafter referred as 'intensive silviculture'. Consequently, treatments represent a gradient in the intensity of logging and additional silvicultural treatments, which resulted in a gradual increase in area disturbed by logging gaps and skid trails (and consequently also light) as treatment application increased (Blate 2005; Peña-Claros *et al.* 2008a,b). Depending on treatment, 9–19 species were harvested (among which mahogany was not included) with a harvesting intensity varying from 2·1–4 trees ha^{-1}. Silvicultural treatments applied were liana cutting from future crop trees (FCT), liberation of FCT from competing trees through girdling (i.e. removal of a strip of bark around the tree circumference to cause its death), stand refinement by girdling large senescent trees, and soil scarification in felling gaps (see Table 1). Mahogany trees were included as FCTs since the company is interested in harvesting the species in the future. Plots were logged for species other than mahogany in 2001 (block 1, September to November; block 2, March to July) and 2002 (block 3, January to July), and silvicultural treatments were applied immediately after logging.

All mahogany poles and trees > 1·3 m tall found in the plots (total area 326 ha) were marked, mapped and measured in March–April 2002, July–August 2003, and March–May 2006. DBH was measured and two variables were recorded: crown position index, and liana load (Alder & Synott (1992), Clark & Clark (1992); see Supporting Information Table S1). Seedlings and saplings (< 1·3 m tall) were recorded around 58 mahogany trees (23·3–94·2 cm DBH). Selected trees were reproductively mature and > 50 m apart from each other. All seedlings within a 2-m radius around the base of each of these trees and along six evenly spaced 1 × 48 m transects radiating from the inner circle were marked, mapped and measured (making an area of 300·6 m^2 tree^{-1} and 1·74 ha in total). Height and distance to the parent tree were recorded. During the 2003 and 2006 censuses, newly recruited seedlings were recorded and tagged in the same areas as used in 2002. Stumps of mahogany trees harvested in the past were still visible and were mapped in 2002.

DATA ANALYSIS

Population structure

The population structure of mahogany is described using 10 size categories: two height categories (seedlings 0–50; saplings 50–130 cm); two juvenile categories (> 1·3 m tall but < 10 cm DBH; 10–20 cm DBH) and six reproductive categories (20–30, 30–40, 40–50, 50–60, 60–70, > 70 cm DBH). We reconstructed the original mahogany population before exploitation (i.e. before 1974) from the stumps found in the plots. Population structure was compared visually.

Growth, survival and recruitment

Growth rates were calculated for each individual plant as the slope of the linear regression between height (for seedlings and saplings, $n = 223$) or DBH (for all other size classes, $n = 266$) and the three measurement dates. An ANCOVA was used to analyse the effect of treatment and block on growth rates, using initial height or initial DBH as a covariate. Growth rate, initial DBH and initial height were ln-transformed [ln(variable + 1)] before the analysis. Additionally, to determine to what extent variation in diameter growth rates can be attributed to individual tree characteristics, ANCOVA tests were performed using tree characteristics (Supporting Information Table S1) as factors and DBH as a covariate. Finally, to assess direct effects of silvicultural treatments on tree growth, we analysed a group of 71 mahogany future crop trees (FCTs) that were liberated by girdling adjacent trees and/or by cutting the lianas covering them. These trees were distributed among logged treatments (normal, 32 trees; light silviculture, 19; intensive silviculture, 20). The effect of the specific silvicultural treatments on growth rate of mahogany FCT was analysed with a two-way ANCOVA, using liana cutting (naturally free of lianas, lianas cut, and with lianas) and liberation (naturally free, overtopped, free through harvesting, or girdling) as factors and initial DBH as covariate. The interaction term was excluded for the model as it was not significant (ANCOVA, for girdling × liana cutting, $F_{4,72} = 1{\cdot}33$, $P = 0{\cdot}27$).

Plant survival during the study period (2002–2006) was analysed using logistic regression analysis with treatment and block as the categorical covariate, and initial size as the independent variable (for seedlings and saplings, $n = 1542$; for larger plants, $n = 371$). Given that block did not have any effect on survival (data not shown), the analyses were redone with only treatment as a categorical covariate. The probability of survival was then calculated on an annual basis for each size class, using the mid-point of each size class in the logistical regression equations obtained.

