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Regeneration of commercial tree species following silvicultural treatments in a moist tropical forest

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Abstract

Silvicultural treatments are generally performed to improve yields of commercially valuable tree species by increasing their recruitment and growth rates. In this study we analyze the effects of three different sets of silvicultural treatments on the densities and growth rates of seedlings, saplings and poles of 23 commercial tree species in a moist tropical forest in Bolivia. The treatments vary in intensity of logging and silviculture application, and are compared to a control treatment. Silvicultural treatments applied were liberation of future crop trees from lianas and neighboring competing trees, soil scarification and stand refinements. Treatments were applied to twelve 27-ha plots. In each plot 4 transects were established to assess the density and growth of the regeneration of the 23 commercial species. Effects were measured 1 and 4 years after treatment application and were described using three ecological guilds; shade-tolerant species, partially shade-tolerant species, and long-lived pioneers. We found that the intensive silviculture treatment had the largest impact on the density and growth rates of the regeneration of the commercial species. Overall, the density of regeneration of the commercial species was higher in the control treatment than in the logged treatments 1 year after treatment application, but 3 years later these differences had disappeared. Nevertheless, there were marked shifts in densities when different size classes were considered. In nearly all treatments, the number seedlings decreased over time, while the number of saplings and poles increased. Overall shade-tolerant species were more abundant than the other two ecological guilds. Treatment had a positive effect on density only for long-lived pioneers. Growth of commercial tree regeneration was strongly affected by treatment and was highest in the intensive silvicultural treatment plots where growth of long-lived pioneers was twice that of shade-tolerant species and partial shade-tolerant species. Apart from silvicultural treatments and ecological guild, light availability had the strongest effect on growth rates. These results show that different silvicultural treatments have different effects on the regeneration of commercial tree species and that ecological guilds-specific treatments should be considered in management plans for sustainable timber production in tropical lowland forests.

Keywords: Bolivia; Regeneration; Sustainable forest management; Silvicultural treatments; Tropical forest

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1. Introduction

The goals of sustainable forest management is to provide a steady flow of resources and income, while at the same time preserving forest cover, biodiversity and ecosystem integrity (e.g., Sayer et al., 1995). Numerous measures have been proposed to improve forest management including, among other recommendations, full commercial tree censuses, improved road planning, liana cutting on harvestable trees, seed tree retention, higher harvest diameter limits and liberation of future crop trees and (e.g., Graaf, 1986; Lamprecht, 1989; Fredericksen, 2000; Louman et al., 2001; Fredericksen and Putz, 2003). Such management interventions are not only needed to reduce felling damage while extracting trees from the forest (Heinrich, 1995), but also to ensure future timber yields (Jackson et al., 2002). One problem with the silvicultural interventions mentioned above is that they are focused mainly on maintaining forest structure and protecting ecological

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functions (e.g., soil productivity and nutrient retention) through controls on harvesting practices, not on securing the regeneration needed for future harvests (Fredericksen et al., 2003).

Once logging damage has been controlled, perhaps the single most important impediment to achieving long-term sustainability of managed forests is securing sufficient regeneration of commercial tree species (e.g., Lamprecht, 1989). This problem is particularly acute in Bolivia where previous studies have shown that many species suffer regeneration failures (Mostacedo and Fredericksen, 1999) except in disturbed areas, such as gaps, skid-trails and or log landings (Fredericksen and Mostacedo, 2000; Fredericksen and Pariona, 2002). Many studies conducted in other neotropical forests report similar results (Verissimo et al., 1992; Negreros-Castillo and Mize, 1993; Snook, 1996; Guariguata and Dupuy, 1997; Dickinson et al., 2000).

Most tropical forests consist of a large number of species with relatively low abundance per species. Experiments on the effects of silvicultural systems thus need to be large in scale and need to have sufficient replication to yield statistically sound conclusions and appropriate management recommendations. Also, small-scale experiments may give erroneous results because of spatial variation in community composition and dynamics. The Long-term Silvicultural Research Program (LTSRP) in lowland Bolivia has established a network of large-scale (20–27 ha) replicated plots that received one of four treatments ranging in intensity of logging and silviculture application from no intervention to high-intensity logging and numerous other silvicultural treatments (Table 1). Such large plots are necessary because, like most tropical forests, those in Bolivia have large numbers of species each represented by relatively few individuals. The LTSRP is being carried out in three different forest types – wet, moist, dry – of the country representing the major timber production regions (Dauber et al., 2000); in this paper we focus on the three blocks of plots established in the moist forest site.

Even with large plots, grouping species into a few ecological guilds or functional groups greatly facilitates data analysis (Philips et al., 2001), and helps overcoming the problem of low densities of tropical tree species and erratic regeneration. Classifying species into regeneration guilds uses similarities in regeneration requirements and behavior as a basis for grouping (Swaine and Whitmore, 1988; Lamprecht, 1989; Finegan, 1996). In the present study focused on commercial timber producing species, we distinguished three regeneration guilds described by Finegan (1996): shade-tolerant species (ST) that can establish and survive in the shade; partially shade-tolerant species (PST) that can establish in the shade but need a gap to grow to larger sizes and long-lived pioneers (LLP) that have high light requirements for regeneration and live longer than 30 years (Finegan, 1996). A fourth guild, short-lived pioneers (P), that has high light requirements for regeneration and lives <30 years are not included here because none are commercial species at this study site.

