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Silvicultural treatments enhance growth rates of future crop trees in a tropical dry forest

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ABSTRACT

Silvicultural treatments are often needed in selectively logged tropical forest to enhance the growth rates of many commercial tree species and, consequently, for recovering a larger proportion of the initial volume harvested over the next cutting cycle. The available data in the literature suggest, however, that the effect of silvicultural treatments on tree growth is smaller in dry forests than in humid forest tree species. 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 of future crop trees (FCTs; i.e., trees of current and potentially commercial timber species with adequate form and apparent growth potential). The study was carried out in a tropical dry forest in Bolivia where a set of 21.25-ha plots were monitored for 4 years post-logging. Plots received one of four treatments that varied in intensity of both logging and silvicultural treatments as follows: normal (reduced-impact) logging; normal logging and low-intensity silviculture; increased logging intensity and high-intensity silviculture; and, unlogged controls. The silvicultural treatments applied to FCTs involved liberation from lianas and overtopping trees. Results showed that rates of FCT stem diameter growth increased with light availability, logging intensity, and intensity of silvicultural treatments, and decrease with liana infestation degree. Growth rate increment was larger in the light and intensive silvicultural treatment (22–27%). Long-lived pioneer species showed the strongest response to intensive silviculture (50% increase) followed by total shade-tolerant species (24%) and partial shade-tolerant species (10%). While reduced-impact logging is often not sufficient to guarantee the sustainability of timber yields, application of silvicultural treatments that substantially enhanced the growth rates of FCTs will help move the management of these forests closer to the goal of sustained yield.

1. Introduction

Tropical dry forests are among the most endangered ecosystems in the world (Janzen, 1986; Hoekstra et al., 2005). Most of the remaining area covered by tropical dry forest in the Americas is located in Mexico and Bolivia (Janzen, 1986), with the largest extant patch in the latter country (Killeen et al., 2006) that also boasts one of the most biologically diverse dry forests in the world (Parker et al., 1993). Until the 1990s, the tropical dry forests of Bolivia were mostly intact, but rates of conversion for intensive soybean production and cattle ranching have recently increased (Rojas et al., 2003; Killeen et al., 2007). Consequently, this forest type suffers high deforestation rates (Rojas et al., 2003; Killeen et al., 2007) and one of the highest incidences of wildfires in the country (Resnikowski and Wachholtz, 2007). One option for reducing the conversion pressure on tropical dry forest is to promote other economic alternatives, such as forest management for timber production (Lamprecht, 1990). In 2007, about 27% of the areas under forest management in Bolivia was in tropical dry forests, of which 550,670 ha was certified as well managed according to the Forest Stewardship Council (FSC) standards (CFV, 2007).

Recent studies show that tropical trees in Bolivia grow at lower rates than expected when the current cutting cycles were

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established (Dauber et al., 2005; Brienen and Zuidema, 2006). In the case of tropical dry forests in Bolivia, models have shown that only 13% of the volume harvested during the first commercial timber harvest will be recovered in time for the next planned harvest, i.e., at the end of the second cycle (25 years later; Dauber et al., 2005). Hence, at least in terms of volume recovery, Bolivian tropical forests are not as resilient as was believed. One way to increase volume recovery is to enhance the growth rates of future crop trees (FCTs) by increasing light availability to their crowns by reducing competition from neighboring trees and lianas (Dauber et al., 2005; Wadsworth and Zweede, 2006; Peña-Claros et al., 2008). The effects of such silvicultural treatments have mostly been studied in tropical moist forests (Wadsworth and Zweede, 2006; Peña-Claros et al., 2008), whereas little is known about their effects in tropical dry forests. Models simulating an improvement in growing conditions of FCTs in Bolivian dry forests resulted in a rather small increase in yield recovery rate between cutting cycles (from 13% to 16%; Dauber et al., 2005), but this estimate was not based on data from experimentally replicated plots where actual silvicultural treatments have been applied.

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 that ranged in logging intensity and the intensity in application of additional silvicultural treatments (Peña-Claros et al., 2008). The LTSRP is currently underway in three different forest types that represent the major timber production regions in Bolivia. The large size of the LTSRP plots permits estimation of logistical feasibility and cost-effectiveness of different silvicultural interventions while providing for realistic studies of the long-term impacts of silvicultural treatments on biodiversity, stand dynamics and 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 (Blate, 2005). In this paper, we focus on the effects of different silvicultural treatments on growth rates of FCTs using two blocks of treatment plots established at the dry tropical forest site.

