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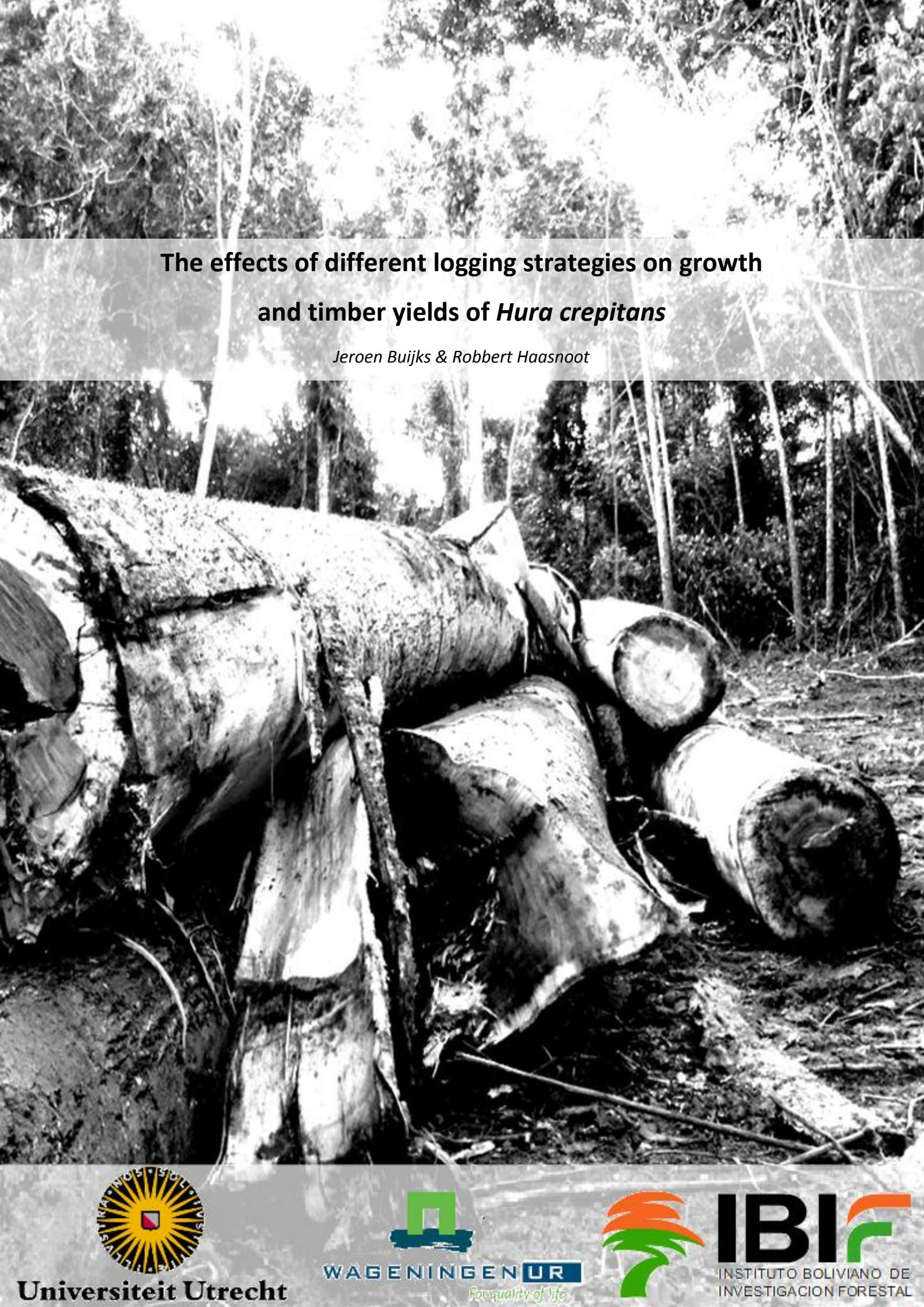
Jeroen Buijks & Robbert Haasnoot



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“People who will not sustain trees,

will soon live in a world that will not sustain people.”

Bryce Nelson

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Abstract

As the use of conventional selective logging has shown to significantly damage and degrade tropical forests, reduced-impact logging techniques and guidelines were developed worldwide. Reduced-impact logging has repeatedly shown to reduce the impact of logging on tropical forests. Unfortunately, these techniques are not sufficient enough to guarantee sustainable timber yields of commercial tree species. The addition of silvicultural treatments has proven to be an effective strategy to increase the growth rates of future crop trees (FCTs) in the period after logging. In this study we combined life time growth rates obtained from tree ring-analysis with variables from permanent plot data to construct an individual tree based growth model for *Hura crepitans.* Because the use of growth rates obtained from permanent plots may lead to underestimating long term tree growth and therefore future timber yields, growth rates obtained from tree ring analysis were used in this study. This model was used to determine future timber yields after the application of different logging strategies in a Bolivian semi-deciduous tropical forest. We analyzed the effects of reduced-impact logging (RIL), with or without Low-intensity (LS) or High-intensity silvicultural treatments (HS), different logging intensities (38% and 80% of all trees > the Minimum Cutting Diameter) and different logging cycles (20 or 30 years) on growth and future timber yields of *Hura crepitans*. Growth rates of future crop trees in the different DBH classes (10-30 cm, 30-60 cm and >60 cm) increased with 11-36% in the RIL treatment, 11-60% in the LS treatment and 23-68% in the HS treatment, compared to the control treatment. These effects lasted up to 4 years for RIL and LS and up to 6 years when high-intensity silvicultural treatments were used. The largest increase in growth rates were found in trees above 60 cm DBH. With the current Bolivian logging legislation (RIL, 80% logging intensity, 20yr cycle) the recuperation of timber volume was only 52% compared to the initial harvest. This timber recuperation rate increased to 64% when high intensity silvicultural treatments were applied. Thus, silvicultural treatments increase future yields, but under current logging regulations these yields are substantially lower than initial yields. Our results show that by reducing the logging intensity to 38% of all trees above Minimum Cutting Diameter (MCD), 91-102% of the initial volume can be harvested after 20 years. Alternatively, by increasing the time between logging events to 30 years, 70-82% of the initial volume recuperates under a logging intensity of 80% and 104-117% under a logging intensity of 38%. These results indicate that decreasing logging intensities, increasing the logging cycles and the application of high-intensity silvicultural treatments improves sustainability of tropical timber production, although the implementation of these actions would be at the expense of the current income of logging companies.

Keywords: Bolivia; Sustainable tropical forest management; Individual-tree based growth model; Tree ring analysis; Permanent sample plots; Reduced impact logging; Silvicultural treatments; Timber recuperation; *Hura crepitans*

1. Introduction

As a consequence of a growing world population and its demands, forests are threatened by degradation and deforestation. Estimates of the amount of forest converted to other land uses from 2000 till 2010 show that around 13 million hectares of forest (mainly tropical forest) is converted each year [FAO, 2010]. Sustainable selective logging is needed as an alternative for this land use change, while conserving these tropical forests [Howard & Valerio, 1996; Dickinson et al., 1996; Keller et al., 2007; Zarin et al., 2007]. Forest management can be considered sustainable if wood volumes of commercial species harvested at the initial harvest, are similar to the volume of timber available at the second harvest (after a certain re-growth period), while minimally disturbing the environment. However, only 3.5% of the tropical forest estates use responsible practices and is certified as being sustainable (not in terms of recuperation) [ITTO, 2007].