The questions we address in this paper with their corresponding hypothesis are:

(1) How do silvicultural treatments affect densities and growth rates of seedlings and saplings of commercial trees? We expected that the density and the growth rates of regeneration increase with increasing silvicultural treatment intensity.
(2) Do ecological guilds respond differently to silvicultural systems in terms of density and growth rates? We predicted that the partially shade-tolerant and long-lived pioneer species respond positively to increased disturbance whereas shade-tolerant species are expected to be most abundant in the control treatment (Pinard et al., 1999; Arets et al., 2003). Additionally in keeping with the results of other studies (Welden et al., 1991; Burslem and Whitmore, 2003; Sheil, 2003; Ter Steege et al., 2003), we expected tree growth rates to be highest in the most intensive silvicultural system, and shade-tolerant species to have the lowest and long-lived pioneers the highest growth rates.
(3) Does the effect of silvicultural systems on density change over time? We expected total commercial tree regeneration density to increase over time after treatment, as long as the forest is recovering from the disturbance.

Table 1
Treatments applied to the LTSRP plots in La Chonta Forest Concession, Bolivia; (●) Management practice applied. (● ●) Management practice applied with double intensity. C, Control; N, Normal; LS, Light silviculture and IS, Intensive silviculture

Management practices	Treatments			
	C	N	LS	IS
Pre-harvest inventory of merchantable commercial trees, using species-specific minimum cutting diameters (50–70 cm in diameter)	●	●	●	●
Lianas cut on harvestable 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})				●

(4) What environmental conditions (microsite, crown position index, liana infestation) and tree characteristics (ecological guild, initial height) determine tree growth rates? Among factors influencing tree growth rates, we expected microsite to be the most important one because it integrates the most important environment characteristics for tree regeneration (cf. Clark and Clark, 1992).

2. Methods

2.1. Study site

The research was conducted in the 100,000 ha forestry concession of Agroindustria Forestal La Chonta Ltda., 30 km east of Ascención de Guarayos, Bolivia (15°47′S, 62°55′W). This lowland semi-deciduous tropical moist forest is transitional between (Chiquitano) dry forest and Amazonian wet forests (Dauber et al., 2000). Annual precipitation in the region is about 1580 mm, with 4 months receiving <100 mm (May–September) and 1 month (July) during which potential evapotranspiration exceeds rainfall. About 30% of the canopy trees and many lianas are seasonally deciduous. The area is situated on the southwestern border of the Brazilian Shield, characterized by rolling hills with thin soil mostly derived from gneiss, granitic, and metamorphic rocks. The sandy-loam soil is circumneutral in pH and rich in nutrients (Paz, 2003; M. Peña-Claros, unpublished data). About 160 tree species >10 cm dbh have been identified at La Chonta, 23 of which are considered to be commercially valuable and 8–10 of which are currently harvested in substantial volume. Average harvest volumes are about 6 m^3 ha^{-1}. The intended cutting cycle is currently 30 years and the company's management was certified by the Forest Stewardship Council (FSC) in 1998. Fires are prevalent in the landscape matrix surrounding La Chonta; most are set annually during the dry season. In 1995 and 2004, about 30% of the concession burned.

2.2. Study design

La Chonta is one of the areas where the Long-term Silvicultural Research Program (LTSRP) is carried out by the Instituto Boliviano de Investigación Forestal. The LTSRP plots were established using a randomized block design. In La Chonta, there are three blocks, each located in different harvesting compartments. The company harvested the compartments after block establishment between 2001 (block 1 and block 2) and 2002 (block 3). Each block consists of four 27-ha plots (450 m × 600 m), which have received one of four different treatments (Table 1): an unharvested control plot, hereafter referred to as 'Control'; a plot harvested following practices stipulated by the Bolivian forestry law, hereafter referred to as 'Normal'; a plot harvested as in the Normal treatment using additional silvicultural treatments, hereafter referred to as 'Light Silviculture'; and a plot harvested as the normal treatment but doubling logging intensity and application of silvicultural treatments, hereafter referred as 'Intensive silviculture'. Consequently, treatments represent a gradient in the intensity of logging and silvicultural treatments. Silviculture treatments applied were liana cutting from future crop trees (FCTs), liberation of FCTs from competing trees through girdling, stand refinement and soil scarification (see Table 1 for more details on the silvicultural treatments applied).

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 the four treatments, with the exception of the control treatment that was subjectively assigned to maximize the area of unharvested surrounding forest. Trees >10 cm in diameter at 1.3 m height (DBH) growing in the LTSRP plots are sampled following a nested design. Individuals of the 23 commercial species (selected by the timber company; Table 2) <10 cm in DBH are monitored in four 450 m long regeneration transects established 2–5 months after logging in each plot, making a total of 5.4 km of transects for each treatment. Transects are subdivided into 20 m sections marked with pvc stakes. In 2004–2005, 42 of these 48 transects were remeasured. The remaining transects could not be included either because of missing data or because they were destroyed by the 2004 fire.