The objectives of this paper are: (1) to assess the effect of liana infestation and crown position on growth rates of FCTs; (2) to determine the effect of logging and additional silvicultural treatments (release of future crop trees from lianas and overtopping trees) on growth rates of FCTs; (3) to evaluate whether species belonging to different functional groups respond differently to logging and additional silvicultural treatments; and (4) to asses the effect of silvicultural treatments at species level. We predicted that growth rates of FCTs would increase with logging and silvicultural intensity and those treatment responses would be greater for light-demanding than for shade-tolerant species.

2. Methods

2.1. Study area

The study was conducted on the 30,000 ha private property of INPA PARKET Ltda (hereafter INPA), 50 km southeast of the town of Concepción (16°06′S, 61°43′W). This area has been classified as supporting deciduous tropical dry forest, locally known as Chiquitano dry forest (Killeen et al., 2006). The area is part of the Precambrian Chiquitano Shield, characterized by rolling hills with superficial thin oxisols, mostly derived from gneiss or other granitic rocks (Cochrane, 1973; Navarro and Maldonado, 2002). The elevation varies between 400 and 500 m asl. Annual precipitation in the region is 1160 mm with a 4-month dry season from June to September, during which nearly all trees are deciduous. The annual mean temperature is 23.8 °C. For trees with diameter at 1.3 m aboveground (DBH) ≥ 10 cm, the forest has an average density of 437 trees ha^{-1}, basal area of 21 m^2 ha^{-1}, and 34 species ha^{-1}. There are at least 98 canopy tree species identified in INPA, 16 of which were harvested for timber at the beginning of this study (2002). The intended cutting cycle is 25 years and the company obtained Forest Stewardship Council certification for its management plan in 1999.

2.2. Experimental design

The study was carried out within the LTSRP plots established at INPA by the Instituto Boliviano de Investigación Forestal. At INPA, there are 8 plots with an average size of 21.25-ha, grouped in two blocks. Each block was established in a different logging compartment logged in a different year, using a randomized block design, for a total of 160 ha of study plots. All plots were first delineated on the ground using an inventory map to select areas with similar densities of harvestable trees. Plots were then randomly assigned to one of four treatments, except that the control treatment plots were located so as to maximize the area of adjacent unharvested forest.

Plots received one of four treatments that vary in management intensity consisting of: (a) unharvested, “control”; (b) harvested following the technical norms of the Bolivian forestry law, which requires the application of reduced-impact logging techniques, “normal”; (c) “light silviculture” plots harvested as the normal treatment but with application of additional, low-intensity silvicultural treatments; and, (d) “intensive silviculture” plots that were harvested at twice the intensity of the normal treatment and with application of more intensive silvicultural treatments (Table 1). The more intensive treatments were intended to enhance the growth of potential commercially marketable individuals, especially FCTs. FCTs are individuals of commercial species (Table 2) that are too small to be harvested in the first cutting cycle (i.e., 10–50 cm DBH for current commercial species and 20–50 cm DBH for potentially commercial species) but that have adequate form (excellent to good stem quality and perfect to tolerable crown form; see Section 2.3 for more details) and are expected to be harvested in the future. In the intensive silviculture treatment, a longer species list based on expected future marketability was used for defining FCTs (Table 2).

LTSRP plots have a nested design in which trees ≥40 cm in DBH are included in the entire plot, trees ≥20 cm in DBH in the central

Table 1
Basic information on experimental design used to test the effect of logging and additional silvicultural treatments on future crop trees. The study is carried out in the LTSRP plots in a tropical dry forest in Bolivia that are on average 21.25-ha in size. LS = Light silviculture. IS = Intensive silviculture.

Management practices	Treatments		
	Normal	LS	IS
• Number of 21.25 ha plots	2	2	2
• Density of future crop trees (FCTs; in trees ha^{-1})	17.2	14.6	19.6
• Pre-harvest marking of FCTs ≥ 10 cm DBH to reduce damage during logging (in trees ha^{-1})	0	14.6	19.6
• Lianas cut on FCTs 2–5 months before logging (in trees liberated ha^{-1})	0	7.1	10.2
• Merchantable trees harvested using species-specific minimum cutting diameters (40–50 cm in DBH) (in trees harvested ha^{-1})	4.3	4.0	8.1
• Post-harvest liberation of FCTs from overtopping non-commercial trees by girdling (in trees liberated ha^{-1})	0	4.7	5.5
• Number of non-commercial trees girdled to liberate FCTs after logging (trees girdled ha^{-1})	0	2.6	2.5
• Post-harvest girdling of non-commercial trees >40 cm DBH (trees ha^{-1})	0	0	0.8

Table 2
The 24 species considered in INPA's forest management plan as currently and potentially commercial grouped into one of three functional groups: long-lived pioneers (LLP), partially shade-tolerant (PST), and totally shade-tolerant species (TST). LS = Light silviculture, IS = Intensive silviculture. MDC = minimum diameter for cutting.

