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Beyond reduced-impact logging: Silvicultural treatments to increase growth rates of tropical trees

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Abstract

Use of reduced-impact logging (RIL) techniques has repeatedly been shown to reduce damage caused by logging. Unfortunately, these techniques do not necessarily ameliorate the low growth rates of many commercial species or otherwise assure recovery of the initial volume harvested during the next cutting cycle. In this study, we analyze the effect of logging and application of additional silvicultural treatments (liana cutting and girdling of competing trees) on the growth rates on trees in general and on of future crop trees (FCTs) of 24 commercial timber species. The study was carried out in a moist tropical forest in Bolivia, where we monitored twelve 27-ha plots for 4 years. Plots received one of four treatments in which logging intensity and silvicultural treatments were varied: control (no logging); normal (reduced-impact) logging; normal logging and low-intensity silviculture; and, increased logging intensity and high-intensity silviculture. Tree growth rates increased with intensity of logging and silvicultural treatments. The growth rates of FCTs of commercial species were 50–60% higher in plots that received silvicultural treatments than in the normal logging and control plots. Responses to silvicultural treatments varied among functional groups. The largest increase in growth rates was observed in FCTs belonging to the partially shade-tolerant and the shade-tolerant groups. These results indicate that silvicultural treatments, in addition to the use of RIL techniques, are more likely to result in a higher percentage of timber volume being recovered after the first cutting cycle than RIL alone.

Keywords: Bolivia; Reduced-impact logging; Sustainable forest management; Silvicultural treatments; Tropical forest

1. Introduction

Once logging damage is controlled by the application of reduced-impact logging (RIL) techniques, the next major challenge to secure sustained yields of commercial timber species is increasing tree growth rates to allow for economically attractive cutting cycles (Fredericksen and Putz, 2003; Fredericksen et al., 2003; Schulze et al., 2005; van Gardingen et al., 2006; Wadsworth and Zweede, 2006; Zarin et al., 2007; Putz et al., this issue). Recent studies in lowland Bolivia have shown that commercial trees grow at lower rates than assumed by policy-makers when the currently designated cutting cycles were selected (Dauber et al., 2005; Brienen and Zuidema, 2006). Consequently, it is estimated that only 3–38% of the volume harvested during the first commercial timber harvest will recover in time for the next planned harvest, i.e., at the end of the second cycle (Dauber et al., 2005; Brienen and Zuidema, 2006; Keller et al., 2007). One option to increase volume recovery is to provide improved growth conditions for future crop trees (FCTs), including high light availability to tree crowns and freedom from lianas. When growing under these conditions, volume increments of FCTs in Bolivia have increased 9–64% (Dauber et al., 2005; Keller et al., 2007). Studies conducted elsewhere in the tropics have also shown that applying silvicultural treatments to FCTs, such as liberation

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from competition by girdling nearby trees and liana cutting, can significantly increase their growth rates (e.g., Wadsworth and Zweede, 2006). In this paper, we present the results of an industrial-scale study in lowland Bolivia on the application of combinations of RIL and silvicultural treatments.

Logging in Bolivia is typically selective but it was also unnecessarily destructive, with numerous negative impacts on forest ecosystems and severe depletion of valuable timber species such as *Swietenia macrophylla*, *Amburana cearensis* and *Cedrela* spp. In the decade following passage of the 1996 Forest Law, substantial advances were made in forest management to the point that Bolivia became a model for the certification of managed natural tropical forests (Nittler and Nash, 1999). By 2007, about 25% of the total area under forest management (about 2.1 million ha of lowland tropical forest) was certified as making substantial progress towards sustainable forest management by Forest Stewardship Council (FSC) accredited certifiers (CFV, 2007). One factor that promoted FSC certification in Bolivia is that the forestry law requires the use of RIL techniques during forest operations (MDSP, 1998; Fredericksen et al., 2003).

The many benefits of RIL notwithstanding, forest management in Bolivia rarely goes beyond selective logging despite the demonstrated need to apply silvicultural treatments to improve regeneration, maintain stand quality and improve tree growth (Fredericksen, 2000a; Fredericksen et al., 2003; Dauber et al., 2005; Keller et al., 2007). Various individual silvicultural practices have been investigated and determined to be effective in Bolivia including harvesting systems (Mendieta, 1998; Alarcon, 1999; Krueger, 2004), vine cutting (Fredericksen, 2000b; Pérez-Salicrup, 2001; Alvira et al., 2004), prescribed burning (Kennard, 2004; Heuberger et al., 2002), regeneration treatments (Fredericksen and Pariona, 2002; Pariona et al., 2003), and other timber stand improvement (Olson-Kiehn et al., 2006). For various reasons, however, these small-scale experiments have not been tested or applied at operational scales. Also lacking are experiments in which individual treatment combinations are tested together as silvicultural systems.

The Long-Term Silvicultural Research Program (LTSRP) in lowland Bolivia established a network of large-scale (20–27 ha) replicated plots that received one of four treatments ranging in logging intensity and the application intensity of additional silvicultural treatments (Table 1). The LTSRP is currently underway in three different forest types that represent the major timber production regions in Bolivia (Dauber et al., 2000). The LTSRP plots are large in scale and thus permit estimation of logistical feasibility and cost-effectiveness of different silvicultural interventions, as well as the long-term impacts of silvicultural treatments on biodiversity, stand dynamics and forest ecosystem functions. These plots can also be used to assess the viability and trade-offs of other management options, such as the development of carbon sequestration reserves (e.g., Blate, 2005a). In this paper, we focus on the effects of different silvicultural treatments on tree growth rates in three blocks of plots established at the moist forest site.