To determine to what extent the number of new seedlings produced can be attributed to seed tree DBH, treatment, block, and observation period (2002–2003 and 2003–2006), we used an ANCOVA with tree DBH as a covariate and treatment, block, and observation period as factors. The number of new seedlings produced between 2002–2003 was used directly in the analysis, while the number of new seedlings produced between 2003–2006 was corrected for seedlings dying in-between censuses (number of new seedlings per year = $N_{\text{field}}/(\sigma^3 + \sigma^2 + \sigma)$; where N_{field} is the number of new seedlings counted in the field in 2006, and σ is the annual seedling survival probability obtained using a logistic regression equation (see previous paragraph) to the power of number of years that had passed since the last census (2003) for the different seedling cohorts).

Matrix model construction and analysis

The population dynamics of mahogany was analysed with stage-based matrix models (Caswell 2001), constructed using the same 10 size categories. A transition matrix was parameterized using three vital rates for each treatment: annual survival probability (σ), annual probability of growing to the next size class (γ), and annual number of seedlings produced (f). The probability of staying in the same size class was calculated using σ and γ. Survival rates were calculated with logistical regression equations, using the midpoint of each size class. In the case of seedlings and saplings, we used a different equation for each treatment, as treatments differed in survival (see Results). Growth rates were calculated by regressing (height or DBH) growth on initial size. In the case of poles and trees, we used a different regression for each treatment because (i) the application of specific silvicultural treatments on FCTs improved growth rates (see Results; Fig. 2B); (ii) 42 to 80% of the trees found in a given treatment had been classified as FCT; and (iii) diameter growth rate 2003–2006 was correlated with diameter growth rate 2002–2003 (Pearson correlation, $r = 0{\cdot}60$, $P < 0{\cdot}001$), which indicates that fast-growing trees will maintain their fast growth over time (Brienen & Zuidema 2006, 2007). Finally, the number of seedlings produced by each size class was the average number of seedlings produced by a given size class, regardless of treatment (Supporting Information Table S2).

The transition matrix **A** was used to simulate population dynamics as $\mathbf{n}(t + 1) = \mathbf{A} \times \mathbf{n}(t)$, in which **n** is a vector containing the population structure at time t and $t + 1$ (Caswell 2001). Such a simulation yields a fixed population growth rate equivalent to the dominant eigenvalue (λ), which is a mathematical property of matrix **A**. We simulated the population growth rates (λ) of the different silvicultural treatments and performed elasticity and sensitivity analysis (Zuidema & Franco 2001) to determine how population growth responded to changes in vital rates. Additionally for each logged treatment, a Life Table Response Experiment (LTRE; Caswell 2001) was performed to determine how the vital rate variation between logged treatments and the control treatment contributed to changes in the population growth rate (λ).

Logging simulations

The matrix models were ultimately used to simulate alternative logging scenarios and to explore the population response of mahogany to those scenarios. For this purpose, we used the modelling approach as described by Lloyd *et al*. (2005). We calculated the composite matrix M from logging matrix L and treatment matrix T as follows:

$$M = T^{t-1} \times L,$$

where matrix T contains the vital rates obtained from either the normal, light silviculture or intensive silviculture treatment, and t stands for the number of years after harvesting. The logging matrix L is similar to T but with reduced survival (σ) of commercial size trees, depending on the intensity of mahogany harvesting. Other vital rates were not changed because we assumed that logging of other commercial species has similar effects on vital rates than logging of mahogany (and matrix T includes those changes already). Lambdas were calculated for the resulting populations experiencing harvesting cycles from 20 to 100 years, and for the following logging scenarios: (i) mahogany logging using the normal treatment matrix and two management prescriptions: minimum cutting diameter (MCD) of 50 cm DBH and 100% harvesting intensity as previously done in Bolivia, and MCD of 70 cm DBH and 80% harvesting intensity as stipulated by the current technical norms of the Bolivian Forestry Law (MDSP 1998); (ii) mahogany logging with harvesting intensities of 50%, 80% and 100% of commercial trees > 70 cm DBH; (iii) same as in (ii) but with a diminishing effect of silvicultural treatments over time to better mimic the changes of forest conditions after logging through time. For this, we used the different matrices for different periods of time (t_1; 10 years for the normal and light silvicultural treatment and 15 years for the intensive silvicultural treatment), followed by the control matrix (C) for the remaining years to complete the cutting cycle (t_2). For this purpose, the composite matrix M was adjusted to:

$$M = C^{t2} \times T^{t1-1} \times L.$$

Lambdas obtained were annualized (Lloyd *et al*. 2005) and standardized to the lambda of the control treatment to compare them across the different scenarios. A harvesting prescription was considered sustainable when the standardized lambda was equal or above 1. All logging simulations were done using Mathematica software.