Scientific name	Family	Functional group	Density (# ha^{-1})	Species being treated in	
Acosmium cardenasii	Fabaceae	ST	7.06		IS
Amburana caerensis	Fabaceae	LLP	0.06	LS	IS
Anadenanthera culubrina	Fabaceae	LLP	6.97		IS
Aspidosperma cylindrocarpon	Apocynaceae	PST	0.11		IS
Aspidosperma subincarnum	Apocynaceae	PST	0.80		IS
Aspidosperma tomentosum	Apocynaceae	PST	1.34		IS
Astronium urundeuva	Anacardiaceae	LLP	1.06	LS	IS
Caesalpinia pluviosa	Fabaceae	PST	5.56	LS	IS
Cedrela fissilis	Meliaceae	LLP	0.20	LS	IS
Centrolobium microchaete	Fabaceae	LLP	4.03	LS	IS
Cordia alliadora	Boraginaceae	LLP	0.46		IS
Guibourtia chodatiana	Fabaceae	PST	0.98	LS	IS
Hymenaea courbaril	Fabaceae	PST	0.63	LS	IS
Machaerium acutifolium	Fabaceae	PST	0.27		IS
Machaerium scleroxylon	Fabaceae	LLP	1.09	LS	IS
Phyllostylon rhamnoides	Ulmaceae	PST	0.34		IS
Platymiscium ulei	Fabaceae	LLP	0.08		IS
Pterogyne nitens	Fabaceae	LLP	0.04	LS	IS
Schinopsis brasiliensis	Anacardiaceae	LLP	0.15	LS	IS
Spondias mombin	Anacardiaceae	LLP	0.30	LS	IS
Sweetia fruticosa	Fabaceae	PST	2.01	LS	IS
Tabebuia impetiginosa	Bignonaceae	LLP	0.06		IS
Tabebuia serratifolia	Bignonaceae	LLP	2.01	LS	IS
Zeyheria tuberculosa	Bignonaceae	LLP	0.76	LS	IS

half of the plot, and trees ≥10 cm in DBH in four 1-ha subplots. However, to increase the sample size of FCTs to which silvicultural treatments were applied, all trees fulfilling the FCT criteria were located in the entire 21.25-ha of the light silviculture (577 trees) and intensive silviculture (761 trees) treatment plots (i.e. trees were sample in 42.50 ha per treatment). FCTs in the normal treatment were defined in the lab by selecting trees that had excellent to good stem quality and perfect to tolerable crown form (see Section 2.3. for more details; 763 trees selected). The FCTs in the normal treatment were used for comparison as these trees were growing in logged plots, but did not receive additional silvicultural treatments. Silvicultural treatments applied to FCTs to enhance growth rates were the following: cutting of lianas growing on FCTs that had their stems below the projected crown area of the tree (on average 5–6 lianas per tree were cut using a machete); and girdling of competing trees with a chainsaw, followed by application of the 2.4-D herbicide (at 20% solution) in the girdle cuts (Table 2).

Plots were installed in 2002 (block 1) and 2003 (block 2) and they were harvested by the concession workers 2–6 months after plot installation. Depending on the treatment, harvesting intensity ranged from 4 to 8 trees per ha, which resulted in 6.3–7.1% of the area being included in logging gaps or skid trails (Mostacedo et al., 2006). All plots were harvested using reduced-impact logging techniques, which included pre-harvest inventory of merchantable trees larger than the species-specific minimum cutting diameters (40–50 cm DBH), lianas cut on merchantable trees 3–5 months before logging, skid trial planning, retention of 20% of merchantable commercial trees, and directional felling.