The objectives of this paper were: (1) to assess the effect of logging and additional silvicultural treatments on tree growth; (2) to evaluate if species belonging to different functional groups respond differently to logging and additional silvicultural treatments and (3) to determine how FCTs respond to liberation treatments such as liana cutting and girdling of competing trees. We predicted that growth rates of FCTs would increase with logging and silvicultural intensity and that treatment responses would be greater for light-demanding than for shade-tolerant species.

2. Methods

2.1. 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 moist Amazonian forests (Dauber et al., 2000). Annual precipitation in the region averages 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

Table 1
Treatments applied to the 27 ha LTSRP plots in La Chonta Forest Concession, Bolivia: C = control; N = normal; LS = light silviculture and IS = intensive silviculture. ● = management practice applied; ●● = management practice applied with double intensity. See Table 3 for the species included in LS and IS

Management practices	Treatments			
	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 trial 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})				●

Table 2
The 20 most abundant species in the LTSRP plots in La Chonta Forest Concession, Bolivia. Density and basal area per species are given. Data are for trees >10 cm DBH, based on the 48 1-ha subplots (4 subplots per 27-ha plot)

Species name	Density (# ha^{-1})	Basal area (m^2 ha^{-1})
Pseudolmedia laevis	90.96	3.69
Ampelocera ruizii	17.35	0.89
Ocotea sp. 6	17.27	0.64
Hirtella triandra	15.73	0.25
Ocotea sp. 1	15.42	0.31
Terminalia oblonga	13.17	1.39
Urera caracassana	12.40	0.40
Stylogyne ambigua	11.23	0.13
Licaria triandra	10.17	0.13
Pouteria macrohylla	8.85	0.26
Hura crepitans	8.71	1.41
Pourouma cecropiifolia	7.40	0.27
Dendropanax arboreus	6.63	0.34
Guarea guidonea	6.52	0.11
Alibertia verrucosa	5.63	0.08
Neea hermaphrodita	5.40	0.12
Aspidosperma rigidum	4.90	0.23
Pouteria nemorosa	4.88	0.55
Sapindus saponaria	4.25	0.16
Ocotea guianensis	3.42	0.08
Other species	97.87	8.24

lianas are seasonally deciduous (IBIF, unpublished data). The study site is situated on the southwestern border of the Brazilian Precambrian Shield and has sandy-loam soils that are circumneutral in pH and rich in nutrients (Paz-Rivera, 2003; IBIF, unpublished data). For trees >10 cm DBH, the forest has an average density of 367 stems ha^{-1}, basal area of 19.3 m^2 ha^{-1} and 59 tree species ha^{-1} (Table 2). There are 160 tree species identified at La Chonta, 24 of which are considered to be merchantable for timber. The intended cutting cycle is 30 years and the company obtained FSC certification for its management plan in 1998. Fires are prevalent in the landscape matrix surrounding La Chonta, most of which are intentionally set during the dry season for agricultural purposes. In both 1995 and 2004, approximately 30% of the concession was burned after escaped agricultural fires entered the concession (Blate, 2005b; IBIF unpublished data).

2.2. Experimental design

The study was carried out in twelve 27-ha plots grouped in three blocks. Each block was established in a different logging compartment using a randomized block design, for a total of 326 ha of study plots. All plots were first delineated on the ground using an inventory map to select areas with similar harvestable tree densities, vegetation type and topography. Plots were then randomly assigned to one of four treatments, with the exception of the control treatment plots that were selected so as to maximize the area of unharvested surrounding forest; at least 50 m separates control plots from the nearest harvesting activity. Trees were marked, mapped, measured and identified to species in nested plots as follows: trees ≥40 cm in diameter at 1.3 m height (DBH) in the whole plot (27 ha); trees ≥20 cm in DBH in half of the plot (13.5 ha); and, trees ≥10 cm in DBH in four 1-ha subplots. Data on smaller trees of commercial species were also

Table 3
The 24 species considered in La Chonta's forest management plan as currently commercial and potentially commercial, grouped into one of three functional groups: long-lived pioneer species (LLP), partial shade-tolerant (PST) and shade-tolerant species (ST). LS = light silviculture, IS = intensive silviculture, MDC = minimum diameter for cutting