The use of conventional selective logging has shown to significantly damage tropical forests [Pereira et al., 2002] and has led to severe depletion and degradation of commercially valuable species [Gullison et al., 1996]. To reduce the impact of logging activities on tropical forests, detailed reduced-impact logging (RIL) techniques and guidelines are developed worldwide [Putz et al., 2008]. By applying RIL techniques such as directional felling, skid trial planning and liana cutting, considerably less damage is done to future crop trees (FCTs) [Pinard & Putz, 1996] and to soil and regeneration [Putz et al., 2000]. Unfortunately, research shows that these

techniques are not sufficient enough to guarantee sustainable timber yields of commercial species. Only 3-50% of the harvested volume recuperated and would be available for harvest in the next logging cycle [Dauber et al., 2005; Sist & Ferreira, 2007; Brienen & Zuidema 2006a; Rozendaal et al., 2010, Rozendaal & Zuidema, 2011]. This indicates that the application of RIL alone is far from sustainable when using a cutting cycle of 20 years. An effective strategy to increase the commercial timber yields in the period after logging is the addition of silvicultural treatments [Dauber et al., 2005; Keller et al., 2007]. Silvicultural treatments aim on increasing growth conditions of FCTs, by liberating FCTs from overtopping non-commercial trees and lianas [Wadsworth & Zweede, 2006]. Recent studies have shown that silvicultural treatments can increase growth rates of FCTs with 22–27% in a Bolivian tropical dry forest [Villegas et al., 2009] and even up to 50-60% in a Bolivian tropical moist forest [Peña-Claros et al., 2008a]. With this increase in growth of FCTs, which can last for about 6 years [Peña-Claros et al., 2008a; Toledo et al., 2011], future logging volumes could be increased.

Until recently, the most important source of data for growth of tropical trees was obtained from repeated diameter measurements in permanent sample plots. This data is then used in combination with data on mortality, recruitment and size structure of the population to construct growth and yield models for tropical tree species or species groups [e.g. Alder, 1995; Arets, 2005; Dauber et al., 2005; Picard et al., 2008]. There are some important limitations to this method. The short time span of growth measurements in these studies, the assumption of deterministic growth trajectories and the lack of accounting for autocorrelation, may lead to underestimating long term tree growth and therefore future timber yields. [Brienen, 2005; Brienen & Zuidema, 2006a]. Temporal correlations may be found between growth rates in subsequent years (autocorrelation between years) and in growth rates between trees in the same area (autocorrelation between trees). This autocorrelation may strongly influence the variation in growth trajectories and size-age variation in tree populations [Bullock et al., 2004] and therefore the output of growth simulations and population models, especially with data from shorter time spans e.g. obtained from permanent plots. Therefore, quantifying autocorrelation and implementing this into growth models is essential for reliable model output [Brienen et al., 2006]. Another disadvantage of permanent plot data is that slow-growing, suppressed juvenile trees are also included in the data, of which only a small fraction will eventually attain harvestable size. Therefore, including these small trees also underestimates the growth of FCTs [Rozendaal et al., 2010]. As an alternative to the use of short term growth rates obtained from permanent plots, tree ring measurements were introduced as a valuable and reliable tool to evaluate the sustainability of forest management. The formation of annual growth rings in most tree species provides reliable data on lifetime growth rates of (tropical) tree species [Brienen & Zuidema, 2006a; Brienen & Zuidema, 2006b]. These growth rates can be directly applied to estimate timber yield using relatively simple models [Brienen & Zuidema, 2006b; Rozendaal et al., 2010]. Although tree rings provide detailed, long-term data on growth, they do not provide data on other variables (abundance, size class distribution, natural mortality and logging mortality), necessary for modeling population dynamics.

This paper focuses on the effect of reduced impact logging and additional silvicultural treatments on the growth and timber yields of *Hura crepitans,* a common commercial timber species in the lowlands of Bolivia. In Bolivia, the 1996 Forestry act requires the use of RIL techniques during logging. This act also requires a minimum cutting cycle of 20 years and a maximum logging intensity of 80% of all trees (leaving 20% of the trees as seed trees) above the defined Minimum Cutting Diameter (MCD) of 50-70 cm (species dependent) [MDMSA, 1997]. After the introduction of this act, Bolivia became a model for management of tropical forest and its certification [Nittler & Nash, 1999]. This resulted in substantial progress towards sustainable management of tropical forests, with 25% (2.1 million ha) of the total area under forest management now being certified by the Forest Stewardship Council (FSC) by 2007 [CFV, 2007]. Although research has shown that RIL techniques are not sufficient in sustaining timber yields of commercial species, and there is a need of additional silvicultural treatments to make tropical logging activities more sustainable, forest management in Bolivia rarely goes beyond RIL techniques [Fredericksen et al., 2003; Dauber et al., 2005; Keller et al., 2007; Peña-Claros et al., 2008a]. It is therefore important to obtain realistic estimates of timber yields after logging with the use of additional silvicultural treatments, to validate these techniques for forest managers.

In this paper we combine tree ring data with data obtained from the permanent plots of the Long-Term Silvicultural Research Program (LTSRP) in lowland Bolivia, a network of large scale replicated plots (20-27ha) which received different logging treatments. The growth rates are obtained from tree ring measurements, while other variables (population structure, natural mortality, logging intensity, logging mortality and treatment induced increased growth) are obtained from permanent plot data. In this paper we focus on the effects of different logging techniques on growth rates and future timber yields of *Hura crepitans* in tropical forests of lowland Bolivia. Specific questions addressed in this study are; (1) What is the effect of different logging strategies on the growth of *Hura crepitans*? (2) What is the difference between growth rates of *Hura crepitans* trees obtained from permanent plot data compared to data obtained from tree ring analysis? (3) What harvestable volumes of timber will recuperate under different logging strategies? (4) Which logging cycle and strategy is most recommendable for *Hura crepitans?*

2. Materials & Methods

2.1 Study area and species

Fieldwork was conducted in a semi-deciduous tropical moist forest, east of the town of Guarayos, Santa Cruz province, Bolivia (15°47'S, 62°55'W). The study area is a transition between Chiquitano dry forests and Amazonian moist forests. Average annual precipitation is 1580 mm, with a dry season from May till September in which precipitation is <100 mm per month [Peña-Claros et al., 2008a]. Due to this dry season annual rings are formed in many trees [Lopez, 2003; Rozendaal et al., 2010]. The forest has an average density of 367 trees (DBH > 10 cm) ha^{-1} with a basal area of 19.3 m^2 ha^{-1}. The tree (DBH > 10 cm) biodiversity is 59 species ha^{-1} with a total of 160 different tree species [Peña-Claros et al., 2008a]. The species used in this study is *Hura crepitans* (Euphorbiaceae), a commercial valuable timber species which has a minimum cutting diameter of 70 cm. This partly shade tolerant tree has density of 8.7 trees ha^{-1} with an average basal area of 1.41 m^2 ha^{-1} [Peña-Claros et al., 2008a].

Table 1; Silvicultural treatments used in the different logging scenarios. LS = RIL + LS, HS = RIL + LS + HS.
* Minimum Cutting Diameter, ** Future Crop Trees.