2.3. Measurements

Two of the 23 commercial species designated by La Chonta are shade tolerant, 8 are partially shade tolerant and 13 are long-lived pioneers (Table 2, based on Mostacedo et al., 2003; Justiniano et al., 2004; Poorter et al., 2006). Tree regeneration was assigned to three height classes: seedlings (<30 cm in height); saplings (30–150 cm in height) and poles (>150 cm tall but <10 cm DBH). Seedlings and saplings were evaluated in a 2 m wide strip and poles in a 4 m-wide strip. In every 20 m section, a maximum of three plants per species per height class were tagged at the time of plot installation. Additional plants of the same species and height class were only counted. When individuals tagged in 2001–2002 were dead or missing in 2004–2005, new plants were tagged. The following data were collected for each tagged individual: height for seedlings and saplings; DBH of poles; microsite (undisturbed, skid trail, skid trail edge, logging gap, logging gap edge, natural gap, natural gap edge); liana infestation (1, free of lianas; 2, with lianas) and crown position index (CPI; Clark and Clark, 1992; 1, no direct light; 1.5, some lateral light; 2, moderate lateral light; 2.5, a 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). Plants with zero or negative height or diameter increments were re-checked in the field and any that were physically damaged (14.5% of tagged individuals) or had negative growth rates (3.5% of tagged individuals) were excluded from the analyses.

2.4. Data analysis

Densities were obtained from the total number of tagged and untagged individuals per guild, and were ln-transformed for analyses. Effects of time, block, treatment and guild on

Table 2
The 23 commercial species monitored in regeneration transects in the LTSRP plots, grouped into one of three ecological guilds (based on Mostacedo et al., 2003; Justiniano et al., 2004; Poorter et al., 2006). The species relative density (%) is based on all treatments

Ecological guild	Scientific name	Family	Relative density
Shade tolerant	*Ampelocera ruizii*	Ulmaceae	24.04
Shade tolerant	*Pseudolmedia laevis*	Moraceae	35.27
Partially shade tolerant	*Clarisia racemosa*	Moraceae	8.39
Partially shade tolerant	*Pouteria nemorosa*	Sapotaceae	10.32
Partially shade tolerant	*Aspidosperma polyneuron*	Apocynaceae	0.49
Partially shade tolerant	*Cariniana ianeirensis*	Lecythidaceae	1.68
Partially shade tolerant	*Hura crepitans*	Euphorbiaceae	3.02
Partially shade tolerant	*Hymenaea courbaril*	Caesalpiniaceae	0.08
Partially shade tolerant	*Swietenia macrophylla*	Meliaceae	0.60
Partially shade tolerant	*Terminalia amazonica*	Combretaceae	3.44
Long-lived pioneer	*Caesalpinia pluviosa*	Caesalpiniaceae	2.22
Long-lived pioneer	*Cariniana domestica*	Lecythidaceae	0.01
Long-lived pioneer	*Cariniana estrellensis*	Lecythidaceae	0.69
Long-lived pioneer	*Cedrela fissilis*	Meliaceae	0.08
Long-lived pioneer	*Ceiba pentandra*	Bombacaceae	0.02
Long-lived pioneer	*Centrolobium microchaete*	Fabaceae	0.20
Long-lived pioneer	*Cordia alliodora*	Boraginaceae	0.15
Long-lived pioneer	*Ficus boliviana*	Moraceae	0.12
Long-lived pioneer	*Gallesia integrifolia*	Phytolaccaceae	4.76
Long-lived pioneer	*Tabebuia serratifolia*	Bignoniaceae	0.02
Long-lived pioneer	*Schizolobium amazonicum*	Caesalpiniaceae	0.48
Long-lived pioneer	*Spondias mombin*	Anacardiaceae	0.35
Long-lived pioneer	*Sweetia fruticosa*	Fabaceae	6.28

densities were analyzed using a three-way repeated-measurement ANOVA, with density as the dependent, time as the within-subject variable and block, treatment and guild as between-subject fixed factors. Transects were used as the sample units, as the minimum distance between transects established in a given plot is 80 m. Given that the maximum crown diameter that species achieve in La Chonta ranges from 1.7 to 35 m (mean 12.1, median 9.8 m; Lourens Poorter, personal communication), tree crowns do not overtop more than one transect at the same time. Consequently, we believe that it is possible to consider transects as independent units.

Growth rates were calculated for each tagged individual as the slope of a regression between the height or DBH and the measurement date. A one-way ANOVA was then used to analyze the effects of treatment and ecological guild on growth rates. Growth data were ln-transformed to increase normality and decrease heteroscedasticity. Additionally, growth rates were analyzed as a function of CPI and guild (two-way ANOVA) as well as by microsite class (one-way ANOVA). Because only four individuals had a CPI of 4, they were pooled into CPI class 3. To determine relative effects of treatment, initial height, CPI, liana load, ecological guild and microsite, growth rates were analyzed with multiple regression analysis, using dummy variables assigned to the categorical factors. Where data were transformed, back-transformed data are shown in graphs and tables. All statistical analyses were carried out using SPSS 12.