Scientific name	Family	Functional group	Commercial value	MDC (cm)	Included in treatment	
Ampelocera ruizii	Ulmaceae	ST	Potential	50		IS
Aspidosperma cylindrocarpon	Apocynaceae	PST	Potential	50		IS
Caesalpinia pluviosa	Caesalpiniaceae	LLP	Potential	50		IS
Cariniana domestica	Lecythidaceae	LLP	Potential	50		IS
Cariniana estrellensis	Lecythidaceae	LLP	Current	50	LS	IS
Cariniana ianeirensis	Lecythidaceae	PST	Current	50	LS	IS
Cedrela fissilis	Meliaceae	LLP	Current	50	LS	IS
Ceiba pentandra	Bombacaceae	LLP	Potential	50		IS
Centrolobium microchaete	Fabaceae	LLP	Current	50	LS	IS
Clarisia racemosa	Moraceae	PST	Potential	50		IS
Cordia alliodora	Boraginaceae	LLP	Current	50	LS	IS
Ficus boliviana	Moraceae	LLP	Current	70	LS	IS
Gallesia integrifolia	Phytolaccaceae	LLP	Potential	50		IS
Hura crepitans	Euphorbiaceae	PST	Current	70	LS	IS
Hymenaea courbaril	Caesalpiniaceae	PST	Current	50	LS	IS
Pouteria nemorosa	Sapotaceae	PST	Current	50	LS	IS
Pseudolmedia laevis	Moraceae	ST	Potential	50		IS
Pterogyne nitens	Caesalpiniaceae	LLP	Potential	50		IS
Schizolobium amazonicum	Caesalpiniaceae	LLP	Current	50	LS	IS
Spondias mombin	Anacardiaceae	LLP	Current	50	LS	IS
Sweetia fruticosa	Fabaceae	LLP	Potential	50		IS
Swietenia macrophylla	Meliaceae	PST	Current	70	LS	IS
Tabebuia serratifolia	Bignoniaceae	LLP	Current	50	LS	IS
Terminalia oblonga	Combretaceae	PST	Current	50	LS	IS

Table 4
Initial basal area, numbers of trees and volume harvested and basal area (BA) immediately after logging in the different treatments of the LTSRP plots in La Chonta. Area in logging gaps and skid trails are given as percentages of the total area of each treatment. Data are mean ± 1S.D. based on three replicates (blocks). Based on Mostacedo et al. (2006)

Treatment	Initial BA ($m^2\ ha^{-1}$)	Trees harvested (# ha^{-1})	Volume harvested ($m^3\ ha^{-1}$)	BA after harvesting ($m^2\ ha^{-1}$)	Area in logging gaps (%)	Area in skid trails (%)
Control	19.6 ± 2.6	0	0	19.6 ± 2.6	0	0
Normal	19.5 ± 1.8	2.3 ± 1.1	10.4 ± 6.4	18.1 ± 1.2	6.3 ± 3.5	4.3 ± 1.1
Light silviculture	18.7 ± 1.0	2.1 ± 0.9	9.4 ± 3.6	17.6 ± 0.8	5.3 ± 1.8	3.9 ± 1.1
Intensive silviculture	19.4 ± 0.2	4.0 ± 0.8	14.4 ± 1.6	17.5 ± 0.4	9.0 ± 1.4	5.1 ± 0.8

collected (Peña-Claros et al., 2008), but are not presented here.

Each plot received one of four treatments representing a gradient in management intensity (Table 1): an unharvested control plot, hereafter referred to as ‘control’; a plot logged following practices stipulated by the Bolivian forestry law with RIL techniques, hereafter referred to as ‘normal’; a plot harvested as in the normal treatment but with application of silvicultural treatments at low intensity, hereafter referred to as ‘light silviculture’; and, a plot harvested at twice the intensity of the normal treatment and with application of more intensive silvicultural treatments, hereafter referred to as ‘intensive silviculture’. The more intensive treatments aimed to enhance the growth and regeneration of commercial individuals, especially FCTs. FCTs are individuals of commercial species that are too small to be harvested in the first cutting cycle (i.e., 10–70 cm DBH for a few commercial species and 10–50 cm for all other commercial species; Table 3), but that have adequate form and growth potential and are expected to be harvested in the future. Silvicultural treatments applied included cutting lianas on FCTs, liberation of FCTs from competing trees through girdling, stand refinement by girdling large senescent non-commercial trees, and soil scarification in felling gaps (see Table 1 for a summary of silvicultural treatments applied). In the intensive silviculture treatment, a longer species list of FCTs was included based on expected future marketability (Table 3); many of these species were not being harvested in the concession when the study commenced. Plots were harvested by the concession workers 2–6 months after plot installation in 2001 (block 1 and block 2) and 2002 (block 3). Depending on the treatment, harvesting intensity ranged from 2.1 to 4.0 trees ha^{-1}, which resulted in 9.2–14.1% of the area being disturbed by logging gaps or skid trails (Table 4; Mostacedo et al., 2006). Some RIL techniques were applied by the company 6–9 months prior to harvesting (e.g., liana cutting on trees to be felled); the silvicultural treatments compared in this study were applied before, during, or after the harvest treatment (Table 1).

2.3. Measurements

Trees were identified to species and the following measurements, among others, were made: DBH; crown position index (modified after Clark and Clark, 1992: 1 = no direct light, 2 = moderate to substantial lateral light, 3 = overhead light on part of the crown, 4 = full overhead light and 5 = emergent crown that receives light from all directions); and liana load (Alder and Synott, 1992: 1 = no lianas, 2 = lianas on stem, 3 = lianas on stem and crown and 4 = lianas completely covering crown). Species were assigned to one of the following four functional groups based on existing classifications (Jardim et al., 2003; Mostacedo et al., 2003; Justiniano et al., 2004; Poorter et al., 2006) and field observations: shade-tolerant species; partial shade-tolerant species; long-lived pioneer species and pioneer species. Of the 160 tree species with DBH $\geq$ 10 cm, only 7% could not be assigned to any functional group because they were too rare or there was insufficient ecological knowledge available about them. All plots were remeasured 1, 2 and 4 years after establishment, and will continue to be monitored every 2 years. Dead and newly recruited trees were recorded during each census.

