Effects of soil scarification on the regeneration of commercial tree species in the moist tropical forest of La Chonta, Santa Cruz, Bolivia

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ABSTRACT

Silvicultural treatments application has been shown to be a practical tool to deal with the lack of regeneration of many commercial timber species in the tropics. In this study, the effect of soil scarification treatment was evaluated in the response of 25 commercial tree species in terms of density and growth rates (15 long-lived pioneers, eight partially shade-tolerant and two shade-tolerant species). Changes in environmental conditions related to treatment application were also addressed per plot: biotic factors as vegetation cover (lianas and herbs) and abiotic factors (litter, woody debris, light and compaction). The study was carried out in a moist tropical forest in Bolivia along nine 27 ha plots monitored for six years. Plots were established in three blocks belonging to different harvesting compartments and received one of three different treatments where logging and additional silvicultural treatments were varied: "normal" a normal logging intensity treatment; "light silviculture" treatment with normal logging and low intensity silvicultural practices and "intensive silviculture" with double harvesting intensity and additional silvicultural practices. Soil scarification was applied only in the last treatment. A total of 180 parcels of 25 m^2 were established in each of the plots: 90 in intensive silviculture treatment receiving soil scarification application and 90 in normal and low-silviculture treatment (45 in each) without soil scarification application. This study compared the effects of soil scarification in logging gaps. We took plots in normal and light silviculture treatments together as "non-scarified plots treatment" because we assumed no differences between both treatments in the scarification parcels. Plots established in intensive silviculture treatment were taken as "scarified plots treatment". Five census measurements were done during the six years monitored: 0, 4, 12, 27 and 71 months after treatment application.

Herbs and lianas cover increased in scarified and decreased in non-scarified plots along the first four measurements but after six years herb cover had significantly increased in non-scarified plots while lianas were significantly lower in scarified plots. Litter and woody debris increased with time in scarified and decreased in non-scarified plots. There was an effect of treatment after plot establishment but after six years differences between treatments had disappeared. Light availability decreased in both treatments through time and there was an effect of the treatment only in the last measure where light availability significantly increased in scarified plots. Compaction was significantly higher after six months treatment application in scarified plots. There was a positive effect of the treatment in total density of commercial species through time. Density regeneration was significantly higher in scarified plots in all the censuses and it was about double in scarified plots even after six years. Responses to soil scarification treatment varied between functional group, being the long-lived pioneer species the most benefited by the treatment application in comparison with partially shade-tolerant and shade-tolerant species. Total growth rates were significantly higher for long-lived pioneers than for the other functional groups and there was a negative effect of the treatment for shade-tolerant species. Long-lived pioneer regeneration after six years had a negative correlation with initial vegetation and litter cover while only a slight relation was found between initial light conditions and shade-tolerant regeneration density after six years. The results showed that environmental conditions created by soil scarification enhance regeneration and establishment of commercial species although we cannot assure that growth rates were improved.

1. INTRODUCTION

1.1. Problem statement and justification

The successful establishment of commercially valuable tree species is crucial to the successful long-term management of tropical forests (Park et al., 2005). In managed tropical forest in Bolivia, the regeneration of commercial tree species is sparse (Mostacedo and Fredericksen, 1999; Pariona and Fredericksen, 2003). Knowledge about seed dispersal and the conditions needed for successful regeneration is fragmentary or non-existent for many Bolivian commercial tree species (Mostacedo and Fredericksen, 1999). Therefore, further study of short- and long- term regeneration dynamics is needed, particularly with respect to the response of commercial tree species to environmental conditions in logging gaps (Park et al., 2005).