3. Results

Densities of commercial tree regeneration varied with block, treatment, ecological guild and time since treatment (Table 3). Even in the control plots, overall densities (all size classes combined) were higher in 2004 than in 2001 (Fig. 1). A

Table 3
Results of three-way repeated measurement ANOVA with density as the dependent variable, time as the within-subject variable and block, treatment and guild as between-subject fixed factors

Test of within-subjects contrasts			Test of between-subjects contrasts		
Factor	F	p	Factor	F	p
Time	30.26	***	Block	3.39	*
Time × block	16.55	***	Treatment	6.36	***
Time × treatment	0.86	ns	Guild	113.50	***
Time × guild	17.87	***	Block × treatment	3.78	**
Time × block × treatment	0.84	ns	Block × guild	1.21	ns
Time × block × guild	9.61	***	Treatment × guild	4.65	***
Time × treatment × guild	1.55	ns	Block × treatment × guild	1.21	ns
Time × block × treatment × guild	1.44	ns			

Significance level; n.s., Non-significant, $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

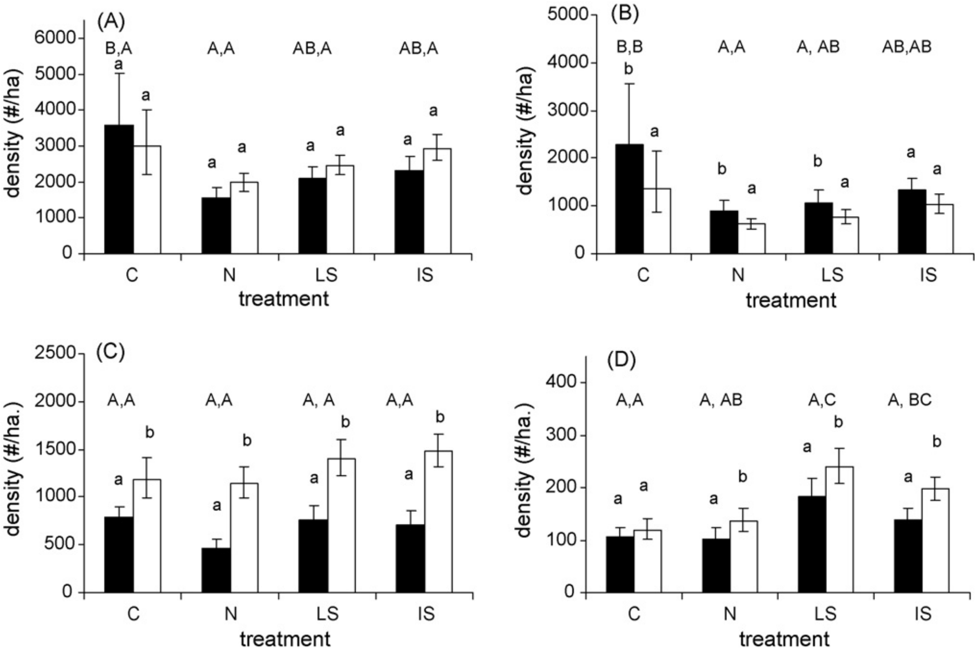

Fig. 1. Densities (mean ± S.E.) of plants <10 cm DBH of 23 commercial tree species in 2001/2002 (black bars) and 2004/2005 (open bars), for four silvicultural treatments. (A) All individuals combined, (B) seedlings, (C) saplings and (D) poles. C, Control; N, Normal; LS, Light silviculture and IS, Intensive silviculture. Different capital letters represent a significant ($p < 0.05$) difference among treatments for the same year (2001, 2004). Different small letters represent a significant (at $p = 0.05$) difference between years for the same treatment. Back-transformed data are presented but the analyses were performed on ln-transformed numbers.

time × block interaction was observed; over time, density increased in blocks 2 and 3, but decreased in block 1. A time × guild effect was also observed; although density of all guilds increased with time, the increase was much larger for long-lived pioneers. In 2004 there were significantly more shade-tolerant individuals than partially shade tolerant or long-lived pioneer individuals in all treatments (Fig. 2). Treatment effects interacted with block and guild. When treatment effects were analyzed for the guilds separately, only long-lived pioneers showed a significant response to treatments, having a higher density in the intensive silviculture treatment, compared to control and normal logging plot (Fig. 2). When the same analysis was done at the species level, treatment had an effect only on the density of *Gallesia integrifolia* (a long-lived pioneer species; ANOVA, $F_{3;38} = 3.7$, $p = 0.02$). The density of *Gallesia* increased with treatment intensity (17.6 plants ha^{-1} in the control treatment versus 332.7 plants ha^{-1} in the intensive treatment), which is in line with the response found at the guild level.

In 2001, total plant densities were higher in the control than the normal treatment (Fig. 1A, black bars), but by 2004 this difference disappeared (Fig. 1A, open bars). Otherwise, total plant density did not change much over time (Fig. 1A), but within size classes, marked shifts occurred. In nearly all treatments, except the intensive silviculture treatment, the number of seedlings decreased over time (Fig. 1B). The increase in the number of saplings (Fig. 1C) and poles (Fig. 1D) over the same time period implies that many seedlings and saplings shifted to the next height classes.

Silvicultural treatments had a strong effect on the height growth rates of seedlings and saplings (ANOVA, $F_{3;2121} = 23.14$; $p < 0.001$), and on height and diameter growth rates of poles (ANOVA, $F_{3;808} = 6.86$; $p < 0.001$ for height; $F_{3;586} = 16.14$; $p < 0.001$ for DBH; Fig. 3). For all height classes, growth rates increased as the intensity of logging and other silvicultural treatments increased. Ecological guilds varied clearly in their height growth rates (for seedlings and saplings: ANOVA, $F_{2;2393} = 18.38$; $p < 0.001$; Fig. 4A) and in their DBH growth rates (for poles: ANOVA, $F_{2;601} = 15.07$; $p < 0.001$; Fig. 4B). In both cases plants of long-lived pioneers grew faster than those of the other guilds.