2.4. Data analysis

To determine treatment effects on light exposure of remnant trees, a repeated-measures ANOVA was performed with crown position as the dependent variable, and treatment and time as factors. The Student–Newman–Keuls (SNK) procedure was used for post hoc treatment comparisons. The same analysis could not be performed for liana infestation because trees growing in the different treatments varied significantly in liana infestation even before treatment application (Fig. 1B). Consequently, the difference in liana infestation between the last (4 years post-treatment) and the first (pre-treatment) measurement was calculated; a negative value indicates a decrease in liana infestation while a positive value indicates an increase in liana infestation over time. To determine the effect of treatment on the change in liana infestation, we used a Kruskal–Wallis test, followed by Mann–Whitney tests of differences among treatments (p-value was corrected using a Bonferroni correction; $p = 0.008$).

Growth rates were calculated for each tree as the slope of DBH and measurement date. Growth rate were calculated on an annual basis for each measurement period (hereafter referred as “$GR_{0–1}$”, “$GR_{1–2}$”, “$GR_{2–4}$”) and for the whole period including as many measurement dates as possible (henceforth referred to as “GR_{total}”). The first measurement used to calculate $GR_{0–1}$ and GR_{total} is the measurement done during plot installation (time 0). Trees with growth rates <-0.5 cm y^{-1} were not included in the analysis. To determine the upper growth rate limit, the 99.9 percentile of growth rates was calculated for each functional group, and the value

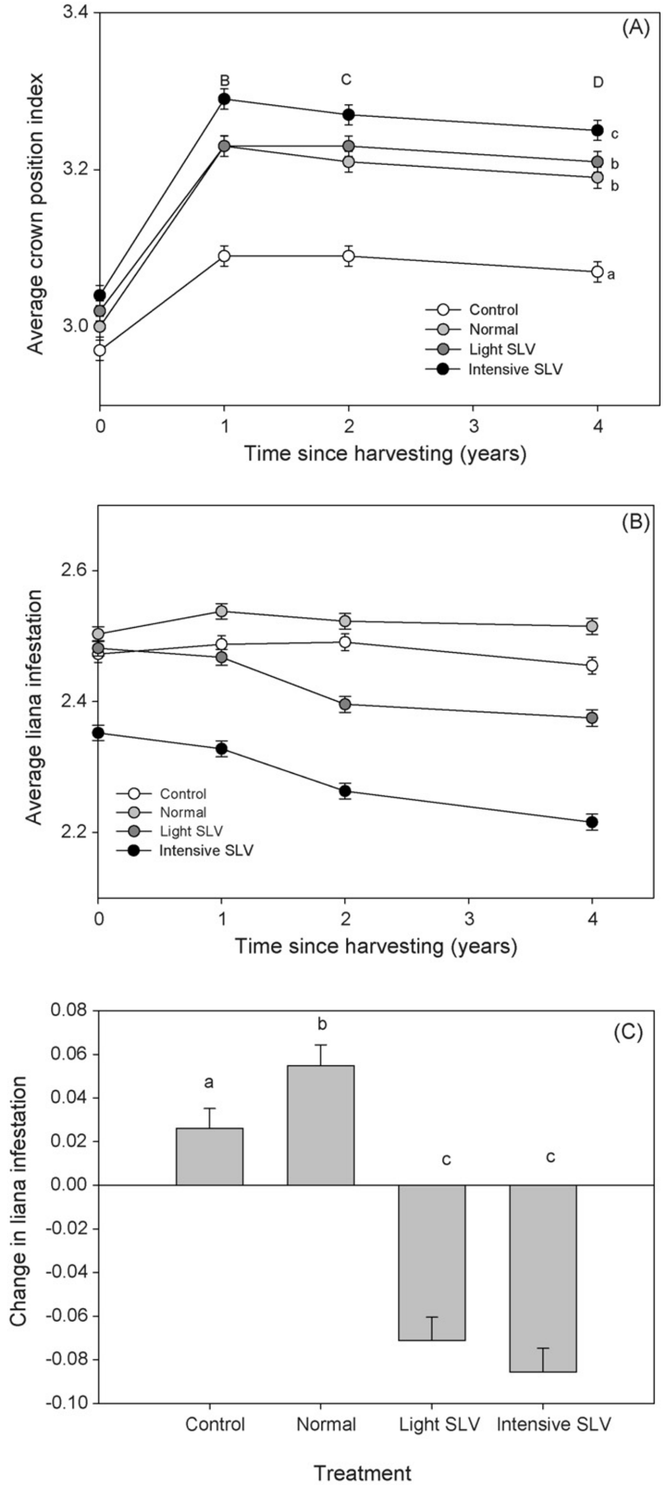

Fig. 1. Changes in crown position index (A) and liana infestation (B) through time after different management treatments, and average change in liana infestation pre-and post-treatment application (C) in a tropical moist forest in Bolivia. Each line or bar represents a different treatment. Different capital letters in A represent significant differences among years after treatment application. Lower case letters in A and C represent significant differences among treatments over time. SLV = silviculture. Data are mean ± 1S.E.

obtained was used at the species level to exclude trees having extreme growth rates. Trees with estimated DBH, incorrectly measured DBHs due to the presence of buttresses or lianas, and palms were also discarded from the analysis. From the total 42,688 trees in the database, we finally included 72–88% of the trees depending on the growth rate calculated ($GR_{0–1}$, $GR_{1–2}$ and $GR_{2–4}$).