2.3. Measurements

Trees were measured at plot installation and then 1, 2, and 4 years after treatment application. All FCTs growing in the light and intensive silvicultural treatments were also measured at those times. During each evaluation, we measured for each FCT the DBH, crown position index, crown form, degree of liana infestation and stem quality. The crown position index (referred hereafter as the light availability) had the following categories (Clark and Clark, 1992): 1 = no direct light, 2 = moderate to substantial lateral light, 3 = over-head light on part of the crown, 4 = full overhead light and 5 = emergent crown that receives light from all directions. The crown form had the following categories (Alder and Synnott, 1992): 1 = perfect, 2 = good, 3 = tolerable, 4 = bad or damage, 5 = severely damage or without crown. Liana infestation was categorized using the following categories (Alder and Synnott, 1992): 1 = no lianas; 2 = lianas on stem; 3 = lianas on stem and crown; and 4 = lianas completely covering the crown. Stem quality was categorized using the following categories (Alder and Synnott, 1992): 1 = perfect stem, 2 = stem with some irregularities, 3 = irregular, hollow, damaged stem. Commercial and potentially commercial species were assigned to one of the following three functional groups based on existing classifications (Jardim et al., 2003; Mostacedo et al., 2003; Justiniano et al., 2004; Poorter and Bongers, 2006): long-lived pioneer species; partial shade-tolerant species; and total shade-tolerant species.

2.4. Data analysis

Growth rates were calculated for each tree using a simple linear regression with DBH as the dependent variable and time as the independent variable (i.e. the 4 measurement dates). The slope of the regression gives the growth rate in cm day^{-1}, which was consequently multiplied by 365 to obtain the growth rate in cm $year^{-1}$. Trees whose DBH was estimated due to presence of buttresses or lianas, were excluded from the analysis to avoid errors on individual computed growth rates.

To determine treatment effects on crown position and liana infestation of remnant trees, we first tested if trees growing in the different treatments varied significantly in these variables at plot installation (time 0). Given that both average light availability and liana infestation were significantly different among treatments before treatment application (for light availability, Kruskal–Wallis, d.f. = 2, $\chi = 7.02$, $p = 0.03$; for liana infestation, Kruskal–Wallis, d.f. = 2, $\chi = 14.87$, $p = 0.01$), we could not use a repeated-measurements ANOVA. Therefore, we calculated the change in light availability and liana infestation between the last (4 years post-treatment) and the first (pre-treatment) measurements. A positive change in crown position denotes an improvement in light availability over time, while a negative change in liana infestation denotes a decrease in liana infestation over time. To determine the effect of treatment on the change in light availability and liana infestation, we used a Kruskal–Wallis test, followed by Mann–Whitney tests of differences among treatments.

To determine the effect of treatment and functional group on FCT growth rates, a two-way ANOVA was performed with treatment and functional group as factors, and DBH at plot installation as covariate. Additionally, to determine to what extent variation in diameter growth rates can be attributed to individual tree characteristics, a two-way ANOVA was performed using tree characteristics (liana infestation and light availability, both 1 year after logging as factors, and DBH as covariate. We used the tree characteristics measured 1 year after logging in the ANCOVA because this measurement was more highly correlated with growth rate than the other measurements taken (data not shown).

The direct effects of silvicultural treatments on tree diameter growth were analyzed using ANOVAs, with girdling (naturally free, overtopped, liberated through logging, and liberated through girdling) and liana cutting treatments (naturally free of lianas, liberated from lianas, and infested with lianas) as factors. In addition, to assess the combined effect of the two FCT liberation treatments, all 12 possible combinations between the two treatments were grouped in 5 categories: "no treatment", including FCTs that needed one or both treatments but did not receive either of them; "naturally free" were FCTs growing naturally without lianas and without overtopping competitors; "both treatments" included FCT that were liberated actively both from lianas and from overtopping trees either by girdling or harvesting; "liberated through girdling/harvesting" included FCT that were only liberated from overtopping competitors through girdling or harvesting; and "liberated from lianas" included FCT that were liberated from lianas only. This new grouping was chosen to avoid having none or few individuals in some of the 12 possible combinations of the two treatments. To test if there were differences among categories of the combined treatments in terms of growth rates, an ANOVA was used.

To study the treatment effects at the species level, ANOVAs were performed with treatment as factor and growth rates as the dependent variable. Species having <15 individuals were excluded from the analysis; consequently, the analysis was carried out for only 12 of the 24 commercial and potentially commercial species included in the study (Table 2).

We transformed growth rates using a square root function to meet normality and homogeneity of variances assumptions. For all the analyses, each tree was used as replicate and the Tukey pair comparisons were used as a post hoc test. Differences were considered significant at $p < 0.05$. All statistical analyses were carried out using SPSS 12.0.1.

3. Results

Changes in light availability through time did not differ among treatments (Kruskal–Wallis, d.f. = 2, $\chi = 2.37$, $p = 0.31$), although there was a tendency for an increase in light availability as treatment intensity increased (Fig. 1A). On the other hand, changes in liana infestation varied with treatment (Kruskal–Wallis, d.f. = 2, $\chi = 54.5$, $p < 0.001$). Liana infestation diminished more in the light silviculture treatment than in the intensive silviculture treatment, while it increased in normal treatment (Fig. 1B).