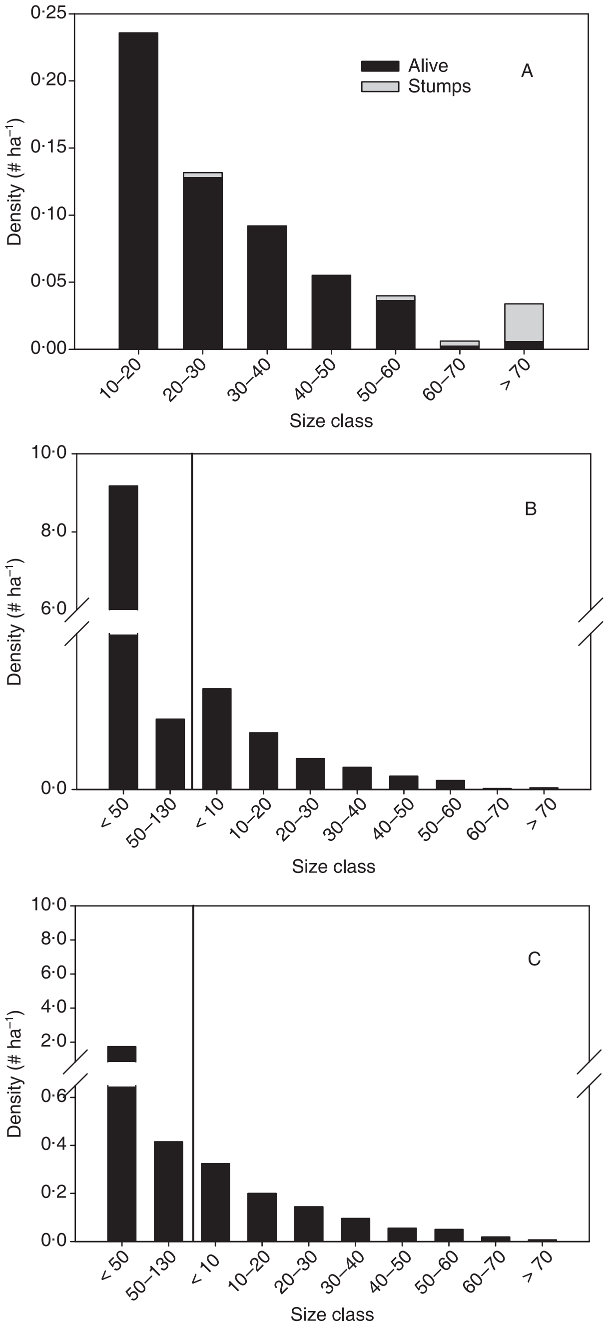

Fig. 1. Population structure of mahogany per size class in the Long Term Silvicultural Research Program plots in a tropical moist semi-deciduous forest in Bolivia. Original population structure reconstructed using observed stumps (trees logged 1970–1995) (A), population structure in 2002 (B) and 2006 (C). Different scales are used for the *y* axis. Two sampling methods are used for B and C, depending on size of the plants. See Methods section for more details.