In 1996 a new forestry law was enacted in Bolivia to promote sustainable forest management (Mostacedo and Fredericksen, 1999). After the 1996 Forest Law substantial advances were made in forest management and Bolivia became a model for the certification of managed natural tropical forests (Nittler and Nash, 1999). This law includes, among others measures, the requirement of the use of reduced-impact techniques to control logging damage during forests operations (Fredericksen et al., 2003), as well as the stipulation of a minimum cutting cycle of 20 years (Dauber et al., 2005). The law is, however, very general regarding the use of silvicultural treatments for improving commercial tree growth and for promoting the regeneration of commercial species. Nevertheless recent studies have demonstrated the benefits of the application of silvicultural treatments to improve regeneration, tree growth and maintain stand quality (Fredericksen, 2000[a]; Peña-Claros et al., 2008[a]; Peña-Claros et al., 2008[b]). It seems clear, then, that forest managers are directly responsible for the creation of conditions that will influence the regeneration of silviculturally important tree species (Lindenmayer and Franklin, 2002).

Several silvicultural treatments can be applied to promote regeneration of commercial tree species. In Bolivia some of these practices have included prescribed fire (Pinard et al., 1998; Heuberger et al., 2002; Kennard et al., 2002), chemical and mechanical weed control (Pariona and Fredericksen, 2000; Heuberger et al., 2001) and other timber stand improvements (Olson-Kiehn et al., 2006). Some of these methods, however, have been proved to be only partially effective in providing adequate commercial tree regeneration and in most of the cases they are too costly. One alternative and economic method to deal with the lack of commercial regeneration in the tropics is soil scarification due to the low application cost that it requires. Various studies have observed improved recruitment of seedlings and saplings in areas where soil scarification has been applied by logging equipment (Fredericksen et al., 1999; Fredericksen and Mostacedo, 2000; Pariona and Fredericksen, 2000). The idea of this treatment originated from field observations and studies showing that commercial species were more abundant in areas disturbed during logging (such as skid trail, disturbed areas by machinery in logging gaps and log-decks) (Fredericksen and Mostacedo, 2000; Pariona and Fredericksen 2000, 2002). Similar results have been reported in other tropical forests (Snook, 1996; Guarigata and Dupuy, 1997; Dickinson and Whigham, 1999; Dickinson et al., 2000).

The present study is an experiment integrated within the Long-term Silvicultural Research Program (LTSRP). The LTSRP is an experiment being carried out at operational scale by the Instituto Boliviano de Investigación Forestal (IBIF) to assess the effect of silvicultural treatments in different forest types in Bolivia. The experiment consists of a network of large-scale (20-27 ha) replicated plots where four different levels of silvicultural treatments have been applied, ranging from no intervention to high-intensity logging combined with additional silvicultural treatments (Peña-Claros et al., 2008[b]). One of the additional silvicultural treatments being evaluated in the LTSRP plots is soil scarification. The LTSRP is currently being developed in the three most representative forest types of the country where the major timber production occurs. The focus of this research is only on the effect of soil scarification on the regeneration of 25 commercial tree species in a moist forest site (La Chonta forestry concession)

1.2. Theoretical framework

1.2.1. Species regeneration guilds

Whithin a given forest species vary in their light requirements for seed germination (e.g. Vázquez-Yanes 1974; Vázquez-Yanes and Smith 1982), seedling establishment (e.g Riera,1985; Nunez-Farfan and Dirzo 1988) and sapling growth and survival (Brokaw, 1987; Van der Meer et al., 1998). These differences have been considered when classifying species into a few ecological guilds. Based on similarities in regeneration requirements, four regeneration guilds can be defined (Finegan, 1996): short-lived pioneer species that have high light requirements for regeneration and live less than 30 years, long-lived pioneer species that have high light requirements for regeneration and live longer than 30 years, partially shade-tolerant species that can establish in the shade but need a gap to grow to larger sizes and shade-tolerant species that can establish and survive in the shade. This grouping is an effective way to analyze species in tropical forests because facilitates data analysis and helps overcoming the problem of low densities of tropical tree species and erratic regeneration.

Tree species belonging to different ecological guilds differ in their ability to capture, use and conserve limiting resources, which affects their ability to compete successfully with other plants (Poorter et al., 2005). In general terms, light-demanding species would have a competitive advantage for regeneration under high irradiance conditions (Poorter et al., 2005) where root competition is reduced (Brokaw, 1985) and rapidly can reach the resources. Shade-tolerant species would have a competitive advantage under moist and shaded conditions because they maximize their persistence in the low-resource environment of the forest understorey (Poorter et al., 2005).