To evaluate the effects of liana infestation and crown position on growth rates, a two-way ANOVA was performed, with liana infestation and crown position (both at time 0) as factors and GR_{total} as the dependent variable. Additionally, we evaluated the effect of logging impact on GR_{total} by using a forward multiple regression analysis using as independent variables the number of trees harvested and basal area left after harvesting. Only the number of trees harvested was included in the analysis because it was highly correlated with volume harvested, basal area harvested and area disturbed by logging (Pearson correlations, respectively, $r = 0.97$, $r = 0.98$ and $r = 0.98$, all $p < 0.001$). Because logging impact data were available only at the plot level, an average GR_{total} per plot was calculated.

Treatment effects on growth rates of trees in different functional groups were determined by using a repeated-measures ANOVA with time, treatment and functional group as factors, and $GR_{0–1}$, $GR_{1–2}$, $GR_{2–4}$ as the dependent variables. To test if different commercial timber species groups (commercial, potentially commercial and non-commercial) were affected differently by treatments, we performed a one-way ANOVA, followed by a SNK post hoc test. Finally, to evaluate the growth responses of FCTs to the treatments, we performed a two-way ANOVA with treatment and functional group as factors, and GR_{total} as the dependent variable using only trees identified as FCTs in the different treatment plots. A similar analysis was conducted at the species level with treatment as factor, and GR_{total} as the dependent variable. Species having less than five individuals in each treatment were excluded from the analysis; consequently, the analysis was carried out for only 17 of the 24 species. Differences were considered significant at $p < 0.05$. All statistical analyses were carried out using SPSS 12.0.1.

3. Results

Light exposure of tree crowns based on CPI increased after treatment application. The increase in crown exposure observed in the control treatment was due to natural gaps that formed during the study period. Crown exposures reached their highest values 1 year after logging after which they decreased (repeated-measures ANOVA; for time, $F_{1.94,31198} = 1547$; $p < 0.001$). The rate of decrease in crown exposure through time varied with treatment; the fastest decrease being observed in the normal treatment (repeated-measures ANOVA; time - × treatment, $F_{1.94,31198} = 1547.3$; $p < 0.001$) (Fig. 1A). On average, tree crowns in the control treatment were more shaded than those in the logged treatments; in the logged plots, trees in the intensive silviculture treatment were the most exposed to light (ANOVA, $F_{3,31998} = 33.31$; $p < 0.001$). Similarly, over

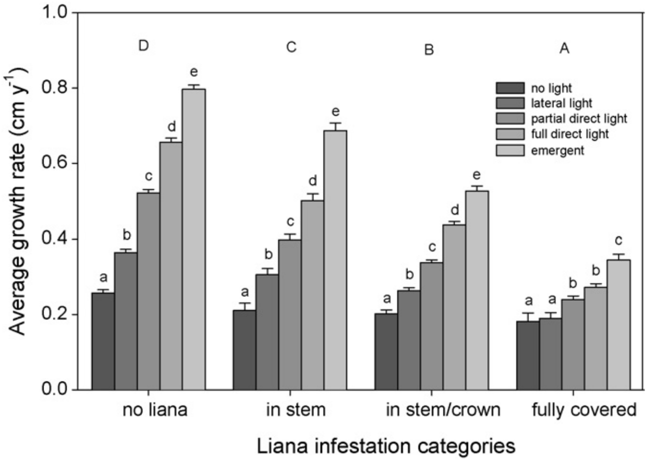

Fig. 2. The effect of crown position and liana infestation on average tree growth rate (4 years post-treatment) in a managed tropical moist forest in Bolivia. Trees from all management treatments combined. Data are mean ± 1S.E. based on all trees present at the beginning of the study. Liana infestation and crown position correspond to data collected during plot establishment. Capital letters indicate significant differences among liana infestation categories. Lower case letters indicate significant differences among crown position categories inside each liana infestation category.

the 4-year observation period liana infestation increased in the normal and control treatments, and decreased at a similar rate in the light and intensive silviculture treatments (Kruskal–Wallis, d.f. = 3, $\chi^2 = 149.9$, $p < 0.001$) (Fig. 1C). The decrease in liana infestation in the light and intensive silviculture treatments is due to the additional liana cutting done in these treatments to liberate future crop trees (Table 2), while the increase in liana infestation observed in the control and normal treatment is due to the continuous expansion of lianas in tree crowns.

Trees, in general, grew faster as crown light exposure increased (ANOVA, $F_{4,31464} = 409.6$; $p < 0.001$) and more slowly with increasing degrees of liana infestation (ANOVA, $F_{3,31464} = 461$; $p < 0.001$). The response to improved light exposure varied with the degree of liana infestation; compared to liana-infested trees, growth responses of liana-free trees were much stronger (ANOVA; for liana infestation × crown position, $F_{12,31464} = 25.4$; $p < 0.001$) (Fig. 2). Additionally, growth rates over the first 4 years post-treatment increased with number of trees harvested and decreased with basal area retained after harvesting (forward multiple regression analysis, $F = 13.05$, $p < 0.002$, $r^2 = 0.744$).