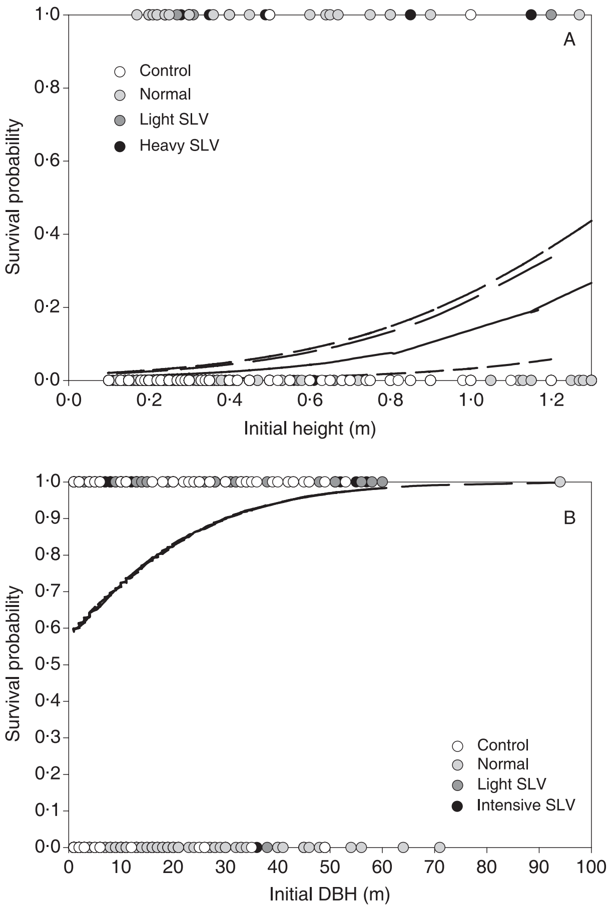

Fig. 2. Annual survival rate for mahogany seedlings and saplings (A) and larger trees (B). Each dot represents a plant growing in one of the four treatments, each treatment being represented by a different symbol. Dots at the bottom represent plants that died during the study period, while dots at the top represent plants surviving during the study period. When treatment has a significant effect, then separate regression lines are shown (small dash, control; medium dash, normal; long dash, light silviculture; solid line, intensive silviculture). SLV, silviculture.

Results

Both the current mahogany population and the original population reconstructed from stumps found in the plots showed a decrease in the number of individuals with increasing size class (Fig. 1A–C). The population structure in 2002 differed from that in 2006 mainly because of the steep drop in seedling density (Fig. 1B–C). The overall population structure of trees > 1·3 m tall was quite similar in both years (Fig. 1B–C).

Seedling and sapling survival varied with treatment and initial size (Table 2; Fig. 2). It was lower in the control treatment, higher in the normal and light silviculture treatment, and intermediate in the intensive treatment. On the other hand, pole and tree survival increased with initial DBH but was not affected by treatment (Table 2; Fig. 2B).

Seedling and sapling height growth rate was not affected by treatment or block, but increased with initial height (Table 2). Similarly, average DBH growth rate was only affected by initial diameter and not by treatment or block (Table 2; Fig. 3A). Trees had a higher DBH growth rate as their crown position improved (ANCOVA, $F_{4,252} = 10{\cdot}52$, $P < 0{\cdot}001$) and as their liana infestation decreased (ANCOVA, $F_{3,250} = 5{\cdot}22$, $P = 0{\cdot}002$). The response of mahogany FCTs to silvicultural

Table 2. Results of statistical analyses on survival and growth rates of mahogany plants found in the LTSRP plots in La Chonta forestry concession. For seedlings and saplings initial size is in height (m), and for other size classes initial size is in DBH (cm). Block was not included in the analysis of survival data as it was not significant. *< 0·05; **< 0·01; ***< 0·001; ns, non-significant; na, non-applicable; C, control; N, normal; LS, light silviculture; and IS, intensive silviculture

						Sample size			
Variable	Initial size	Treatment	Block	Treat × block	Period	C	N	LS	IS
Survival (seedlings and saplings)	37·8***	11·12*	na	na	na	417	610	146	369
Survival (other size classes)	25·32***	1·12^{ns}	na	na	na	60	162	49	100
Growth rate (seedlings and saplings)	4·50*	2·49^{ns}	0·58^{ns}	0·20^{ns}	na	74	88	8	53
Growth rate (other size classes)	81·77***	0·39^{ns}	1·66^{ns}	1·97^{ns}	na	43	112	41	66
Number of new seedlings produced	2·74^{ns}	0·38^{ns}	0·03^{ns}	1·42^{ns}	0·23^{ns}	16	15	11	16