Reduced Impact Logging (RIL)
- Pre-harvest inventory of merchantable commercial trees (according MCD*) - Lianas cut on merchantable trees 6 months before logging - Skid trial planning - Retention of 20% merchantable commercial trees as seed trees - Directional felling - Merchantable trees harvested using species-specific MCD
Low-intensity Silvicultural Treatments (LS)
- Pre-harvest marking of 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
High-intensity Silvicultural Treatments (HS)
- LS is also applied to potential timber species - 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})

The study area is part of a 100.000 ha forestry concession of the logging company Agroindustria Forestal La Chonta. This company has been certified by the FSC since 1998, and uses a cutting cycle of 30 years. The permanent plots of the Long-Term Silvicultural Research Program of the Instituto Boliviano de Investigación Forestal (IBIF) are located within this concession. These plots are measured since 2000, with the last measurement in the end of 2009. Three main blocks consists of 4 plots which each have undergone different logging strategies in 2001 or 2002; Reduced-impact Logging (RIL), RIL with additional low-intensity silvicultural treatments (LS), RIL with additional high-intensity silvicultural treatments (HS) and a control subplot (C) where

no logging occurred (**Table 1**). In each entire plot all trees >40 cm DBH are measured, trees with a DBH of 20-40 cm are only measured in half of the plot while trees 10-20 cm DBH are only measured in four 1-ha subplots. In total, the plots of the LTSRP cover an area of 324 ha, divided into three 108 ha blocks each containing four 27 ha plots (**Fig. 1**).

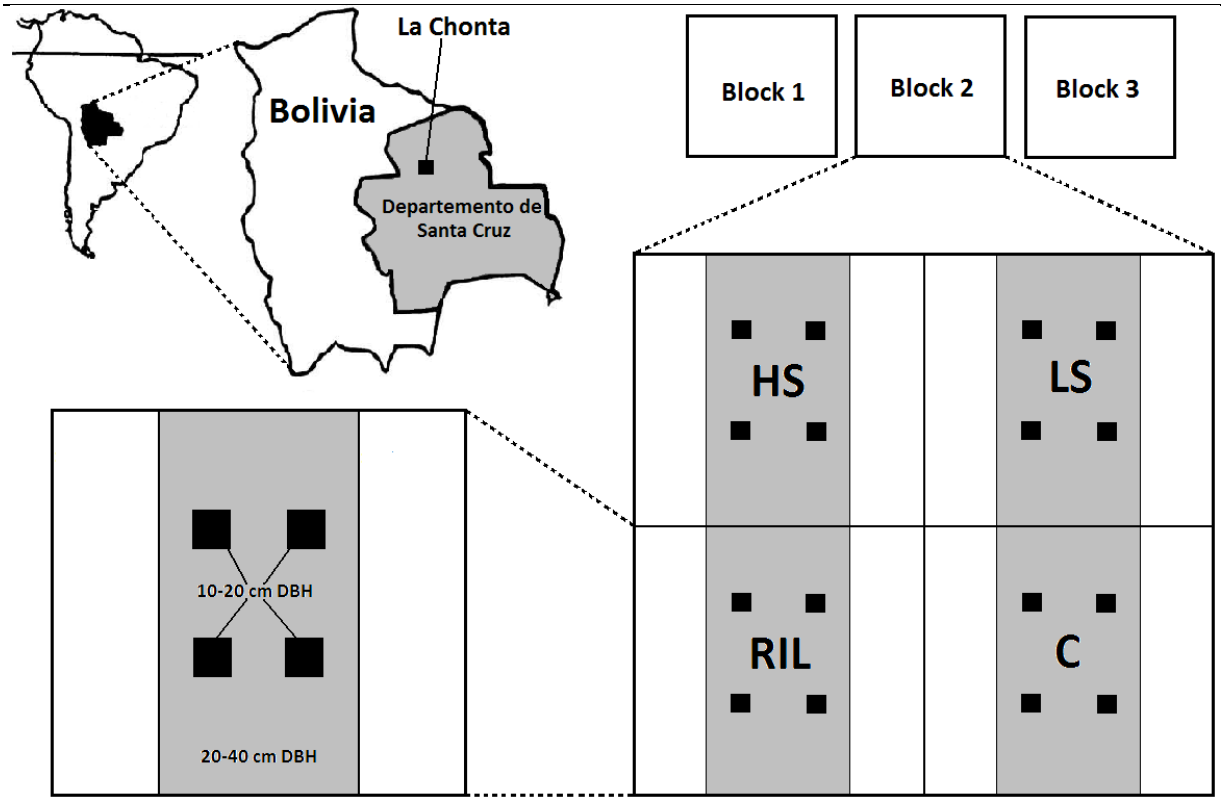

Fig. 1; Location of study site (left-top) and experimental design of the LTSRP in La Chonta Forest Concession, Bolivia: HS = High-intensity Silviculture; LS = Low-intensity Silviculture; RIL = Reduced Impact logging and C = Control. Black = Trees with DBH 10-20 cm measured; Grey = Trees with DBH 20-40 cm measured; Trees with DBH >40 cm are measured in the entire plot.

2.2 Sample collection and measurements

Tree discs and cores of *Hura crepitans* were collected in an undisturbed forest in March and April of 2011. Seventeen discs were obtained at breast height with a chainsaw. In addition, cores were collected from 10 living trees. From each tree, 3 cores were taken at breast height. All samples were taken according to the following sampling strategy; In a 9 hectare plot a random GPS point was assigned, this point was used as the centre of our sampling circle with a 50 m radius (0.79 ha). Within this circle we sampled all trees of >10 cm DBH. This was repeated in 3 other 9 hectare plots. This sampling strategy was used to minimize spatial autocorrelation between trees due to a larger scale, while still representing a realistic DBH distribution due to clustered sampling. Samples were collected right after logging, and thus represent trees from an undisturbed forest. For each sampled tree we also measured the total height and height till the first branch. After collecting, both disks and cores were dried and sanded up to 3000 grit. For the discs we counted the rings on 3 different radii and measured ring width with a LINTAB 6 and TSAPWin software (Rinntech, Germany). The cores were scanned with high resolution scanner (Epson 10000X) and measured on a minimum of 3 radii with WinDENDRO.

2.3 Sample analysis

Ring-widths of all different radii were measured, averaged and then multiplied by two to calculate the annual diameter growth for each tree. The cumulative annual diameter growth was then used to construct age diameter relations for the complete lifetime of each tree. To determine diameter-growth relations, trees were divided into DBH categories of 3 cm and average diameter increments with variances were calculated for each

category. As tree diameter growth is typically non-linear related to DBH, with lower growth values for both large and small sized individuals, the Hossfeld IV equation [Zeide, 1993] was used to describe this pattern. This equation was fitted through the DBH growth data using a non-linear regression procedure with a least-squares loss function. The Hossfeld IV equation is of the following form (**eq. 1**):

$$G(DBH) = \frac{b \times c \times DBH^{(c-1)}}{\left(b + (DBH^{(c/a)})\right)^2}$$

Where *G(DBH)* is the annual DBH growth rate (cm yr^{-1}) for a certain *DBH*, and *a*, *b* and *c* are fitted parameters.

2.4 Growth rates: ring data vs. permanent plot data

To analyse the differences between ring data and permanent plot we divided the ring data in the same DBH classes (10-30 cm, 30-60 cm, >60 cm). The average annual growth rate for the entire data set was calculated but also per DBH class. Differences within and between the data sets were calculated with Mann-Whitney U tests.

2.5 Analysing variables

To determine variables or model parameters, permanent plot data of the LTSRP were used. This data consists of diameter measurements for 1728 individual (>10 cm DBH) *Hura crepitans* trees, measured from 2000 until 2009. The DBH of all trees in the plots were re-measured approximately 1, 2, 4, 6 and 8 years after logging. Regeneration and mortality of *Hura crepitans* trees were also monitored during each census. Trees with extreme growth rates (averages >5 cm yr^{-1}) which were incorrectly measured, due to the presence of lianas, palms and/or buttresses, were excluded from the dataset.