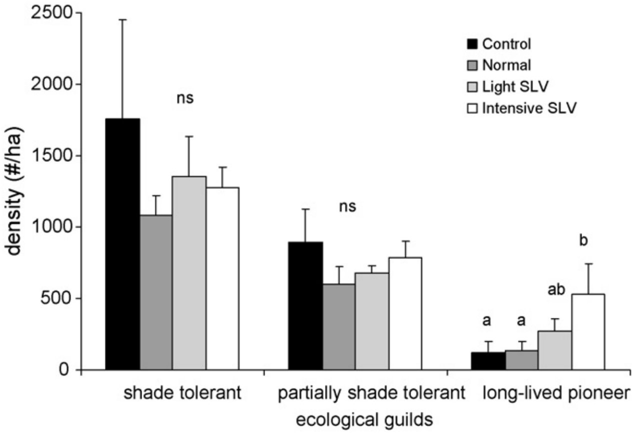

Fig. 2. Densities of plants <10 cm DBH of 23 species of commercial trees in 2004 by ecological guild and treatment (mean ± S.E. with each of the four transects in the three plots of each treatment as replicates). Different letters represent a significant difference ($p < 0.05$) among treatment for the same guild. Back-transformed data are shown. ns, No significant differences; SLV, silviculture.

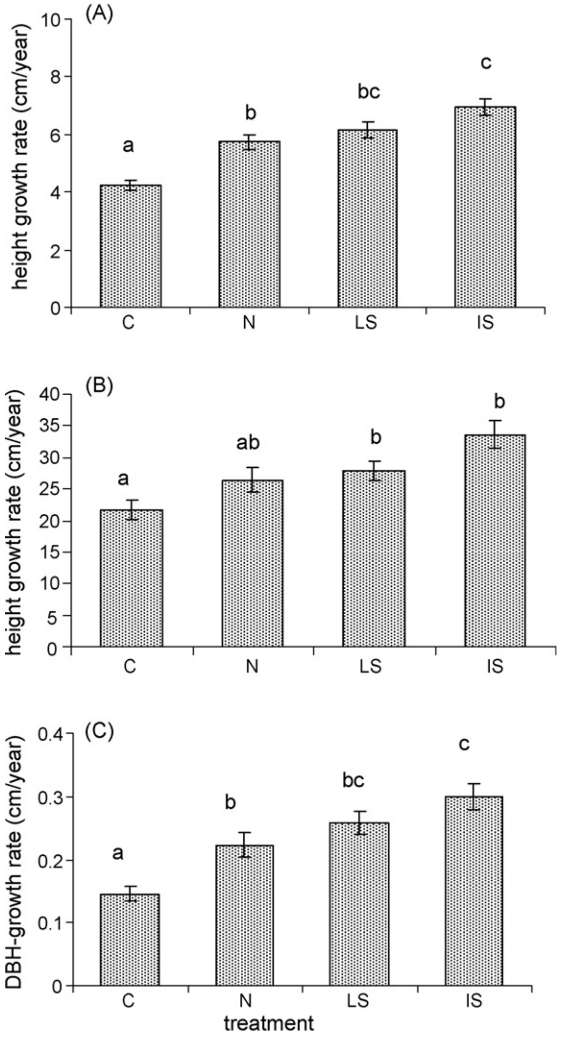

Fig. 3. Height growth rates of seedlings and saplings (A) and of poles (B), and diameter growth rates of poles (C) of 23 commercial timber species (mean ± S.E.) by treatment with individual trees taken as replicates. C, Control; N, Normal; LS, light silviculture; IS, intensive silviculture. Bars with a different letter are significantly different at $p < 0.05$. Note different *Y*-axis scales. Back-transformed data are used. $N = 3180$.

Apart from the influences of silvicultural treatment and ecological guild, CPI, microsite type, liana infestation and initial height also affected plant growth rate. Regardless of their ecological guild, plants growing under high light conditions (high CPI) grew faster than plants growing under lower light levels (low CPI) (ANOVA, $F_{4;2453} = 216.8$; $p < 0.001$; Fig. 5A). Microsite strongly affected growth rates (ANOVA, $F_{6;2933} = 39.0$; $p < 0.001$), with the most disturbed habitats (e.g., logging gaps) showing the highest growth rates (Fig. 5B).

The multiple regression analysis (Table 4) showed that over one third of the variation in growth was explained by the factors used in the model. CPI explained 26% of the variation in height growth rate whereas initial height, silvicultural treatment, liana load, ecological guild and microsite explained together an additional 11% of the total growth data.