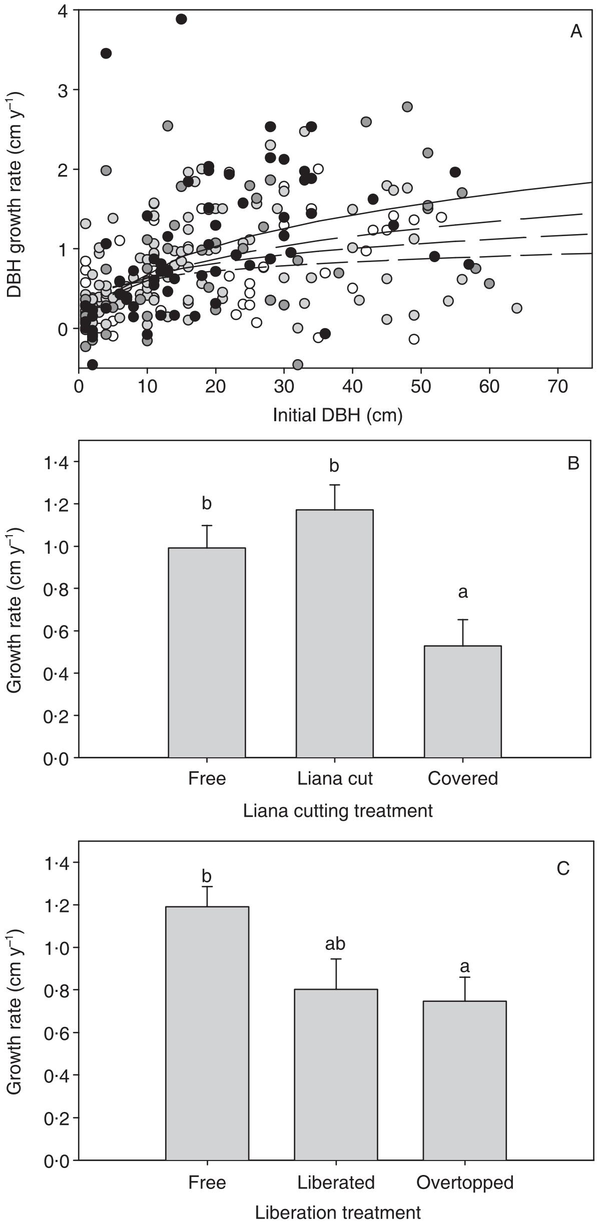

Fig. 3. (A) The relation between growth rate and stem diameter for mahogany trees. Each dot represents a plant in a given treatment. Symbols are as in Fig. 2. (B) The effect of liana cutting on growth rates of future crop trees of mahogany. Data are mean + SE. (C) The effect of liberation through girdling and logging on growth rates of future crop trees of mahogany. Data are mean + SE.

treatments to liana cutting was greater (ANCOVA, $F_{2,76} = 8·94$, $P < 0·001$; Fig. 3B) than to liberation through girdling or harvesting (ANCOVA, $F_{2,76} = 4·07$, $P = 0·021$; Fig. 3C).

Mahogany trees with a > 23-cm DBH had seedlings under their crowns, while smaller trees had none. The number of new seedlings produced was not affected either by seed tree DBH, treatment, block, or by observation period (Table 2). The only significant interaction was between observation period and block (ANCOVA, $F_{2,7·53} = 5·70$, $P = 0·03$).

POPULATION GROWTH, ELASTICITIES AND LIFE TABLE RESPONSE EXPERIMENT

Model simulations predicted that the population growth rate (λ) of mahogany in the control treatment was slightly higher than 1 (1·013). Population growth rate was only slightly higher in the light silviculture treatment than in the normal treatment and, contrary to our expectation, lowest in the most intensive treatment (normal, $\lambda = 1·021$; light silviculture, $\lambda = 1·022$; and intensive silviculture, $\lambda = 1·008$). Elasticity analyses showed that the population growth reacted most strongly to changes in survival of large trees (Table 3). The LTRE suggests that the intensive silviculture treatment negatively influenced the population growth rate due to low survival and growth at the seedling and sapling stage (Fig. 4).

HARVESTING SIMULATIONS

The simulations performed showed that the cutting cycle needed to reach the standardized lambda ≥ 1 is considerably shorter when using a minimum cutting diameter (MCD) of 70 cm DBH (about 50 years) than when using an MCD of 50 cm DBH (> 100 years; Fig. 5A). Additionally, a reduction of logging intensities from 100% to 80% and to 50% of commercial trees (> 70 cm DBH) lowered the length of the cutting cycle needed to reach the standardized lambda only in the case of the light silviculture and the normal treatments (Fig. 5B). When treatment matrices were used only for a limited period of time to simulate closure of the canopy after logging, none of the harvesting intensities tested allowed the reference lambda to be reached (Fig. 5C).

Table 3. Results of the elasticity analysis showing the importance of the three vital rates for the mahogany population growth rate. σ, annual survival probability; γ, annual probability to grow to the next size class; *f*, annual number of seedlings produced

	Control			Normal			Light silviculture			Intensive silviculture		
Size category	σ	γ	*f*	σ	γ	*f*	σ	γ	*f*	σ	γ	*f*
Seedlings and saplings	0·006	0·009	–	0·010	0·013	–	0·011	0·013	–	0·003	0·007	–
Poles (1–20 cm DBH)	0·054	0·009	–	0·068	0·013	–	0·071	0·013	–	0·041	0·007	–
Reproductive trees (> 20 cm DBH)	0·132	0·008	0·002	0·122	0·010	0·002	0·119	0·011	0·002	0·141	0·007	0·001