Growth rates from permanent plots

Growth rates were calculated for each tree of the permanent plot data as the slope of DBH and measurement date. Annual growth rates were calculated for the entire period of approximately 8 years (2000-2009). Trees were divided into three DBH classes to account for the differences in growth rates; 10-30 cm, 30-60 cm and >60 cm DHB. The data was tested for normality by a Kolmogorov-Smirnov test and differences between the classes were tested with a Kruskal-Wallis test and Mann-Whitney U tests. To determine the differences in average annual growth rates between the different logging treatments (C, RIL, LS and HS) and between the different DBH classes Kruskal-Wallis tests and Mann-Whitney U tests were used. The percentage of relative growth increase after each logging treatment was calculated for each DBH class. This was calculated as the growth rates of all trees of a certain DBH category in a logging treatment (RIL, LS, HS), divided by the growth rates of all trees of the same DBH class in the control treatment, times hundred. To determine how long the effects of different treatments on growth lasted, annual growth rates were calculated in each measurement period (0-1, 1-2, 2-4, 4-6 and 6-8 years after establishment) as the slope of DBH and measurement dates. Differences in time for each treatment were tested with Friedman tests, differences among treatments per time step were tested with One-way ANOVA tests with a Bonferroni correction.

Natural mortality

Survival was determined for each individual tree over the entire measuring period of approximately 8 years ($S(8\,yr)$). Trees that had been logged, died as a consequence of logging and new recruits were excluded from the dataset. Then the 10 year mortality rate was calculated as; 1- $[(\sqrt[8]{S(8\,yr)})^{10}$. The same DBH classes as for growth (10-30 cm, 30-60 cm and >60 cm DHB) were used for natural mortality rates. The differences in natural mortality between the DBH classes and between the treatments were tested with Pearson Chi-Square tests.

Logging (mortality)

To simulate logging a random fraction of all trees above the MCD was removed. The applied logging intensity in the plots of the LTSRP was calculated for each treatment as the fraction of trees being logged from the total amount of trees above the MCD. We tested if there were differences in logging intensity between the treatments by a Pearson Chi-Square test. Next to this logging intensity used in the study area we also looked at a scenario with an intensity of 80%, as this is the legal upper limit set by the Bolivian government. Next to the logging intensity, logging mortality was calculated per treatment as the amount of trees per DBH category that died as a consequence of logging. Differences in logging mortality between the DBH classes and treatments were tested with Pearson Chi-Square tests.

2.6 Modelling

We used an individual tree based growth model to project timber yields of *Hura crepitans*. In this model logging, logging mortality (collateral damage), natural mortality and growth are simulated for each individual tree. Recruitment is not taken into account in this model as new recruits are unexpected to attain harvestable size within the logging cycles (20 or 30 years). As an initial population 1000 trees were used with a population structure similar to the population structure in the permanent plots. At t=0 the initial harvest was simulated by randomly removing (logging) a fraction of all trees above the MCD (70 cm). Each individual tree with a diameter above MCD had an equal chance to be removed from the initial population according to the logging intensity (38% or 80% of all trees > MCD). After logging, trees that died as a consequence of logging activities (logging mortality: 2.1%), were randomly removed from the initial population.

For growth simulations we used 10-year growth intervals based on the long-term growth data of our ring measurements. We used tree ring data instead of data from the permanent plots, as the short time span of growth measurements in permanent plots and the lack of accounting for autocorrelation, may lead to underestimating long term tree growth and therefore future timber yields. From the lifetime growth trajectories of measured trees we determined all possible 10-year tree growth per DBH. Initially, one of all possible 10-year growth intervals was randomly assigned to each tree of the initial population (depending on its DBH at t=0), to determine its DBH at t=10. In these growth simulations, autocorrelation was incorporated by maintaining the link between the previous and current growth trajectory. This was done by randomly grouping individual trees of the initial population into a slow or fast 'growth rate class', once a tree was within this slow or fast growth rate class, it stayed in this class during the following simulations. Growth trajectories were divided into fast- and slow-growers based on above and under average annual increment rates. For simulations after the first interval (t=10), 10-year growth was randomly assigned depending on their 'growth rate class' (slow or fast) and DBH.

To account for the effects of the different logging treatments, the growth rates of trees were increased according to the calculated effects in the plots of the LTSRP (§2.4). Only in the first 10-year growth interval after logging, the percentages of increased growth induced by the different logging techniques were added to the normal growth rates. We restricted this to the first ten years because recent research shows that increased growth rates of FCTs are temporary and only lasts up to 6 years [Toledo et al., 2011]. To simulate trees that died naturally during a certain 10-year growth interval, natural mortality was applied on each individual tree before each growth interval. For natural mortality, we used three DBH classes (10-30 cm, 30-60 cm and >60 cm DHB), each individual tree had a chance to be removed from the population according to natural mortality rates of respectively 1,16%, 1,80% and 2,21%. The individual tree based model was repeated 100 times for each treatment in each scenario to calculate average values and standard errors of timber yields.

2.7 Determining timber yields

Relations between DBH and commercial height (h) were established to calculate stem volume. Commercial height i.e. height until the first branch, was measured on all trees sampled for ring analysis. The relation found was h =3.034*ln(DBH)-0.904 (R^2= 0,582). Stem volume of each harvested tree is calculated using the following formula (**eq. 2**) [Brienen & Zuidema, 2006a]:

$$V = h\left(\frac{0.5 \times DBH}{100}\right)^2 \pi \times T$$

Where V is the commercial volume of wood (m^3), [$(0.5DBH/100)^2\ \pi$] gives the basal area (m^2), h is the height (m) until the first branch (or commercial height) and T is the correction factor for tree taper. For T a value of 0.65 is being used as this is the most common applied factor to correct for tree taper in Bolivia [Dauber et al., 2005]. Commercial volumes of all logged trees (yields) were calculated for each logging cycle per hectare. This is done at t=0 and at t=20 or t=30, to determine the differences between the initial and the second harvest (after a re-growth period of 20 or 30 years). Differences in yield between logging intensities and between logging cycles were tested by independent t-tests. The fraction between the initial and second harvest was calculated to determine the amount of recuperation, differences were tested with One-way ANOVA tests with Bonferroni correction. The sustainability of logging under different logging techniques and in different scenarios (logging intensity, logging interval) was then calculated as the percentage of timber volume available in the second harvest compared to the initial harvest. All statistical analyses were done with SPSS 20.0.

3 Results

3.1 Population structure

The population structure (*i.e.* the relative abundance of different sized individuals in the population) of *Hura crepitans* in the plots of the LTSRP has a reverse J-shaped form, with more juveniles than adult trees, typical for an uneven-aged stand. The 1000 trees of the initial population of the model are distributed according this diameter distribution**.** *Hura crepitans* has a density (DBH >10 cm) of 8.37 individuals per hectare. The largest tree in the permanent plot area measured a DBH of 220 cm (**Fig. 2**).

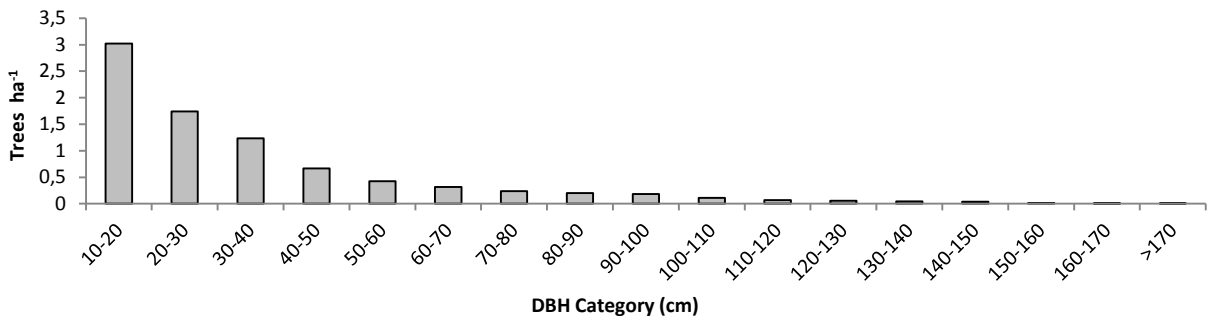

Fig. 2; Diameter distribution per hectare of *Hura crepitans* in La Chonta, Bolivia (2001). Based on 324 ha (N=1417 trees).