FCTs generally grew faster with an increase in size (ANCOVA, $F_{1,1813} = 6.51$; $p = 0.011$), and as light availability increased (ANCOVA, $F_{4,1813} = 2.97$; $p = 0.019$) and degree of liana infestation decreased (ANCOVA, $F_{3,1813} = 3.52$; $p = 0.015$). The response to improved light availability did not vary with liana infestation degree (ANCOVA, for light availability $\times$ liana infestation, $F_{11,1813} = 0.66$; $p = 0.77$), although trees free of lianas tended to respond stronger than trees with lianas (Fig. 2).

Growth rates of FCTs were affected by treatment and functional group but not by DBH (ANCOVA, for DBH: $F_{1,1832} = 1.65$; $p = 0.20$). FCTs grew faster in the light and intensive silviculture treatment than in the normal treatment (ANCOVA, for treatment: $F_{2,1832} = 26.6$, $p \leq 0.001$; Fig. 3A). Partial shade-tolerant trees grew faster than total shade-tolerant and long-lived pioneer trees (ANCOVA, for functional group: $F_{2,1832} = 51.5$, $p \leq 0.001$; Fig. 3B). The response of functional groups to treatments was not the same (ANCOVA, for treatment $\times$ functional group: $F_{3,1832} = 3.14$, $p = 0.024$), as partial shade-tolerant trees grew faster in the light silviculture treatment than in the intensive silviculture treatment (Fig. 3B).

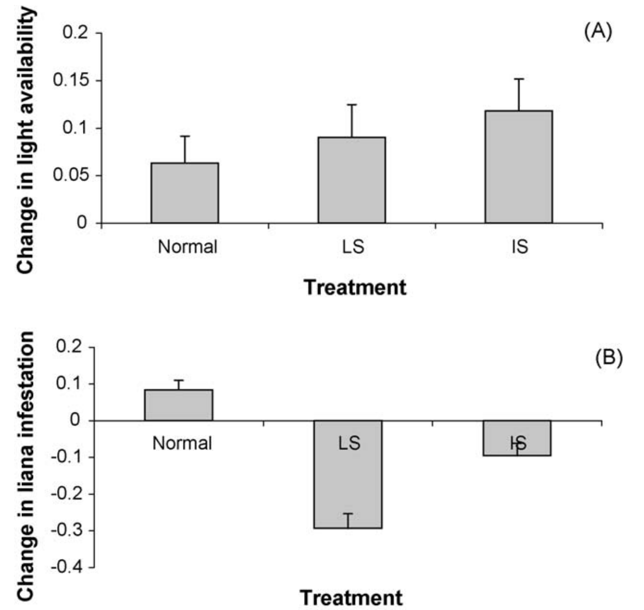

Fig. 1. Average change in light availability (A) and liana infestation (B) pre and post-treatment application in a tropical dry forest in Bolivia. Different letters indicate significant differences in liana infestation at $p < 0.05$. Data are means $\pm$ SE. $n = 2014$.

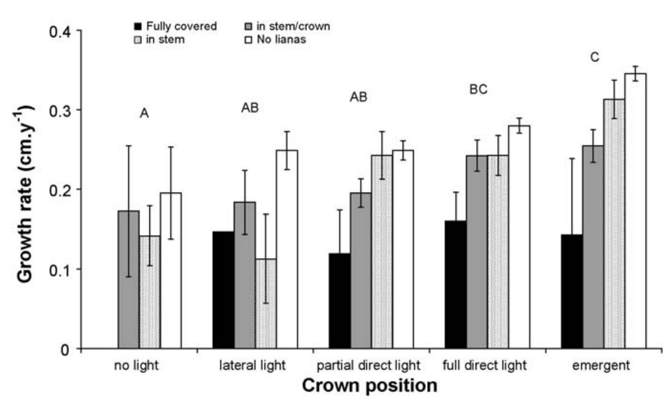

Fig. 2. The effect of crown position and liana infestation on average growth rate (mean $\pm$ 1SE) of future crop trees (4 years post-treatment) in a managed tropical dry forest in Bolivia. Liana infestation and crown position correspond to data collected 1 year after plot establishment. Back-transformed data are presented for a tree with a standardized DBH of 29.6 cm. Different letters indicate significant differences in crown position at $p < 0.05$. $n = 1813$.