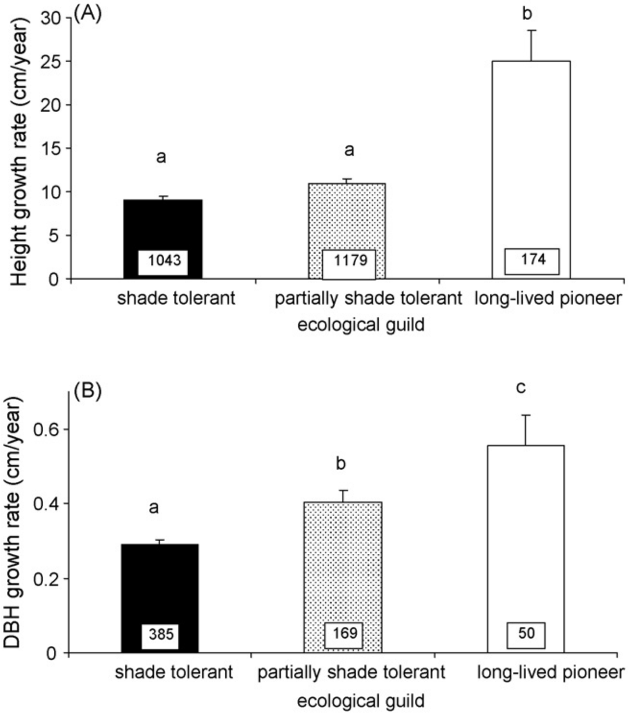

Fig. 4. Height growth rates (mean + S.E.) of seedlings and saplings (A) and DBH growth rates (mean + S.E.) of poles (B) of 23 species of commercial trees by regeneration guilds. Bars with different letters are significantly different at $p = 0.05$. Sample size is given for each size category and ecological guilds in the respective column.

4. Discussion

This study confirmed the results of previous studies in tropical forests that silvicultural treatments can enhance the regeneration of commercial species. In general, commercial regeneration density was decreased by the silvicultural treatments 3–6 months post-treatment, but was enhanced 3 years later at which time there were more commercial poles in the logged treatments than in the undisturbed forest. Growth rates also increased with treatment intensity, so that plants growing in the intensive silviculture treatment plots had higher growth rates than plants growing in the control or normal treatment plots. The effect of silvicultural treatments on growth can be largely explained by the fact that more intensive logging

Table 4
Multiple regression analysis with height growth rate as the dependent variable and CPI, initial height, silvicultural treatment, liana load, ecological guild and microsite as the independent variable. $N = 2460$ plants

Factor	R^2	*F*-value	d.f.
Total model	0.366	82.9^{***}	17
CPI	0.258	213.1^{***}	4
Initial height	0.073	267.9^{***}	1
Silvicultural treatment	0.021	26.2^{***}	3
Liana load	0.008	30.6^{***}	1
Ecological guild	0.003	7.1^{**}	2
Habitat	0.003	1.7^{ns}	6

Significance levels: n.s., non-significant, $^{**}p < 0.01$, $^{***}p < 0.001$.

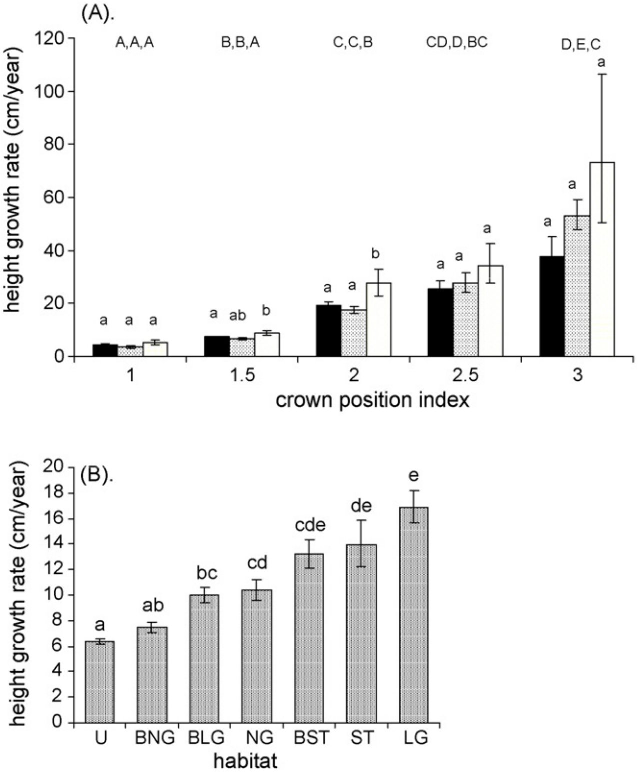

Fig. 5. Height growth rates (mean ± S.E.) of seedlings, saplings and poles of 23 species of commercial trees. (A) Height growth per guild and crown position (CPI; samples sizes per group ranged from 14 to 798). Different capital letters represent significant ($p < 0.05$) differences among CPI for the same ecological guild. Black bars, shade tolerant; shaded bars, partially shade tolerant and open bars, long-lived pioneers. Different small letters represent significant differences among ecological guilds for the same CPI. (B) Height growth per habitat class. U, Undisturbed; BNG, border natural gap; BLG, border logging gap; NG, natural gap; BST, border skid trail; ST, skid trail; LG, logging gap. Bars with different letters are significantly different at $p = 0.05$. Back-transformed data are used.

and silvicultural treatments opened the canopy more, allowing more light to reach the regeneration.

4.1. Silvicultural treatments affect plant densities and growth rates

The low initial densities of seedlings 3–6 months after timber harvesting are probably due to logging damage (Parren and Bongers, 2001; Jackson et al., 2002; Krueger, 2004; Fig. 1 B). By 3 years post-treatment, these differences disappeared because, although seedling densities declined in all areas over the 3-year observation period, they declined more rapidly in the control than in the treated plots. Although we have no data to explain this overall decline in seedling densities, precipitation during the rainy season 2001–2002 was higher than average whereas it was lower than average during the following rainy seasons (2002–2003 and 2003–2004). Due to their relatively low root:shoot ratios (Veneklaas and Poorter, 1998) and the greater belowground competition, control plot seedlings may have suffered more from this drought than those in the treated plots.