Pioneer species are normally better adapted to worse conditions in the soil, like lack of water and nutrients (Poorter et al., 2005). Higher photosynthetic capacity and higher net assimilation rates at higher irradiance (Poorter et al., 2005), as well as faster responses to changes in the light environment (Popma and Bongers, 1991; Ackerly, 1997) make pioneer species better competitors in gaps than shade-tolerant species. Pioneers are also more effective to capture water because they have a greater total root length than shade-tolerant (Huante et al., 1992; Tyree et al., 1998). This characteristic allows them to explore a larger soil volume for water and nutrients and to monopolize growth in gaps. First year's seedlings of pioneer species may suffer less from dry-season drought than shade-tolerant species because of the faster growth rates of pioneers (Poorter et al., 2005). These characteristics allow long-lived pioneer species to outgrow the shade-tolerant species at both low and high irradiance. The higher growth rates of the pioneer species in the understorey enable them to reach a size advantage before the canopy of the stand is closed. However, mortality rate is also higher for pioneer than for shade-tolerant species because pioneers are more attractive to herbivores and more susceptible to pathogens (Coley, 1983; Kitajima, 1996) and physical damages.

Given the size-asymmetric nature of competition for light, it is likely that long-lived pioneer species will be the first to establish (Weiner, 1990). In the long term pioneer species tend to lose importance as new seeds of later successional species arrive. Shade-tolerant species then depend on long-term persistence for long-term competitive success (Poorter et al., 2005). Therefore, shade-tolerant species will probably regenerate after the conditions of the gap have been modified by pioneer species and become better for them.

1.2.2. Natural regeneration in logging gaps in tropical forests.

Disturbance is fundamental to the development, structure and composition of forest ecosystems (Attiwill, 1994). The opening of the forests results in a variation of light availability that leads to a variation in other physical and biotic environmental factors, such as temperature, soil moisture, herbivore abundance and activity of pathogens (Molofsky and Augspurger, 1992). The larger the canopy gap is, the more the microclimatic conditions are changed. The new created conditions will favor some species over others (Denslow, 1980). Since light is the most limiting resource in many humid tropical forests (Whitmore, 1996), successful seedling establishment in gaps depends on species-specific responses to the factors linked to the light environment (Swaine and Whitmore, 1988; Kitajima, 1996; Dalling and Hubbell, 2002).

Timber extraction strongly affects the forest environment and thus tree regeneration (Guariguata and Pinard, 1998). Logging tends to create larger and more gaps than natural tree fall does (Fredericksen and Mostacedo, 2000). Logging gaps, therefore, receive more sunlight and experience higher evapotranspiration rates than natural tree falls. Disturbance by logging machinery also differentiates logging from natural gaps. Disturbed soils are rare in unlogged tropical forests (Dickinson et al., 2000) but in logged forests skidders cause direct soil disturbance in and around gaps.

The higher levels of light availability and soil disturbance created by logging provide a competitive advantage to high-light demanding and fast-growing species (Brown, 1998). In many cases these species are vines and other fast growing species that suppress the regeneration of commercially more valuable species (Fredericksen and Mostacedo, 2000). However, various studies have also found higher commercial regeneration density in areas that had been unintentionally scarified by logging machinery compared to areas unaffected by skidder traffic (Fredericksen et al., 1999; Fredericksen and Mostacedo, 2000; Pariona and Fredericksen, 2000).

Apart of light and soil disturbance many other factors influence the success of commercial tree regeneration in managed tropical forests. The reduced abundance of seed trees after logging may limit seed supply (Fredericksen and Licona, 2000). Large logging gaps may favor wind-dispersed, shade-intolerant pioneers at the expense of shade-tolerant timber trees that have a competitive advantage in smaller gaps (Denslow, 1987; Bazzaz, 1991). Seed-dispersing birds or mammals may also avoid entering large logging gaps, restricting regeneration opportunities for animal-dispersed species (Schupp et al., 1989).

Over time, the changing character of logged forests may affect the relative regeneration success of trees with different dispersal characteristics and degrees of shade tolerance (Denslow, 1980; Whitmore, 1996). To secure future regeneration of commercial species it is important to understand the response of commercial tree species to changes in microhabitats caused by logging.