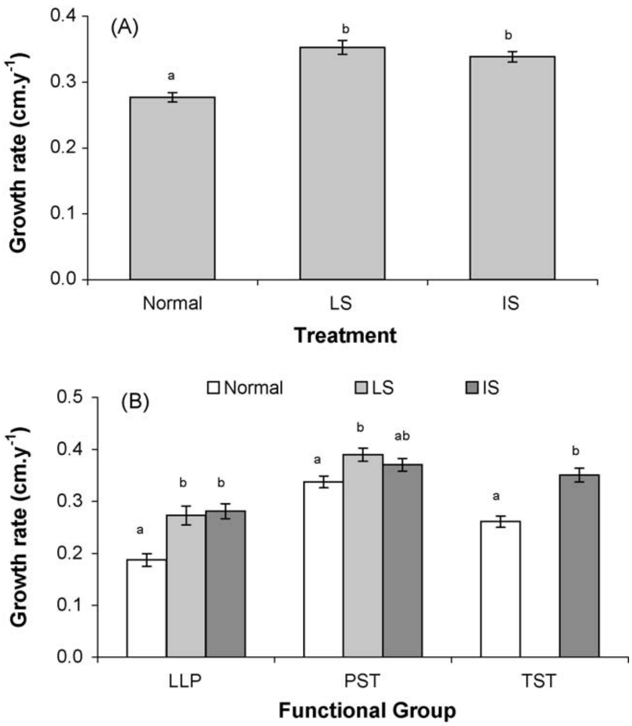

Fig. 3. Average growth rates (mean ± 1SE; 4 years post-treatment) of future crop trees (FCTs) growing in plots that received different treatments in a Bolivian tropical dry forest; per treatment (A) and per treatment and functional group (B). Data are presented are back-transformed and for a tree with a standardized DBH of 29.6 cm. There were not total shade-tolerant trees in the light silvicultural treatment because this species is not currently being harvested. Different letters indicate significant differences at $p < 0.05$. Normal, n = 761; LS = Light silviculture, n = 577; IS = Intensive silviculture, n = 763; LLP = Long-lived pioneer, n = 599; PST = partially shade-tolerant, n = 1078; ST = shade-tolerant, n = 424.

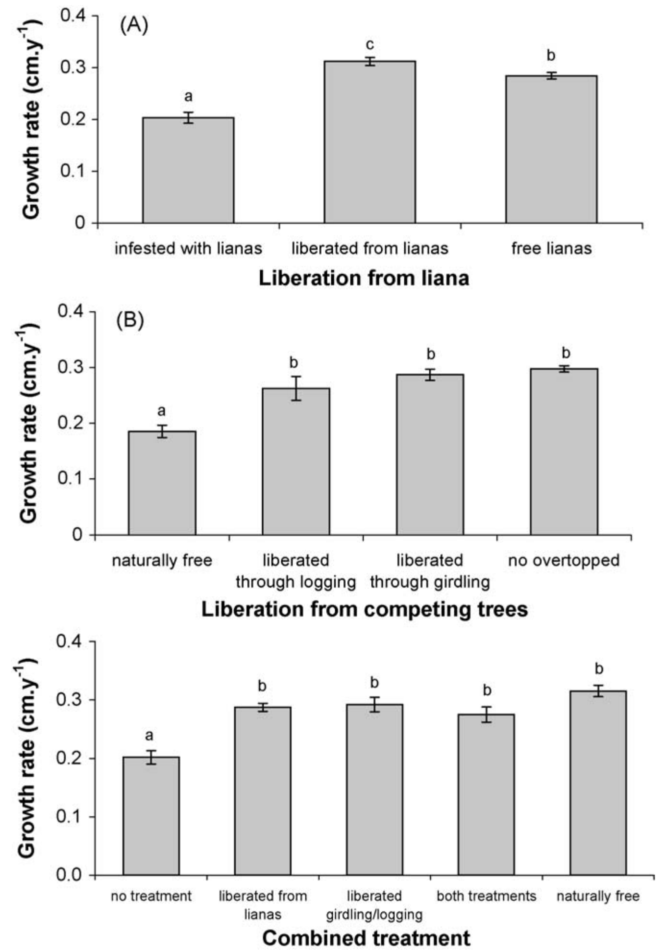

Fig. 4. The effect of specific silvicultural treatments on the growth rate of future crop trees (4 years post-treatment); liana cutting (A), liberation from overtopping trees (B) and both treatments combined (C). Back-transformed data are presented (mean ± 1SE). Different letters indicate significant differences at $p < 0.05$. LS = Light silviculture. IS = Intensive silviculture. n = 2101.