3.2 Age-diameter and diameter-growth relations

We observed large differences in growth within all sampled *Hura crepitans* trees (**Fig. 3a**). A tree could reach the MCD within approximately 50 years, but this might as well take over 100 years or more. On average a tree would reach the MCD at an age of 73 years. The oldest tree sampled reached a DBH of 119 cm at an age of 151 years. Diameter growth relations also showed considerable variation both among and within the DBH classes of 3 cm width (**Fig. 3b**). Growth rates increased up to 54 cm DBH and gradually declined with higher DBH. Annual DBH increments of > 1.5 cm yr^{-1} were often observed in the size range with higher growth rates (21–60 cm DBH). Overall, *Hura crepitans* has an average annual DBH growth rate of 0.86 ± 0.03 cm yr^{-1}, with a maximum of 3.02 cm yr^{-1} and a minimum of 0.15 cm yr^{-1}.

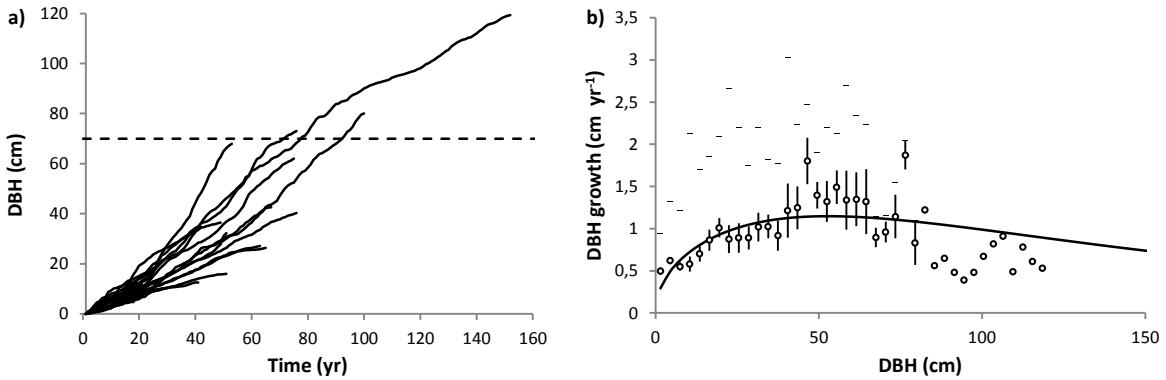

Fig. 3; Age-diameter relations of *Hura crepitans,* based on tree discs and cores (**Fig. 3a**). Each line represents one individual tree. Minimum cutting diameter is indicated by the dashed line. Diameter-growth relations of *Hura crepitans,* based on tree discs and cores (**Fig. 3b**). Data are mean of 3cm categories ±1S.E. and maximum (-) of all tree disks and cores. Shown is the fitted Hossfeld IV equation (line), fitted parameters *a*, *b* and *c* (**eq. 1**) equalled 299.6, 6.15 and 1.48 (R^2 =0.22, *n*=280).

3.3 Growth rates over time

The average annual growth rate of trees in each logging treatment but also in the control differed over time (Friedman tests; all treatments, *P* = 0.000) (**Fig. 4**). Differences in growth rates increased from the first growth period (0-1 years after logging) to the second period (1-2 years after logging), but declined over time after the second growth period. In the first year after logging there was no difference in growth rates between the treatments (One-way ANOVA; *P* = 0.138), until the sixth year we found a difference in growth rate between the treatments (One-way ANOVA; *P* = 0.000). In the eighth year the treatments showed no difference anymore (One-way ANOVA; *P* = 0.280). RIL and LS treatment showed no differences in growth (Bonferroni; all years, *P* ≥ 0.400). In the sixth year after logging only the HS treatment differed from the rest (Bonferroni; *P* ≤ 0.012). Overall, growth rates increased with silvicultural intensity and this effect was still visible up to 6 years after logging (**Fig. 4**).

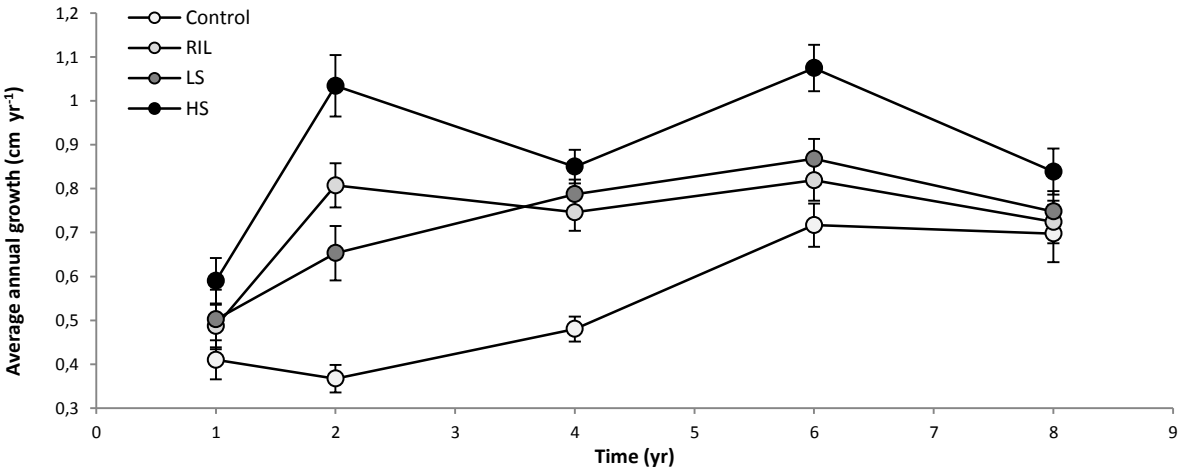

Fig. 4; Average annual growth rates of *Hura crepitans* over time after different management treatments in a Bolivian tropical moist forest. Different logging techniques (RIL, LS, HS) were applied at t=0. Data are mean ±1S.E. based on all trees measured in each treatment.

3.4 Ring data vs. permanent plot data

In the control plots trees had an average annual growth rate of 0.63 ± 0.04 cm yr^{-1}. This is significantly lower compared to the average growth rate obtained from the ring measurements of 0.86 ± 0.03 cm yr^{-1} (Mann-Whitney U; *P* = 0.000). When looking at the growth rates per DBH class, the ring data also showed higher growth rates in each class (Mann-Whitney U; All, P ≤ 0.001). Within permanent plot data no differences between DBH classes were found (Mann-Whitney U; All, *P* ≥ 0.448), ring measurements however showed higher growth rates in the DBH class 30-60 cm (Mann-Whitney U; All, P = 0.000) (**Table 3**).

Table 3: Mean growth rates (± 1S.E.) permanent plot and ring data. Differences were tested with Mann-Whitney U tests (*P* = 0.05). Ring data was in all cases significantly higher than permanent plot data. Differences are shown with letters (vertical).