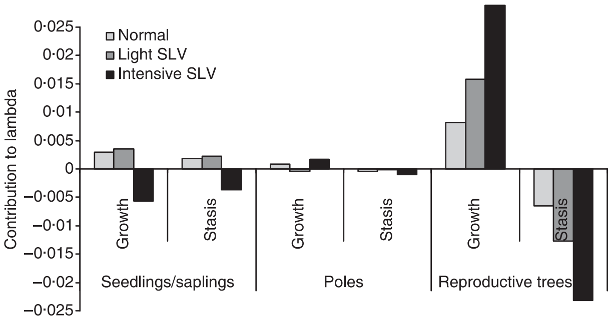

Fig. 4. Results of the Life Table Response Experiment (LTRE) showing the contribution of each vital rate to the population growth rate (lambda). Results are shown for seedlings and saplings, poles (1–20 cm DBH) and for reproductive trees (> 20 cm DBH) in the different logged treatments. The population in the control treatment was taken as the reference. SLV, silviculture.

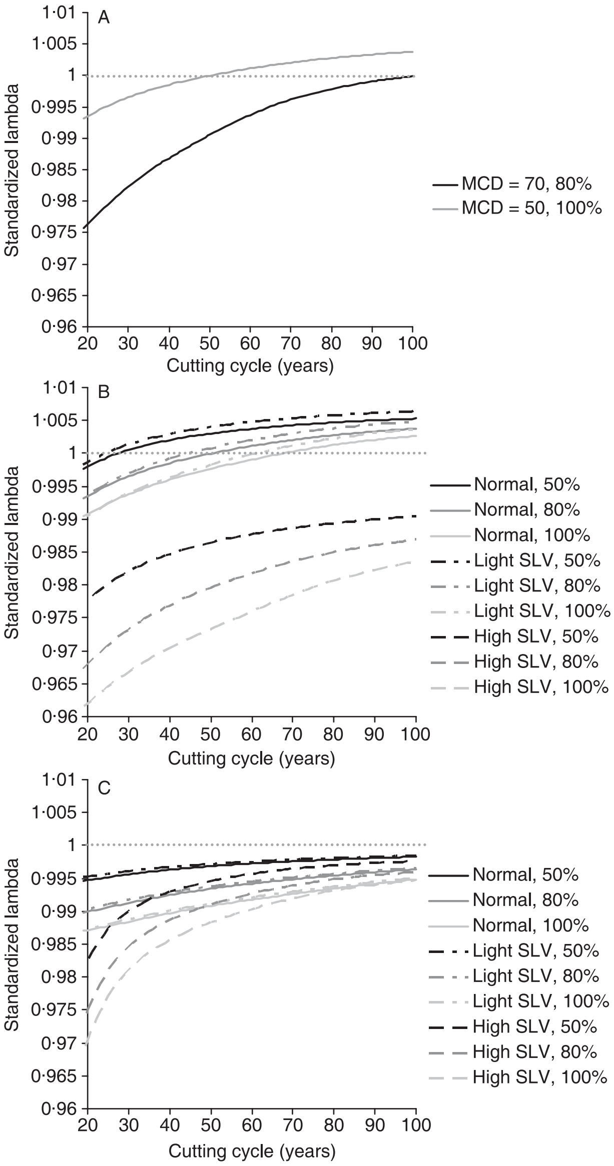

Fig. 5. Annualized lambdas (*sensu* Lloyd *et al.* 2005) for three different logging scenarios for mahogany. The lambdas are standardized to the lambda of the control treatment (lambda = 1, straight dashed grey line). (A) Mahogany population growth rate using the normal treatment matrix and applying minimum cutting diameter (MCD) of 50 cm DBH and 100% harvesting intensity and an MCD of 70 cm DBH and 80% harvesting intensity. (B) Population growth rates using different treatment matrices and different harvesting intensities of commercial trees, assuming a MCD of 70 cm DBH and no changes in vital rates through time. (C) The same as in B, but including changes in vital rates through time by using the control treatment matrix to complete the cutting cycle. SLV, silviculture.

Discussion

Previous exploitation of mahogany has resulted in local commercial extinction of the species in our study area in lowland Bolivia. Based on the number and sizes of stumps of logged mahogany trees in the area, pre-logging population structure differed considerably from the current one (Fig. 1A). The current scarcity of large reproductive trees is the result of previous overexploitation, and the elasticity analysis shows that larger trees make the greatest contribution to population growth rates (Table 3). The results of the matrix modelling, using data from 4 years of monitoring, suggest that the mahogany population in La Chonta will recover faster from overharvesting if intermediate levels of silvicultural treatments are applied to individual mahogany trees and to the forest in general. Moreover, our harvesting simulations strongly suggest that silvicultural treatments need to be applied repeatedly to achieve sustainable harvesting levels of mahogany.