1.2.3. Soil scarification

Soil scarification is defined as a method of seedbed preparation that consists of removing with a skidder blade the first layer of the forest floor and woody debris resulting from the logging operation. It is applied right after the log has been removed by the skidder and usually takes 3–5 min to carry out per gap (M. Peña-Claros, unpublished data). The objective of soil scarification is to liberate gaps from obstacles such as litter and woody debris that may obstruct germination and establishment of commercial seedlings, and remove vegetation that could compete with tree regeneration, such as herbs and lianas. Logging gaps have to fulfill three conditions to receive this treatment: no slope, no advanced regeneration of commercial species and presence of seed trees around.

Litter cover in gaps has been proved to be an obstacle for seed germination and seedling establishment and survival, either if seeds are situated under or above the litter (Schiotz et al., 2006). The effects are particularly negative for those species with small seed size because these species depend for establishment on areas where roots easily get soil contact (Coomes and Grubb, 2003). A study carried out in La Chonta to evaluate the factors influencing regeneration of *Terminalia oblonga* (Schiotz et al., 2006) suggested that soil disturbance and a thin litter layer favored seedling emergence. Another study carried out in Barro Colorado showed that litter removal increased seedling emergence almost three-fold over control plots whereas litter addition reduced seedling emergence almost by half (Mofolsky and Augspurger, 1992).

Lianas generally increase in density after natural and anthropogenic forest disturbance (Hegarty and Caballe, 1991) and thrive in unmanaged timber operations (Pinard and Putz, 1994). The high degree of phenotypic plasticity both in space and time and the capacity to recruit from a variety of sources gives lianas the potential to respond rapidly to dynamic light conditions (Avalos and Mulkey, 1999). Many liana species are capable of producing roots and shoots that can form liana tangles that dominate the vegetation in logging gaps (Appanah and Putz, 1984) and then suppress commercial tree regeneration. Additionally herbs and other non-commercial species are common invaders of areas characterized by high solar radiation (Rundel et al., 1998) and thus compete with commercial regeneration.

Scarification has been proved to increase the germination and survival of tree species relative to areas without scarification (Fredericksen and Pariona, 2002) because it provides commercial species enough light to grow and replace short-lived pioneers in recovering gaps. In La Chonta, most of commercial species require substantial competition reduction for their establishment (Kennard, 1999; Perez-Salicrup, 2001). The association between disturbance processes and the resulting plant community (Denslow, 1980) is of direct relevance to forest managers trying to ensure that selective logging is ecologically and silviculturally sustainable (Lindenmayer and Franklin, 2002). Therefore, it is important to understand the responses of commercial species in terms of regeneration in scarified gaps.

1.3. Objectives

The general objective of the study is to assess the regeneration response of commercial tree species to the application of soil scarification treatment over time.

The specific objectives are:

1. To evaluate the differences in environmental factors (biotic or abiotic) between scarified and non-scarified gaps over time;
2. To determine the effect of treatment application on density and growth rates of commercial species;
3. To determine which abiotic and biotic factors influence the most the regeneration density of commercial species after six years.

1.4. Research questions

The questions to be addressed in this study to reach the objective are listed below with their corresponding hypothesis.

Regarding changes in abiotic and biotic factors due to soil scarification:

1- What are the differences in herb and liana cover, litter and woody debris between scarified and non-scarified logging gaps over time?
Hypothesis: Scarified gaps will have less litter, less woody debris and less herb and liana cover than non-scarified plots right after treatment application but after six years differences between treatments will have disappeared.

2- What are the effects of soil scarification on light availability in the gap right after treatment application and 6 years later?
Hypothesis: Light availability will not differ between scarified and non-scarified gaps right after treatment application nor after six years of treatment application.

3- What is the effect of soil scarification on soil compaction 6 years after treatment application?
Hypothesis: Soil compaction will be higher in scarified than in non-scarified gaps after six years of treatment application.