Tree growth rates varied with time since harvesting, treatment and functional group (Table 5). Growth rates varied

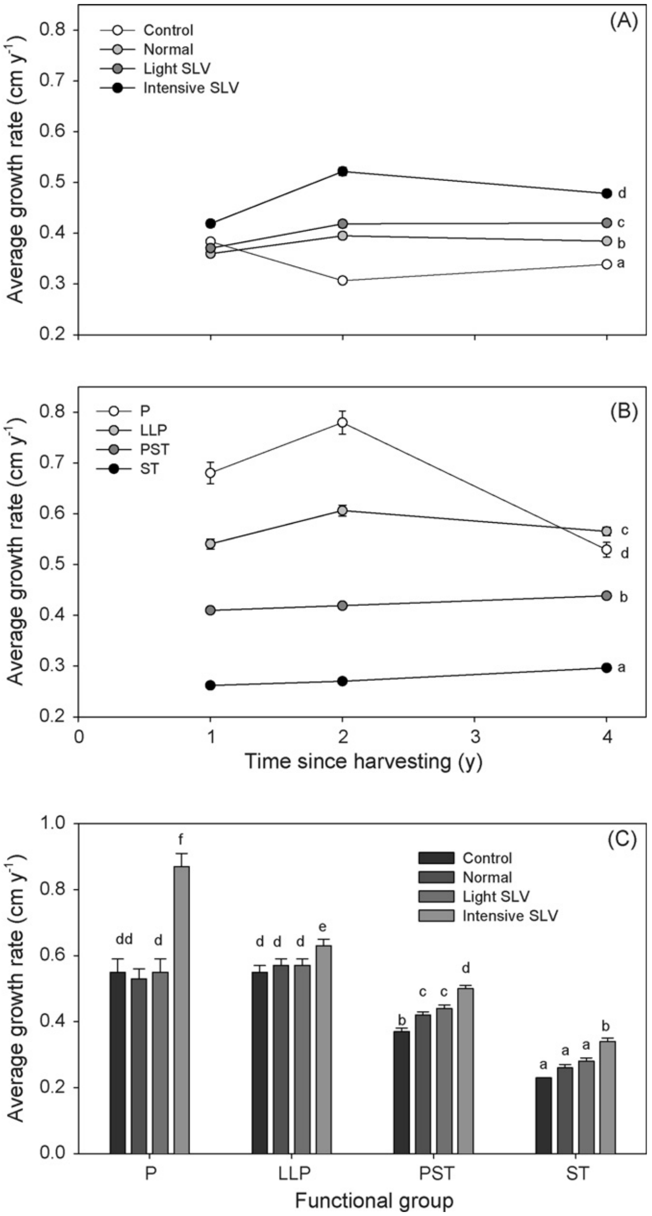

Fig. 3. Average tree growth rates through time after different management treatments in a Bolivian tropical moist forest. The effect of treatment (A), functional group (B) and functional group and treatment 4 years after treatment application (C) on growth rate are presented. Data are mean ± 1S.E. based on all trees sampled in each treatment. Different letters represent significant differences over time in A and B. SLV = silviculture.

Table 5

Results of a two-way repeated-measures ANOVA with growth rate (GR_{total}) as the dependent variable, time as the within-subject variable, and treatment and functional group as between-subject fixed factors

Test of within-subject contrasts			Test of between-subject contrasts		
Factor	F	P	Factor	F	P
Time	248.3	***	Treatment	86.8	***
Time × treatment	57.6	***	Treatment × functional group	8.5	***
Time × functional group	118.6	***	Functional group	693.8	***
Time × functional group × treatment	8.0	***			

***Significance levels: $p < 0.001$, $N = 26511$.

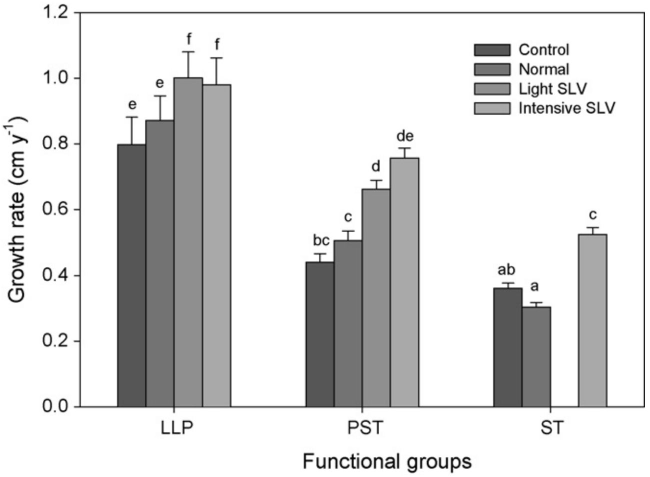

Fig. 4. Average growth rates (4 years post-treatment) of future crop trees (FCTs) of different functional groups growing in plots that received different treatments in a Bolivian tropical moist forest. Data are mean ± 1S.E. based on FCTs sampled in all plots. There were only two shade-tolerant trees in the light silvicultural treatment, thus they were excluded from the analysis. Different letters indicate significant differences at $p < 0.05$. SLV = silviculture.

through time, with $GR_{1–2}$ significantly higher (0.41 ± 0.003) than the $GR_{0–1}$ (0.38 ± 0.003) and $GR_{2–4}$ (0.40 ± 0.003). During the 4-year evaluation period, trees grew faster in the intensive silvicultural treatment plots than in the other treatments (Fig. 3A). In regards to functional groups, light-demanding species grew faster than shade-tolerant species during the first 2 years after logging, but these differences declined 4 years after treatment application (Fig. 3B). Growth rates of trees in all functional groups were highest in response to the intensive silvicultural treatment. Pioneer species showed the strongest response to intensive silvicultural interventions followed by the long-lived pioneer species (Fig. 3C).