EFFECT OF SILVICULTURAL TREATMENTS ON POPULATION DYNAMICS

The difference found in the mahogany population structure between 2002 and 2006 was mainly due to a decline in seedling density (Fig. 1B–C), caused by high seedling mortality (98% of the seedlings present in 2002 were dead by 2006). The number of newly recruited seedlings in 2002–2003 and 2003–2006 was not high enough to compensate for the number of seedlings lost during the same period (Fig. 1). The fact that more seedlings were found in 2002 than in the other censuses may be due to differences in precipitation among years. It is known that germination of mahogany seeds is primarily triggered by soil moisture (Brown *et al*. 2003), while seedling survival depends on regular rain events to avoid desiccation (Gerhardt 1996; Grogan *et al*. 2003). Mahogany seeds in La Chonta germinate at the onset of the rains in November–December. These rains were 70% higher than average in 2001 (La Chonta company, unpublished data). Precipitation during the same period in 2002 and 2005 was 19 to 33% lower than average. This suggests that the high seedling counts in all treatments in 2002 was probably the result of high precipitation rather than the consequence of increases in light levels due to the application of silvicultural treatments (Blate 2005; Peña-Claros *et al.* 2008a,b), as even in the control treatments, higher densities of seedlings were found in 2002 than in 2006. Interestingly, the same decreasing pattern of seedling density has been found for a further 23 commercial species being monitored in La Chonta (Peña-Claros *et al*. 2008a). These predictions on precipitation-driven variation in annual recruitment will be tested with continued observation in future years.

Mahogany survival varied with tree size, the lowest being among seedlings and saplings (Fig. 2). The low seedling survival rates observed are similar to those reported by Grogan *et al*. (2003). Seedlings are vulnerable to environmental stress such as shade, root competition, herbivory, pathogens, or mechanical damage (Gullison & Hardner 1993; Gerhardt 1996; Gullison *et al*. 1996; Whitman, Brokaw & Hagan 1997). In our study plots, the amount of light reaching the seedlings increased in response to silvicultural treatments (Blate 2005; Peña-Claros *et al*. 2008a,b), and seedling survival was higher after the application of the normal and light silviculture treatments (Fig. 2a). Contrary to our expectation, the intensive silviculture treatment had a negative effect on survival rate, probably because the higher logging intensity applied to this treatment resulted in higher mortality among seedlings and saplings, as a consequence of greater competition with other plant forms due to the opening of the canopy, or due to fewer suitable sites for germination and establishment. On the other hand, survival rate of mahogany trees > 1·3 m tall was not affected by silvicultural treatments (Fig. 2B) and it reached almost 100% among trees > 50 cm DBH, corresponding to the high survival rates observed elsewhere in Bolivia (Gullison *et al*. 1996).

Four years after the treatments, mahogany diameter growth rates did not vary with the intensity of silvicultural treatments, although there was a clear tendency in that direction (Fig. 3A). Given that diameter growth rates were autocorrelated, it is likely that as time passes, treatments will have a stronger effect on growth rates because fast-growing trees maintain their fast growth rates through time (Brienen & Zuidema 2007). Additionally, it was found that diameter growth rate increased with crown position and decreased with liana load, confirming the importance of increasing light levels to promote higher DBH growth rates of mahogany. Furthermore, mahogany FCTs liberated through liana cutting had significantly higher growth rates than non-liberated trees (Fig. 3B). These results are in concordance with other studies that have found that growth rates strongly depend on site-specific light levels and can be increased by artificial canopy openings (Gullison *et al*. 1996; Brown *et al*. 2003; Grogan *et al*. 2003; Negreros-Castillo *et al*. 2003; Snook & Negreros-Castillo 2004; Grogan & Galvão 2006). On the other hand, the growth rates of mahogany seedlings and saplings were not affected by silvicultural treatment. This result might reflect a high inter-specific competition for light with neighbouring plants, such as lianas, *Heliconia* sp., *Costus* sp., and ferns that are abundant in logging gaps in La Chonta (Felton *et al*. 2006). Additionally, many of the seedlings showed signs of insect damage, one of the major factors limiting growth and survival in natural forests (Norghauer, Malcolm & Zimmerman 2006).