	Permanent plot data (cm yr^{-1})	Ring data (cm yr^{-1})
10-30 cm	0,628 ± 0,06	0,673 ± 0,02 **a**
30-60 cm	0,695 ± 0,07	1,016 ± 0,05 **b**
>60 cm	0,501 ± 0,05	0,712 ± 0,04 **a**

3.5 Model input

Variables

Growth rates were not normally distributed (Kolmogorov-Smirnov: statistic = 0.142, *P* = 0.000). In the control plots trees had an average growth rate of 0.63 ± 0.04 cm yr^{-1}. We observed differences in annual growth rates between the DBH classes (in all plots). The 30-60 cm DBH class had a higher average growth rate compared to the other two classes. The 10-30 cm and the >60 cm DBH class did not differ from each other (**Table 2**).

We found large differences in growth rates of trees in the permanent plots between the different logging treatments (**Fig. 5**). In the 10-30 cm DBH class, only the HS treatment differed from the other treatments and the control. In the 30-60 cm DBH class, all treatments differed from the control. The HS treatment differed from the RIL and LS treatment in this DBH class, but no difference was found between the RIL and LS treatment. The growth rates in the > 60 cm DBH class the LS and HS treatments differed from the control and RIL treatment, but LS and HS did not differ among each other. No differences in growth were found between the RIL treatment and the control in this DBH class.

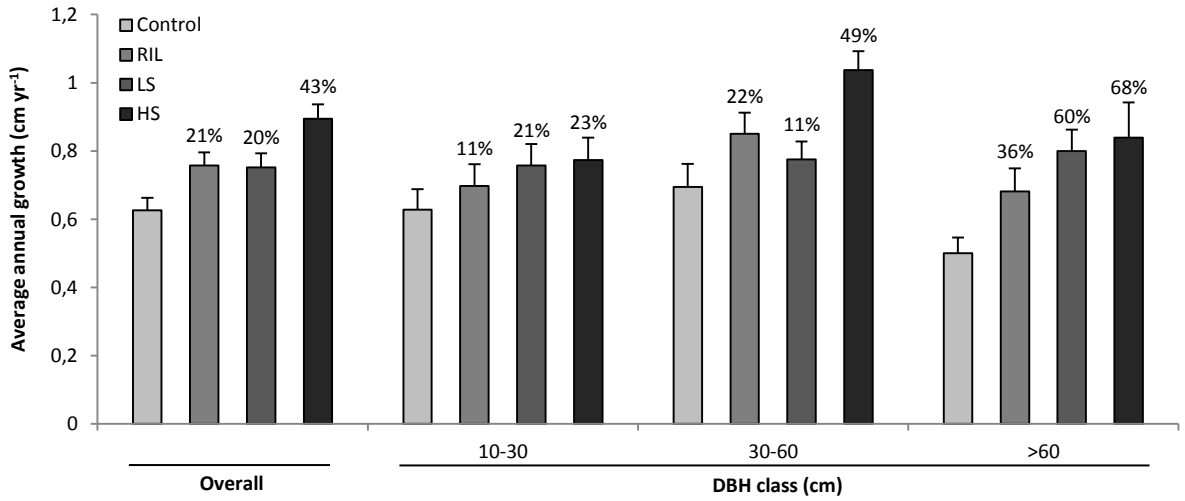

Fig. 5; Mean average annual growth rate (cm yr^{-1}) ±1SE of all trees in the plots of the LTSRP per treatment and per DBH class per treatment. Percentage of increased growth compared to the control (light-grey) overall or in that DBH class is stated above the diagrams.

Natural mortality differed between the DBH classes but not between the treatments (Pearson χ_3^2 = 1.48, *P* = 0.692). Natural mortality was significantly lower in the DBH class of 10-30 cm, compared to the other two DBH classes. The logging intensity of the permanents plots (amount of trees >MCD that had been logged) did not differ among the treatments (Pearson χ_2^2 = 0.15, *P* = 0.935). We used a logging rate of 38% of all trees with a DBH >MCD which is similar to the current logging practices in La Chonta. In addition, a logging rate of 80% was tested, as this is the maximum logging rate allowed by the Bolivian forestry law. As logging mortality did not differ among the DBH classes (Pearson χ_2^2 = 2.22, *P* = 0.338), the calculated value of 2.21% was used for all DBH classes and treatments. All variables used in the individual tree based growth model were calculated from permanent plot data and are summarized in **Table 2**.

Table 2; Variables used in the individual tree based model. Different letters (horizontal) or number of * (vertical) behind the values indicate differences between treatments or DBH classes, using Mann-Whitney U tests for growth rates and Fisher's exact tests for mortality (both $P < 0.05$). Natural mortality (10 year) and logging mortality are the percentage of all trees >10 cm DBH, logging rate is the percentage of all trees above the MCD of 70 cm.

DBH	**Growth (cm yr^{-1})**				**Natural Mortality (10 yr^{-1})**	**Logging intensity**	**Logging mortality**
	Control	RIL	LS	HS	Overall	Overall	Overall
Overall	0.626 ± 0.04 **a**	0.758 ± 0.04 **b**	0.752 ± 0.04 **b**	0.895 ± 0.04 **c**	15.3%	38% or 80%	2.21%
10-30 cm *	0.628 ± 0.06 **a**	0.697 ± 0.06	0.758 ± 0.06	0.774 ± 0.07 **b**	11.0% *		
30-60 cm **	0.695 ± 0.07 **a**	0.850 ± 0.06 **b**	0.775 ± 0.07 **b**	1.037 ± 0.05 **c**	16.6% **		
>60 cm *	0.501 ± 0.05 **a**	0.682 ± 0.07	0.800 ± 0.06 **b**	0.839 ± 0.10 **b**	20.0% **		

3.6 Model output: timber yields

The volumes of harvestable timber at the second harvest compared to the initial harvest differed greatly among logging intensities (Independent t-test; t=30.674, $P = 0.000$), logging cycles (Independent t-tests; 38% logging intensity, t=-8.741, $P = 0.000$, 80% t=-21.015, $P = 0.000$) and among treatments (Bonferroni tests; All $P \leq 0.009$). The amount of recuperation increases with longer re-growth periods, lower logging intensities and with the addition of more intensive silvicultural treatments (**Fig. 6**). The addition of low-intensity silvicultural treatments has in most cases no effect on the recuperation compared to reduced impact logging alone. We observed higher yields using RIL with a cycle of 20 years and a logging intensity of 80%, compared to the LS treatment. With a logging intensity of 80%, the amount of harvestable timber in the second harvest is in all cases lower than in the first harvest (**Fig. 6a**), although volumes harvested are larger than with a logging intensity of 38% (**Fig. 6b**).