Both treatments applied to liberate FCTs resulted in higher growth rates (Fig. 4). FCTs liberated from lianas grew faster than trees infested with lianas and trees that were naturally free from lianas (ANOVA, $F_{2,2098}$ = 29.37, $p \leq 0.001$; Fig. 4A). FCTs from which overtopping neighbors were removed by girdling or through logging had higher growth rates than overtopped trees but grew at rates similar to those that were naturally free (ANOVA, $F_{3,2097}$ = 21.57, $p \leq 0.001$; Fig. 4B). Finally, trees that received at least one of the two silvicultural treatments grew faster than trees that were infested or suppressed. Liberated trees had the same growth rate that trees naturally free (ANOVA, $F_{4,2096}$ = 13.99, $p \leq 0.001$; Fig. 4C).

Species varied substantially in their growth rates, from species like *Schinopsis brasiliensis* with an average growth rate of 0.45 cm y^{-1} to species like *Centrolobium microchaete* and *Aspidosperma cylindrocarpon* with an average growth rate of 0.11 and 0.10 cm y^{-1}, respectively. Of the 12 species for which statistical analysis could be carried out, 6 of them grew faster in the intensive silvicultural treatment than in the normal one. Another 5 species tended to show the same pattern, but treatments were not significantly different, probably due to lower number of individuals.

4. Discussion

Numerous recent studies have called for the application of silvicultural treatments to help move current tropical forest management towards sustainable forestry (Lamprecht, 1990; Silva et al., 1995; Fredericksen et al., 2003; Dauber et al., 2005; Schulze et al., 2005; Keller et al., 2007; Sist and Ferreira, 2007; Zarin et al., 2007; Peña-Claros et al., 2008). Given that tropical dry forest trees have lower growth rates than trees in other forest types (Dauber et al., 2005), we questioned whether dry forests would also show a positive effect of reduced-impact logging and additional silvicultural treatments on future crop tree growth rates.

Growth rates of FCTs increased 22–27% in response to logging and application of additional silvicultural treatments compared to the normal logging treatment (Fig. 3A). Similar responses were observed in more humid tropical forests (Silva et al., 1995; Wadsworth and Zweede, 2006), including a moist tropical forest in Bolivia (Peña-Claros et al., 2008). The increase in growth rates is probably due to an increase in light availability and a decrease in liana infestation (Fig. 1). Logging intensity was higher in the intensive treatment than in the normal treatment, and therefore, a larger proportion of the area was occupied by logging gaps and skid trails (Mostacedo et al., 2006), which likely resulted in an increase in light availability. Although treatments did not differ significantly in terms of changes in light availability (Fig. 1A), the use of additional silvicultural treatments, such as liana cutting and girdling of overtopping trees, has also resulted in increased light availability for FCTs. Moreover, the application of liana cutting on FCTs resulted in less lianas in the light and intensive silviculture treatments than in the normal treatment (Fig. 1B). It is possible that liana cutting has not only resulted in an improvement in light

Table 3
Average growth rates (cm y^{-1}; for 4 years post-treatment) of future crop trees (FCTs) of commercial and potentially commercial species growing in plots that received different treatments in a Bolivian tropical moist forest. Back transformed data are presented. When treatments had effects on growth rates, differences are shown with lower case letters. %change was calculated by dividing growth rate observed after intensive silviculture treatment by growth rate observed after normal logging. N = Normal, LS = light silviculture, IS = intensive silviculture. ns = not significant; nd = no data.

Scientific name	*F*	*p*	N	Treatments LS	IS	N	%Change
Long-lived pioneer							
Anadenanthera culubrina	0.29	ns	0.43	0.42	0.44	458	4
Astronium urundeuva	1.32	ns	nd	0.31	0.26	57	
Centrolobium microchaete	7.90	<0.001	0.14[a]	0.15[b]	0.24[c]	245	65
Machaerium scleroxylon	1.67	ns	0.22	0.28	0.33	66	49
Tabebuia serratifolia	5.01	0.01	0.16[a]	0.32[c]	0.21[b]	99	28
Zeyheria tuberculosa	1.10	ns	0.05	0.07	0.12	43	124
Partially shade-tolerant							
Aspidosperma tormentosum	1.46	ns	0.19	nd	0.22	76	14
Caesalpinea pluviosa	3.43	0.03	0.31[a]	0.33[b]	0.41[c]	294	33
Guibourtia chodatiana	6.23	<0.001	0.14[a]	0.29[b]	0.40[c]	48	185
Hymenaea courbaril	0.32	ns	0.15	0.21	0.20	34	35
Sweetia fruticosa	4.63	<0.001	0.10[a]	Nd	0.17[b]	114	64
Totally shade-tolerant							
Acosmium cardenasii	24.93	<0.001	0.22[a]	nd	0.31[b]	433	40

conditions but also in a reduction in competition for soil water (Perez-Salicrup and Barker, 2000) or soil nutrients. These results support recommendations that additional silvicultural treatments are needed to increase growth rates of trees, and consequently, increase the likelihood of recovery of harvestable volume in the following cutting cycle (Dauber et al., 2005).