Growth of seedlings, saplings and poles generally increased with the intensity of silvicultural treatments (Fig. 3). Similar results have been observed in other studies (Ter Steege et al., 1996; Panfil and Gullison, 1998; Arets, 2005). For example, Ter Steege et al. (1996) showed that annual height increments of saplings in Guyana were two to three times higher in logged and treated plots than in logged and untreated or control forests. In regards to seedling densities, most studies have found more regeneration in logged plots (e.g., Silva et al., 1995; Chapman and Chapman, 1997; Sist and Nguyen-Thé, 2002; Arets et al., 2003), but the opposite has been observed as well (Panfil and Gullison, 1998; Schwarz and Caro, 2003). Surprisingly enough there are few studies examining the effect of different levels of harvest intervention on seedlings and saplings, as most of the studies focus on trees > 10 cm DBH (e.g., Silva et al., 1995; Sist et al., 1998; Finegan and Camacho, 1999; Finegan et al., 1999; Graaf et al., 1999; Sist and Nguyen-Thé, 2002), and it is consequently difficult to compare our results with other studies.

4.2. Ecological guilds differ in their responses to silvicultural interventions

Densities of long-lived pioneers increased with the intensity of logging and silvicultural treatments (Fig. 2). This response was also observed after logging in Guyana (Arets et al., 2003; Rose, 2000) and Surinam (Graaf et al., 1999). Long-lived pioneers also grew faster than either shade-tolerant species or partially shade-tolerant species (Fig. 4), as was reported by Arets et al. (2003) for a forest in Guyana. The high growth rates observed are presumably related to the low wood densities of these species, as suggested by studies done in Surinam (Ter Steege et al., 2003) and Malasia (Verburg and van Eijk-Bos, 2003).

4.3. Environmental and tree characteristics that affect growth

As expected, growth rates increased with increasing intensity of silvicultural interventions. Multiple regression analysis suggests that this effect is mostly due to increasing light after treatment application (Table 4). The intensive silviculture treatment had the highest logging intensity and consequently more logging gaps (Table 5), in addition to gaps created by trees that were girdled to liberate future crop trees and to refine the stand (Table 1). Consequently, there were higher light conditions, which resulted in higher individual CPIs. As CPI was the major factor influencing growth rates (explaining 25.8% of variation; Table 4), growth rates were highest in the intensive silviculture treatment plots, especially among long-lived pioneers that grew two times faster than the shade tolerant and partially shade-tolerant species (Fig. 4). This result is largely a reflection of between guild habitat differences, as long-lived pioneers were more abundant in the high intensity treatments, and had, on average, higher CPIs (data not shown). Growth differences were more modest when compared among trees with similar CPIs, but the long-lived pioneers still showed a stronger response to an increase in CPI

Table 5
Numbers of trees and volumes harvested 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. The sum of area in logging gaps and area in skid trails gives the total area disturbed during logging operations

Block	Treatment	Trees harvested (number ha^{-1})	Volume harvested (m^3 ha^{-1})	Post-logging basal area (m^2 ha^{-1})	Area in logging gaps (%)	Area in skid trails (%)	Bulk density at skid trails[a] (g cm^{-3})
1	Control	0	0	17.0	0	0	na
	Normal	1.1	4	17.0	2.4	3.0	1.12 ± 0.05
	Light silviculture	1.1	5	17.4	3.2	2.6	1.14 ± 0.02
	Intensive silviculture	3.3	13	17.8	7.5	4.3	1.12 ± 0.03
2	Control	0	0	19.5	0	0	na
	Normal	3.3	17	17.9	9.3	4.9	1.17 ± 0.04
	Light silviculture	2.8	12	18.5	6.6	4.6	1.15 ± 0.03
	Intensive silviculture	4.9	16	17.1	10.2	5.2	1.24 ± 0.01
3	Control	0	0	22.2	0	0	na
	Normal	2.5	11	19.5	7.1	5.0	1.02 ± 0.04
	Light silviculture	2.4	10	16.5	6.1	4.5	1.06 ± 0.02
	Intensive silviculture	3.9	15	17.6	9.2	5.8	1.08 ± 0.02

[a] Bulk density (mean ± 1S.E.) was obtained by collecting soil samples (range from 26 to 83 samples per treatment per block) distributed along skid trails opened during logging operations. The bulk density in undisturbed forest is 1.01 ± 0.02 g cm^{-3} (based on 34 samples). Treatments do not differ in terms of bulk density (ANOVA, $F_{2;6} = 0.39$, $p = 0.69$). Data from Ohlson-Kiehn et al. (2003).

than the other two ecological guilds (Fig. 5A). In the multiple regression analysis in which the effects of both treatments and CPIs were taken into account, ecological guild explained only 0.3% of the variation in growth rate (Table 4). The effects of habitat and CPI on growth rate were very similar (Fig. 5A and B) presumably because they both reflect differences in canopy openness. Plants growing in logging gaps had the highest growth rates, probably due to the higher level light levels (Gullison et al., 1996; Johns et al., 1996; Dickinson et al., 2000). Differences in growth rates among treatments can also be partially explained by microsites; 14.1% of the canopy of the intensive silviculture treatment plots was opened by logging whereas less opening occurred in the normal treatment plots (10.6%) and light silviculture treatment plots (9.2%; Table 5). The negative effect of soil compaction on density and growth rates reported in other studies (e.g., Malmer and Grip, 1990; Jusoff and Majid, 1992; Pinard et al., 1996, 2000), was not observed in La Chonta, perhaps because dry season logging resulted in little soil compaction. Neither soil compaction nor area in skid trails vary among logged treatments (Table 5; Ohlson-Kiehn et al., 2003).