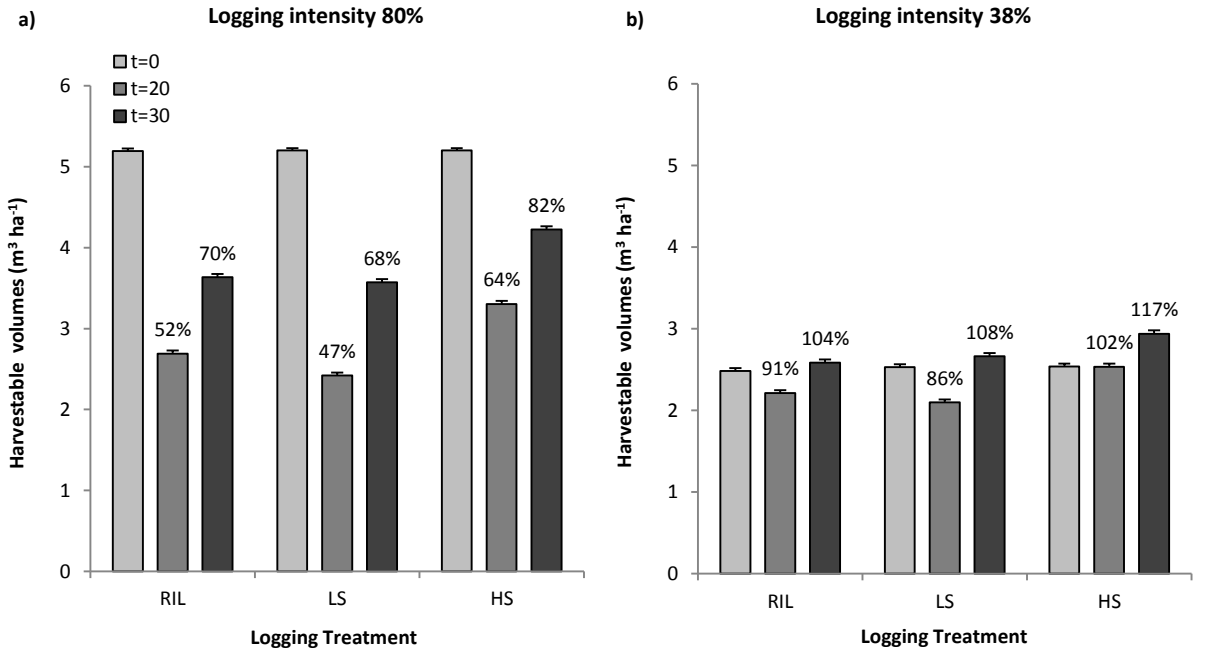

Fig. 6; Harvestable timber volume per hectare for the initial harvest (t=0) and for a second harvest 20 or 30 years later for *Hura Crepitans,* for different logging treatments (RIL, LS and HS) and logging intensities (**Fig. 6a**, 80% and **Fig. 6b**, 38%). Light-grey bars indicate harvestable volumes in the initial harvest, grey and black bars indicate harvestable volumes in the second harvest after respectively 20 or 30 years. Harvestable volume at the second harvest is indicated as a percentage from the initial harvest above the bars. Data are mean ±1S.E. based on 100 model runs.

A logging cycle of 20 years is in all cases, except from a 38% logging intensity and HS treatment, insufficient in sustaining future timber yields. We found sustainable timber yields for *Hura crepitans* when using a logging intensity of 38% and a logging cycle of 30 years, independent of the logging treatment.

When using the logging regime embedded in the Bolivian law (80%, 20yr, RIL), only 52% of the initial volume would be available for harvest in the next logging cycle, showing that this logging regime is not sufficient in sustaining timber yields of *Hura crepitans*. Even with the addition of high-intensity silvicultural treatments, only 64% of the initial volume will be available for logging in the next cycle. With the current logging regime used in the logging concession of la Chonta (38%, 30yr, RIL), 104% of the initial yield will recuperate.

4 Discussion

We found that the addition of silvicultural treatments can significantly increase the growth rates of *Hura crepitans* after logging, although the effects are only temporary. Growth rates of *Hura crepitans* trees increased within 2 years after the appliance of reduced-impact logging (RIL), low-intensity silvicultural treatments (LS) or with the addition of high-intensity silvicultural treatments (HS). RIL and LS led to an equal increase in growth rates, the application of high-intensity silvicultural treatments led to a higher increase. This effect lasted up to 4 years after logging for LS and RIL, with the application of HS this effect lasted up to 6 years (**Fig. 4**).

When comparing permanent plot data with data from ring measurements, ring data showed significantly higher average growth rates. The average growth rate obtained from ring measurements (0.86 ± 0.03 cm yr^{-1}) is higher compared to growth rates from permanent plots (0.63 ± 0.04 cm yr^{-1}). Growth rates also differed per DBH group (10-30 cm, 30-60 cm and >60 cm), with growth rates of respectively 0,63 ± 0,06 cm yr^{-1}, 0,70 ± 0,07 cm yr^{-1} and 0,50 ± 0,05 cm yr^{-1} from permanent plot data and growth rates of 0,67 ± 0,02 cm yr^{-1}, 1,02 ± 0,05 cm yr^{-1} and 0,71 ± 0,04 cm yr^{-1} from ring measurements (**Table 3**).

Compared to an undisturbed forest, overall growth rates of *Hura crepitans* increased by 21% after reduced-impact logging, by 20% with the addition of low-intensity silvicultural treatments and by 43% with the addition of high-intensity silvicultural treatments. We found higher growth rates for intermediate sized trees (30-60 cm DBH), but the greatest differences between the treatments were found for larger sized trees (>60 cm DBH) with an increased growth of respectively 36%, 60% and 68%, compared to an undisturbed forest (**Fig. 5**).

To make predictions about the effects of different logging techniques on future timber yields of *Hura crepitans*, we incorporated these increased growth rates after the use of different logging techniques into an individual tree based growth model. We found that the application of high-intensity silvicultural treatments did positively affect volume recovery, but the application of low-intensity silvicultural treatments had little to zero effect on the future timber yields compared to the practice of reduced-impact logging alone (**Fig. 6**). This indicates that the use of silvicultural treatments is effective in improving the sustainability of forestry, however for *Hura crepitans* only more intensive silvicultural treatments seems to be effective.

Referring to logging regimes, we observed that when using logging techniques mandatory by the Bolivian forestry act (80% logging intensity, 20 year logging cycle, and the use of reduced-impact logging), logging is not sustainable. Even with the addition of high-intensity silvicultural treatments only 64% of the initial timber yield could recuperate for *Hura crepitans* in the second harvest (**Fig. 6a**). Our results show that by reducing the logging intensity to 38% of all trees above MCD, 91-102% of the initial volume recuperates, or by increasing the time between logging events to 30 years, 70-82% of the initial volume recuperates. We found that for the logging concession of la Chonta, which uses RIL, a logging intensity of 38% and a logging cycle of 30 years, that logging of *Hura crepitans* is probably sustainable. When applying additional high-intensity silvicultural treatments in this logging concession, a 20 year cycle could also be sustainable for this species (**Fig. 6b**).

Tree ring analysis has shown to be an accurate method for determining lifetime growth rates [Brienen 2005; Brienen & Zuidema, 2006a; Brienen & Zuidema 2006b]. To model the influence of the different logging strategies on the growth rates, we needed to combine lifetime growth rates obtained from tree ring analysis with permanent plot data, because tree ring analysis does not provide other variables needed to construct an individual tree based growth model. This model, which combines growth rates obtained by tree ring analysis with other variables obtained from permanent plot data seems to be a relatively simple and promising way to make realistic predictions about the yield of a subsequent harvest. However, a larger sample size for ring measurements would be desirable to make more accurate predictions. Because of this relatively small sample size, growth trajectories of especially larger size classes are based on a few individual trees, which could lead to a biased model output. For future research it would also be interesting to have ring samples from multiple plots where different logging treatments have been used in the past. In this way a more realistic model can be made. The logging event could be traced back in the ring data and the period and amount of increased growth could be measured more accurate.

This model cannot make predictions about logging cycles further in the future due to the lack of information on recruitment. In an undisturbed forest there are still sufficient small trees present to secure a sufficient in-growth, but as logging often changes the forest- and canopy- structure there will be some effects on the diameter distribution and growth of this species, especially for seedlings [Okuda et al., 2003; Panfil & Gullison, 1998]. Limited seeds dispersal after human disturbances is often believed to have a large effect on the amount of seedlings [Gullison et al., 1996; Slik et al., 2002; Chazdon 2003]. Especially the amount of seed trees will be limited after logging. Although it is embedded in the Bolivian forestry act that logging companies should leave at least 20% of the trees above the MCD as seed trees. It is questionable if 20% will be enough to sustain similar seedling densities as Mostacedo & Fredericksen (1999) found that 80% of the commercial species in Bolivia do not regenerate sufficiently to replace harvested trees. *Hura crepitans* is able to establish under low-light conditions in an unlogged forest, but might need large openings in the forest structure to become an adult tree. Nabe-Nielsen et al. (2007) found that *Hura crepitans* seedlings will probably benefit from the higher light intensities near roads and in canopy gaps. Another study showed that the growth of *Hura crepitans* seedlings and saplings had a positive relationship with increasing harvest intensity [Panfil & Gullison, 1998]. Therefore it is not assumable that the lack of recruitment in the model can cause biased outcomes for *Hura crepitans*. Besides, this could also indicate that logging could have a positive effect on *Hura crepitans* seedlings, and that possibly more timber could be available in following logging cycles.