Commercial, potentially commercial and non-commercial species groups differed in their growth rates (ANOVA, $F_{2,34479} = 288.22$; $p < 0.001$). The commercial species group had the highest growth rate (0.53 ± 0.009), followed by the non-commercial (0.40 ± 0.004) and the potentially commercial (0.34 ± 0.003) species groups.

FCT growth rates increased with logging and silvicultural treatment intensity and varied among functional groups (ANOVA; for treatment, $F_{3,3407} = 22.2$; $p < 0.001$; for functional group, $F_{2,3407} = 69$; $p < 0.001$); the long-lived pioneer species having the highest growth rates. The interaction between functional groups and silvicultural treatments was not significant (ANOVA, $F_{6,3407} = 2.0$; $p = 0.062$) (Fig. 4). At the species level, seven species increased in growth rate in response to increased logging and silvicultural treatment intensities (Table 6). The other 10 species did not show a significant response to treatment, although most of them tended to have higher growth rates in the intensive silviculture treatment plots.

4. Discussion

Several recent studies indicate that tree growth rates are too low to secure sustained timber yields after conventional or reduced-impact logging of tropical forests, at least using current cutting cycle lengths (Silva et al., 1995; Dauber et al., 2005; van Gardingen et al., 2006; Keller et al., 2007; Valle et al., 2007; Putz et al., this issue). Fredericksen and Putz (2003) suggested that the application of silvicultural treatments to enhance FCT growth rates after logging could help move current tropical forest management closer to sustainable forestry. The positive effect of removing lianas and overtopping trees on future crop tree growth rates observed in our study (Fig. 2) supports the idea that silvicultural treatments beyond RIL are warranted and effective (Dauber et al., 2005; Schulze et al., 2005; Keller et al., 2007; Sist and Ferreira, 2007; Zarin

Table 6
Average growth rates (cm y^{-1}) (4 years post-treatment) of FCTs of different commercial and potentially commercial species growing in plots that received different treatments in a Bolivian tropical moist forest. Data are mean (±1S.E.) based on FCTs sampled in the different plots. When treatment had an effect on growth rates, differences are shown with a lower case letter. C = control, N = normal, LS = light silviculture, IS = intensive silviculture

Scientific name	Treatments					
	F	P	C	N	LS	IS
Ampelocera ruizii	6.5	0.002	0.90 ± 0.06 a	0.76 ± 0.10 a		1.16 ± 0.08 b
Aspidosperma cylindrocarpon	4.2	0.026	0.20 ± 0.07 ab	0.16 ± 0.04 a		0.38 ± 0.07 b
Cariniana estrellensis	1.6	ns	0.38 ± 0.13	0.77 ± 0.11	0.62 ± 0.10	0.66 ± 0.13
Cariniana ianeirensis	1.3	ns	0.56 ± 0.07	0.67 ± 0.12	0.80 ± 0.13	0.48 ± 0.14
Centrolobium microchaete	0.4	ns	0.74 ± 0.13		0.91 ± 0.15	0.87 ± 0.16
Clarisia racemosa	4.5	0.016	0.22 ± 0.05 a	0.32 ± 0.10 ab		0.56 ± 0.13 b
Cordia alliodora	0.2	ns	0.51 ± 0.01	0.55 ± 0.13	0.65 ± 0.13	0.63 ± 0.18
Ficus boliviana	1.2	ns	0.55 ± 0.24	1.51 ± 0.41	1.16 ± 0.31	1.10 ± 0.41
Gallesia integrifolia	1.7	ns	0.62 ± 0.14	1.08 ± 0.18		0.84 ± 0.19
Hura crepitans	13.2	<0.001	0.54 ± 0.05 a	0.85 ± 0.07 b	0.91 ± 0.05 b	1.09 ± 0.05 c
Pouteria nemorosa	1.1	ns	0.31 ± 0.08	0.28 ± 0.10	0.44 ± 0.07	1.09 ± 0.06
Pseudolmedia laevis	35.2	<0.001	0.27 ± 0.01 a	0.27 ± 0.01 a		0.40 ± 0.01 b
Schizolobium amazonicum	0.06	ns	2.12 ± 0.36	1.98 ± 0.29	2.23 ± 0.26	2.13 ± 0.26
Spondias mombin	0.8	ns	0.53 ± 0.08	0.75 ± 0.15	0.74 ± 0.16	0.83 ± 0.19
Sweetia fruticosa	0.2	ns	0.27 ± 0.07	0.26 ± 0.06		0.32 ± 0.06
Swietenia macrophylla	5.9	0.001	0.88 ± 0.14 b	0.64 ± 0.08 ab	1.18 ± 0.20 a	1.29 ± 0.12 ab
Terminalia oblonga	8.0	<0.001	0.26 ± 0.04 a	0.32 ± 0.03 a	0.36 ± 0.03 ab	0.43 ± 0.03 b

et al., 2007). The additional silvicultural treatments required to increase tree growth rates are not components of RIL and are not currently included in the criteria and indicators used for forest certification (e.g., FSC criteria).