There were many severely suppressed individuals in the control plots, mostly of shade-tolerant species, with zero or negative growth rates. The same pattern was found at La Selva, Costa Rica, where 12–37% of individuals <10 cm DBH had negative or zero annual increments (Clark and Clark, 2001). Small individuals of shade-tolerant species can survive long periods of suppression without growth, suffer heavy physical damage, and yet recover, but the long-term data needed to assess this behavior is not yet available from the LTSRP plots.

We were surprised to find so little effect of liana infestations on growth rates of seedlings, saplings and trees <10 cm DBH. One explanation for this finding is that relatively few of these small trees were infested, and few of those that were carried heavy loads of lianas.

4.4. Management recommendations

Of the four treatments applied in La Chonta, the intensive silviculture treatment had the greatest effects on density and growth, with a positive effect on long-lived pioneers, but a slight but non-significant negative one on shade tolerant and partially shade-tolerant species. Before favoring a group of silvicultural treatments, it is obviously necessary to seriously consider the ecological requirements of the species for which the forest is being managed (Fredericksen et al., 2003). In La Chonta, more than half of the commercial species are long-lived pioneer species. Based on the results of this study, the regeneration of these species would benefit from the higher light levels created by doubling the intensity of logging and the application of additional silvicultural practices (girdling of non-commercial trees and liana cutting). If the commercial species being harvested in La Chonta were mainly shade tolerant, this treatment would not be appropriate for enhancing their regeneration. Unfortunately for the forest managers, the species with the most abundant regeneration, *Pseudolmedia laevis* and *Ampelocera ruzii* (both shade-tolerant species), are the lowest valued species, but this might change in the future with market conditions. Additionally if all commercial species would be harvested with the same intensity in La Chonta, it would be necessary to apply a combination of treatments that enhance the regeneration of the full range of species being managed, and not only just species belonging to certain guild. In that case the application of silvicultural treatments would need to account for spatial variability of the species belonging to the different ecological guilds.

A disadvantage of the intensive silviculture treatment is that it leads to large areas under gap, which in our study area are likely to be invaded by lianas, non-commercial tree species and plants belonging to other life forms (e.g., herbs; Park et al., 2005; Felton et al., 2006). Several studies have shown that lianas suppress tree regeneration (Fox, 1976; Buschbacher, 1990; Mostacedo et al., 1998; Fredericksen and Mostacedo, 2000; Schnitzer and Bongers, 2002). Therefore, it may be recommendable to apply post-harvest vine control in gaps (Appanah and Putz, 1984; Vidal et al., 1997) through chemical and mechanical weed control (Pariona et al., 2003) or prescribed burning (Vidal et al., 1997; Gerwing, 2001; Heuberger et al., 2002). These treatments are however expensive. Avoiding lianas proliferation in gaps by more intensive pre-felling liana cutting would be less expensive, but studies conducted in La Chonta have contradictory results about the effectiveness of such treatment (Alvira et al., 2004; Terceros-Gamarra, 2005; Felton et al., 2006). Promisingly, regeneration of long-lived pioneers was enhanced after a recent fire in the area, as was observed in other Bolivian forests (Gould et al., 2002; Heuberger et al., 2002; Kennard and Putz, 2005). Also, mechanical scarification of the surface soil in logging gaps is a cost-effective way to control lianas and other weeds while stimulating regeneration of commercial tree species (M. Peña-Claros, unpublished data). All these treatments, however, increase the costs of forest management.

Decisions about which silvicultural treatments to apply, obviously should be based on understanding of their effects on regeneration in particular and the forest in general. This understanding only grows with continued observations at the same site over long periods of time. For example, although we showed that disturbance promoted increases in the densities and growth rates of many commercial tree species, as found in other studies (e.g., Ter Steege et al., 2003; Arets et al., 2003), the opposite results have also been observed in other tropical forests such as the dipterocarp forests of Malaysia (Pinard et al., 1996) and Indonesia (van Gardingen et al., 1998). Logging impacts on regeneration of commercial tree species thus varies with region and with species. In our forest, for example, regeneration of *Cariniana* spp., *Aspidosperma* spp. and *Caesalpinia pluviosa* only occurs during mast years that occur at 2–4 year intervals (Justiniano and Fredericksen, 2000), while *Cedrela* spp. and *Ficus glabrata* only regenerate in areas with exposed mineral soil (Fredericksen and Pariona, 2002). Species ecological requirements for regeneration generally vary even within the same forests, but need to be taken into account when making forest-specific or even stand-specific silvicultural plans (Fredericksen et al., 2003; Pinard et al., 1999).

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