Our model might underestimate future timber yields; first due to the fact that the is a small chance that trees ≤ 10 cm DBH (excluded in the model) might be able to attain the MCD within one logging cycle of 30 years. Secondly, the increase in growth rates after a logging intensity of 80% is based on and equal to the increase after an intensity of 38%. The increase in growth will likely be higher after a logging intensity of 80% as there will be a greater light availability and therefore less competition for light and possibly other resources between trees. On the other hand this model might also overestimate timber yields as there are no limitations to growth like maximum tree size and competition in the model.

Our results are only valid for *Hura crepitans,* and not for other commercially valuable species in the study area. *Hura crepitans* is a very common species with a relatively high annual growth rate for a partly shade tolerant species. Other, (partly) shade tolerant species in the study area such as *Pouteria nemorosa* (0.31 ± 0.08 cm yr^{-1}), *Pseudolmedia laevis* (0.27 ± 0.01 cm yr^{-1}) and *Termialia oblonga* (0.26 ± 0.04 cm yr^{-1}), have substantially lower growth rates compared to *Hura crepitans* (0.54± 0.05 cm yr^{-1}) in the control plots [Peña-Claros et al., 2008a]. Recuperation of *Hura crepitans* is expected to be higher compared to other more slow growing (hardwood) tropical tree species. Therefore other commercial timber species, especially from other functional groups, should be included to have a better overview of the effects of silvicultural treatments on growth and timber yields and to determine sustainable logging regimes for these functional groups and/or species.

Recent research has shown that when using current legal cutting cycles and logging intensities, growth rates of trees are not sufficient to secure sustained timber yields for commercially valuable tropical tree species [Dauber et al., 2005; Brienen & Zuidema 2006a; Rozendaal et al., 2010]. It has been suggested that the addition of silvicultural treatments could increase the growth rates of future crop trees and that this could make tropical forestry more sustainable [Fredericksen et al., 2003; Dauber et al., 2005; Keller et al., 2007; Peña-Claros et al., 2008a]. This study supports this idea. Our results are similar to the temporary increased growth rates found for other trees in tropical forests of Bolivia [Peña-Claros et al., 2008a; Toledo et al., 2011]. The use of high-intensity silvicultural treatments (HS) is recommendable to increase the growth of *Hura crepitans* trees after logging. The use of Low-intensity silvicultural treatments (LS) is not recommendable for *Hura crepitans* as this does not lead to significant higher growth rates compared to reduced-impact logging (RIL) alone. This result is in accordance with Peña-Claros et al., (2008a) who also did not find significant differences in growth rates between the RIL and LS treatment for *Hura crepitans*. The higher growth rates in the HS plots are possibly caused by the fact that in the HS plots all non-commercial trees >40 cm are being girdled whereas in the LS plots only overtopping trees are girdled (**Table 1**). However, the girdling of only overtopping trees in LS is also expected to result in increased tree growth in the LS plots compared to the RIL plots, but this was not the case in this study. Another reason for the increased growth rates in HS could be a higher logging intensity in HS as is being prescribed [Peña-Claros et al., 2008a]. Although we did not find any significant differences in logging intensity for *Hura crepitans* it seems logical that the formation of larger gaps in these plots could lead to higher growth rates in the HS treatment.

We found higher average annual growth rates based on ring analysis compared to growth data obtained from permanent plots. Rozendaal et al., (2010) also compared growth rates obtained from ring analysis with growth data from permanent plots and found higher growth rates from ring data for some DBH classes in 2 of the 3 studied species (*Cedrelinga catenaeformis* in the 5–10 cm, 30–40 cm and 40–50 cm DBH class, and for *Clarisia recemosa* only in the 30-40 cm DBH class). Brienen & Zuidema (2006b) also found higher average growth rates from ring analysis compared to similar studies using short-term growth data by Clark & Clark (1992, 2001). This indicates that with the use of growth data obtained from permanent plots, growth rates of FCTs and timber yields could be underestimated. Both these studies put forward that this is most likely caused by the fact that large trees sampled for ring-analysis have been successful trees which had higher average growth rates throughout their lives e.g. because of advantages in resource availability due to their location. This could explain the differences we found, although not all our sampled trees are above the MCD and thus do not necessarily represent successful individuals. Another cause for the difference might be climatic variation as the permanent plots show only growth rates from the last decade while ring analysis represent growth over a larger timespan.

When using the logging regime embedded in the Bolivian forestry act (80%, 20yr, RIL), only 52% of the initial wood volume would be available for harvest in the next logging cycle, showing that this logging regime is far from sufficient in sustaining timber yields of *Hura crepitans*. This current Bolivian legal logging regime has also shown to be inadequate in securing sustainable yields for *Amburana cearensis, Cedrela odorata, Cedrelinga catenaeformis, Peltogyne cf. heterophylla* and *Clarisia recemosa* [Brienen & Zuidema, 2006a; Rozendaal et al., 2010]. With the addition of high-intensity silvicultural treatments, only 64% of the initial volume will be available for logging in the next cycle. With the current logging regime used in the logging concession of la Chonta (38%, 30yr, RIL), 104% of the initial yield will recuperate, indicating that according to our model, logging of *Hura crepitans* is sustainable in terms of timber yields.

We recommend that current Bolivian forestry act should be revised. The legal maximum logging rate of 80% of all trees above the MCD has shown to be too high to secure sustainable yields over time for *Hura crepitans* [this study] as well as for numerous other tree species [Dauber et al., 2005; Brienen & Zuidema, 2006a; Rozendaal et al., 2010]. Our research shows that by reducing the logging intensity to 38% (as being used in La Chonta in the permanent plots), more progress towards sustainable forest management could be made, although lower

(short-term) profits will be generated. The minimum logging cycle in the Bolivian forestry act should be changed as the current minimum logging cycle of 20 years is too short to secure sufficient regrowth. As species vary greatly in growth rate [Peña-Claros et al., 2008a], we recommend more species specific logging regimes. Where faster growing species could in some case be logged in intervals of 20 years, while other more slow growing species, could be harvested every 40 or 60 years. With the application of high-intensity silvicultural treatments a logging cycle of 20 years and a logging intensity of 38% could be sustainable for *Hura crepitans*. For *Hura crepitans*, we do not recommend the implication of low-intensity silvicultural treatments as this has no clear positive effects on future yields. The use of high-intensity silvicultural treatments does have a more substantial effect on future yields, and therefore is recommended. Silvicultural treatments have also shown to positively affect regeneration [Peña-Claros et al., 2008b]. Before application of (high-intensity) silvicultural treatments the sustainability of the entire ecosystem should be considered as well as HS could have negative effects on non-commercial species as these are being girdled which would lead to a shift in forest tree composition and structure. Although the application of silvicultural treatments is believed to be of relatively low cost [Peña-Claros et al., 2003; Fredericksen & Pariona, 2002], an economical cost-benefit analysis should be made to convince forest managers of its benefits. Besides, decreasing logging intensities and increasing the logging cycles also improves sustainability of tropical timber production, although the implementation of these actions would be at the expense of the current income of logging companies.

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