In relative terms, the long-lived pioneer species improved their growth rates more than total shade-tolerant and partial shade-tolerant species (Fig. 3B). The long-lived pioneer species grew 50% faster in the intensive silvicultural treatment than after normal logging, while the total shade-tolerant grew 24% and partial shade-tolerant 10% faster, respectively. These results differed from the results found in a similar experiment carried out in our moist forest site in Bolivia, where total shade-tolerant species had the strongest response to silvicultural treatments (Peña-Claros et al., 2008). The fact that different functional groups react differently to silvicultural treatments in dry and moist forests may be related to differences in forest structure between these forests. The moist forest has a taller, denser and more evergreen canopy. Under these conditions, individuals of long-lived pioneer can only persist in relatively large gaps, whereas the other groups can persist under shadier conditions (Peña-Claros et al., 2008); consequently, their growth response to the increase in light due to logging is only modest (12%) compared to the other groups, because they are already growing under relatively well-lit conditions. The dry forest has, in contrast a lower and (seasonally) more open canopy, which is mainly composed of leguminous trees with small leaflets (IBIF, unpublished data) that allow the passage of much light. Under these conditions, long-lived pioneer species can still persist under in the canopy. Therefore, this group benefits as well from increased light levels due to logging and additional silvicultural treatments (i.e. liberation from competing trees and lianas). Because these long-lived pioneers have a higher growth potential than the other functional groups (Delcamp et al., 2008), they show a stronger growth response (Fig. 3B).

Both liana cutting and girdling of overtopping trees resulted in faster growth rates of FCTs (Fig. 4A–C). Liberated trees grew at similar rates as those naturally growing under good conditions, i.e., free of lianas and overtopping trees. This result indicates that the application of liberation treatments creates better growing conditions for treated trees at least for 4 years after treatment application. It is likely that the positive effect of the treatments will disappear over time as was observed in the CELOS system (de Graaf et al., 1999). Due to lack of long-term data, it is currently unclear when and how frequently liberation treatments should be applied to maintain high growth rates, and whether forest managers will be interested in doing so given their low profit margins after the first harvest and the difficulty in re-establishing access to previously harvested areas (Rice et al., 1997; Barreto et al., 1998; de Graaf et al., 1999; Holmes et al., 2002; Pearce et al., 2002). Nevertheless, there is also the possibility that once FCTs are released, they will be able to maintain their high growth rates for longer periods of time. Tree ring analysis suggest that trees have different ways to reach the canopy and that a percentage of them are able to maintain high growth rates for many years after a release event (cf., one sustained release; Brienen and Zuidema, 2006). Additionally, growth differences among trees of a given species often persist over time, which means that fast-growing individuals can maintain rapid growth rates throughout their lives (Brienen and Zuidema, 2007).

The effect of additional silvicultural treatments (i.e., liana cutting and girdling of competing trees) on species-specific growth rates was larger than expected for tropical dry forests. Models simulating an improvement in growing conditions of FCTs in Bolivian dry forests predicted that species-specific growth rates would increase on average by 22% (Dauber et al., 2005). In contrast, we found that when FCTs of commercial and potentially commercial species were liberated from lianas and overtopping competitors, their growth rates increased on average by 58% (Table 3). The higher growth rates observed suggest a greater potential recovery of harvestable volume in the next cutting cycle than predicted by Dauber et al. (2005) if silvicultural treatments are applied. It is also worth mentioning that the application of additional silvicultural treatments to FCTs results in higher increments in the dry forest (58%) than in the moist forest (46%; Peña-Claros et al., 2008), which was not expected considering the fact that dry forests are exposed to longer periods of drought than moist forests.

Silvicultural treatments have positive effects on growth rates of FCTs not only in humid forests but also in tropical dry forests. Using reduced-impact logging techniques to assure reduce damage to the residual stand coupled with the liberation of FCTs from lianas and overtopping non-merchantable trees will lead to higher recovery rates of timber volume for the next cutting cycle.

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