RECOVERY OF OVEREXPLOITED MAHOGANY POPULATIONS

The population growth rates recorded in this study suggest that the mahogany populations at La Chonta are recovering from previous logging and that their recovery is further enhanced by the application of the normal and the light silvicultural treatments. The LTRE results indicate that the positive effects of harvesting other timber species and applying additional silvicultural treatments on the mahogany population growth rate are larger than the negative ones (Fig. 4). However, our results suggest that the intensity at which these treatments should be applied has to be taken into account, as the intensive silvicultural treatment actually reduced the population growth rate. Intensive silvicultural treatments negatively affected the growth and survival of seedlings and saplings, and these negative effects could not be balanced out by an increase in growth rates of reproductive trees (Fig. 4). Positive effects of liberation on population growth rates were expected, given the results of other studies (e.g. Grogan *et al*. 2008), but it is also possible that more time is needed to observe them. Positive effects on population growth rates are expected to occur in the long-term as mahogany growth rate is auto-correlated, a large proportion of trees 10–60 cm DBH were considered FCT, and FCT showed a strong positive response in terms of growth rates to liana cutting (Fig. 3B).

WILL IT BE FEASIBLE TO HARVEST THESE MAHOGANY POPULATIONS IN THE FUTURE?

Our simulations suggest that the current management practices of the Bolivian Forestry Law (reduced-impact logging techniques, MCD of 70 cm DBH, 80% harvesting of harvestable trees; Ministerio de Desarrollo Sostenible y Planificación 1998) represent a large improvement from the previous prescriptions used for mahogany exploitation. However, for the current prescription to be sustainable, it is necessary to use longer cutting cycles (at least > 50 years; Fig. 5A) than are now being recommended in the Bolivian Forestry Law (i.e. minimum cutting cycle of 20 years). Moreover, when harvesting intensity is reduced to 50%, overexploited populations will be sustainably harvestable only if cutting cycles of at least 25 years are used and the effects of treatment (harvesting plus additional silvicultural treatments) are maintained through time (Fig. 5B). If forest conditions return to the pre-logging situation (control treatment in our case), then mahogany harvesting is not sustainable regardless of the harvesting intensity and cutting cycle length applied (Fig. 5C). These results clearly show that mahogany populations need to be actively managed to achieve sustainability and contradict the suggestion that the application of reduced impact logging techniques (as the ones implemented in the normal treatment) are enough to achieve sustainable harvesting of mahogany in semi-deciduous forests (Brown *et al.* 2003). However it is necessary to define the intensity of treatment application as our results indicate that our intensive silvicultural treatment had a negative effect on population growth rates (Fig. 5B). It is possible that appropriate levels of treatment application will vary with forest conditions, requiring even more labour-intensive and costly silvicultural treatments than those implemented in our study. For example, treatments such as enrichment planting with seedlings, direct seeding of logging gaps, and herbicide application in logging gaps to reduce competition, could also be used to promote mahogany regeneration, even in semi-deciduous forests. Some of these treatments are being tested in our study area, and results are very promising (IBIF, unpublished data).

In this study, we have combined a large-scale experimental set up, long-term monitoring of vital rates, and experimental application of silvicultural treatments to simulate how mahogany populations recover after overexploitation. This integrative approach was also used to define effective management practices for mahogany and could be used for other tropical commercial timber species as well. In our case, it enabled us to provide recommendations for the management of mahogany in terms of the length of the cutting cycle, harvest intensity, and the application of additional silvicultural treatments. As mahogany is one of the most valuable timber species in the tropics with an increasing market value, it should be possible to cover the cost of the necessary intensive management recommended here.

Acknowledgements

This research is part of the Long-term Silvicultural Research Program of IBIF. We thank the personnel of La Chonta Agroindustria Forestal for permission to work in the concession and for assistance with plot establishment and monitoring. We owe particular thanks to Laurent Bongers, Todd Fredericksen, William Pariona, Claudio Leaño, Bonifacio Mostacedo, Calvin Ohlson-Kiehn, Carlos Pinto, Lourens Poorter, Ricardo Mendez, Angel Mendez, Eugenio Mercado and Angel Subirana for their assistance during different phases of this study. Jack Putz, Pieter Zuidema, Jimmy Grogan, Matthew Landis and two anonymous reviewers gave thoughtful and helpful comments to improve the manuscript. Pieter Zuidema also assisted greatly with improvements to our matrix modelling. This research was supported by BOLFOR Phase I and Phase II, a forest management project funded by USAID, the Bolivian government, and The Nature Conservancy.

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Received 28 August 2007; accepted 17 August 2008
Handling Editor: Jan Leps

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Categories of crown position index and liana load to which mahogany trees were assigned.

Table S2. Transition probabilities used to describe the population growth of overexploited mahogany populations in a tropical moist semi-deciduous forest in Bolivia.

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