In this study, tree growth rates increased 9–27% in response to (intensive) logging and additional silvicultural treatments compared to RIL alone (Fig. 3A). Disregarding potential below-ground effects, the higher growth rates observed are most likely attributable to the higher light availability to tree crowns (Fig. 1A) and lower liana infestation (Fig. 1B and C) in the light and intensive silvicultural treatments than in the normal (RIL only) treatment. Another benefit of increasing logging intensity and applying additional silvicultural treatments is that future crop trees experience better growing conditions after treatment application than when RIL techniques alone are used. In this study, the better growing conditions persisted for at least 4 years after treatment application and were reflected in higher growth rates over time in the more intensively treated plots (Fig. 3A). We expect that the benefits of these treatments will persist for several more years because, after 4 years, the crown exposures were greater and liana infestations were lower in the light and intensive silviculture treatments than in the normal treatment (Fig. 1). de Graaf et al. (1999) observed that the benefits of the silvicultural treatments applied in the CELOS system persisted for only about 10 years, which prompted the authors to recommend repeated treatments during the cutting cycle to maintain optimal growing conditions. That recommendation is probably also valid for the treatments applied in this study, but it is too soon to define which treatments should be applied and when. It is also uncertain whether tropical forest managers will be willing to implement additional treatments given their low profit margins and the difficulty in reestablishing access to previously harvested areas (Pearce et al., 2002; Rice et al., 1997; Barreto et al., 1998; Holmes et al., 2002).

Our results clearly show that tree growth rates are increased by increasing harvest intensity following RIL guidelines and by applying additional silvicultural treatments. Other studies have found similar results both for harvest intensity (Finegan et al., 1999; Parrotta et al., 2002; Sist and Nguyen-Thé, 2002; Chapman and Chapman, 1997; van Gardingen et al., 2006) and for additional silvicultural treatments (de Graaf et al., 1999; Wadsworth and Zweede, 2006). The relation between harvesting intensity and sustained timber yield has, however, been shown to reach a maximum, after which an increase in harvesting intensity has a negative effect on timber yields after the first cutting cycle (van Gardingen et al., 2006; Karsenty and Gourmet-Fleury, 2006). This negative effect can be attributed to the fact that disturbance increases with harvest intensity (Mostacedo et al., 2006; Sist and Ferreira, 2007), which in turn promotes the regeneration and growth of more light-demanding and fast-growing non-commercial species (Phillips et al., 2004; van Gardingen et al., 2006). This hypothesis is further supported by our observation that, of the four functional groups, pioneer species had the strongest growth rate (Fig. 3C) and recruitment (IBIF, unpublished data) response to the intensive silviculture treatment. Consequently, although future crop tree growth rates increased with the number of trees harvested, it seems necessary to determine the harvesting intensity threshold that promotes accelerated tree growth without reducing future timber yields (cf. van Gardingen et al., 2006). This threshold will likely vary with forest type and with the species being managed. A forest managed for light-demanding species, for example, will probably require more disturbance than a forest being managed for shade-tolerant species.

Tree growth rates varied with functional group and, as expected, pioneer species grew the fastest over the study period (Fig. 3B). By 4 years post-treatment, however, pioneer growth rates declined significantly, probably due to the observed decrease in crown light exposure (Fig. 1A). Furthermore, for all functional groups, growth rates increased with increased intensity of logging and silvicultural treatments (Fig. 3C). Growth rates of the pioneer species increased substantially more in the intensive silviculture treatment, a pattern that was not observed for the other functional groups (Fig. 3C).

As expected, FCT growth rates also increased in response to increasing management intensity. This response was similar among functional groups but was much stronger (in relative terms) for the shade-tolerant and partially shade-tolerant species than for the long-lived pioneers (Fig. 4). Partially shade-tolerant and shade-tolerant species grew 50–70% faster in the intensive silvicultural treatment plots than in the plots treated with RIL alone, while the long-lived pioneers grew only 12% more rapidly in response to the intensive silviculture treatment. It is likely that the response of long-lived pioneers is lower because, compared with trees from other functional groups, these trees were already naturally growing under higher light conditions before treatment (data not presented). It should be noted that the long-lived pioneer species also responded to increased harvest intensity and silvicultural treatments with increased regeneration (Peña-Claros et al., 2008).

Tree growth response at the species level followed the pattern described for the functional groups. Intensive management had a positive effect on the growth rates of 78% of the species belonging to the shade-tolerant and partially shade-tolerant groups, while the treatments apparently had no effect on individual long-lived pioneers species (Table 6). It is perhaps worth noting that although growth rates did not differ among treatments for ten of the studied species, seven of them tended to have grown faster in response to the intensive silviculture treatment than to normal harvesting. Consequently, it is likely that, in the long run, the application of silvicultural treatments will result in a higher volume percentage being recovered during the second cutting cycle (Dauber et al., 2005), regardless of whether growth rates among treatments statistically differ.

Applying silvicultural treatments to increase the growth of FCTs is one method for moving tropical forest management closer to sustained yield. Unfortunately, many tropical forest managers and field foresters are inexperienced with silvicultural treatments; thus, training programs in silviculture, similar to those for RIL, could perhaps be used to promote the use of cost-effective silvicultural treatments. The forest certification movement has also done much to promote reducing undesirable logging damage. Once FCTs are protected from damage, certifiers should move more aggressively towards the promotion of sustained yield in tropical forests through the application of appropriate logging and silvicultural treatments that improve the growth of residual trees.

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