Regarding plant responses to soil scarification:

4- How does soil scarification affect the density over time of commercial species? This question will be addressed at three different levels; for all species together and per functional groups.
Hypothesis 1: Total density of commercial species will be higher in scarified than in non-scarified gaps over time.
Hypothesis 2: Responses to treatment will vary between functional groups in terms of density. Long-lived pioneer species are expected to benefit more from the treatment than partially shade-tolerant and shade-tolerant species. Mortality rates are expected to be higher for long-lived pioneer species than for the other functional groups.
Hypothesis 3: Responses to soil scarification will vary between species.

5- How does soil scarification affect the growth rate of commercial species? This question will be addressed at three different levels; for all species together, per functional groups and per individual species.
Hypothesis 1: Total growth rates of commercial species will be higher in scarified than in non-scarified gaps.
Hypothesis 2: Growth rates of all functional groups will be faster in scarified than in non-scarified logging gaps. Long-lived pioneers will have the highest and shade-tolerant the lowest growth rates.
Hypothesis 3: The effect of soil scarification on growth rate will vary at individual species level.

Regarding to the environmental factors influencing the most the density after six years:

6- What ecological factor explains the most variance in commercial species density between scarified and non-scarified logging gaps after six years of treatment application?
Hypothesis: Variation in density among gaps is mainly explained by the conditions created just after treatment application.

2. METHODS

2.1. Study area

The present study was carried out in the forestry concession La Chonta, managed by La Chonta Agroindustria Forestal. It is located 30 km east of Ascensión de Guarayos town, in Santa Cruz department, Bolivia (15º47'S, 62º55'W). A map of the study area location is provided in ANNEX 1. This lowland semi-deciduous tropical moist forest is transitional between Chiquitano dry forest in the South and Amazonian wet forests in the North (Dauber et al., 2000), and it contains species characteristic of both kinds of forests (Park et al., 2005). Mean annual temperature is 24.5 ºC and annual precipitation averages

1580 mm (Pinard et al., 1999), with five dry months receiving <100 mm, from May to September (Peña-Claros et al., 2008[a]). The altitude varies from 230 to 390 masl (Felton et al., 2006).The forest is in gently rolling terrain where the dominant soils are oxisols, ultisols and inceptisols (Park et al., 2005).

Approximately 160 species >10 cm dbh (diameter at breast height) have been identified in La Chonta, 25 of which are considered to have commercial value and 8-10 of which are currently being harvested. Mean harvested volumes averages 6 m^3 ha^{-1} per year (Peña-Claros et al., 2008[a]). The cutting cycle is 30 years. The company's management has the Forest Stewardship Council (FSC) certification since 1998. Fires are frequent in the area, most of them occurring during the dry season. In 1995 and 2004 about 30% of the concession was burned (Peña-Claros et al., 2008[a]).

2.2. Materials and Methodology

2.2.1. Study design

The Long-Term Silvicultural Research Program (LTSRP) have established three blocks of experimental plots in La Chonta, each located in different harvesting compartments. The company harvested the compartments right after plot establishment between 2001 (blocks 1 and 2) and 2002 (block 3). Each block is composed by four 27 ha plots, randomly assigned, each of them receiving one of four different treatments. These treatments were: "control" a non-harvested plot; "normal" a normal logging intensity treatment plot; "light silviculture" a normal logging and low intensity silvicultural practices treatment plot and "intensive silviculture" a double harvesting intensity and additional silvicultural practices treatment plot (Table 1). All plots in each block were selected in areas with similar harvestable tree densities, vegetation type and topography. Harvesting intensity varied on average from 2.1 trees ha^{-1} in the normal and light silviculture treatment plots to 4.0 trees ha^{-1} in the intensive silvicultural treatment plots, which resulted respectively in 9.2 to 14.1 % of the area being disturbed by logging gaps or skid trails (Mostacedo et al., 2006). The main additional silvicultural treatments applied in each treatment are explained in Table 1.
Soil scarification was applied during logging operations only in the intensive silviculture treatment plots. Logging gaps selected for the application of the treatment in the intensive silviculture treatment plot had to fulfil the following requirements: no advance regeneration present in the area, flat terrain and presence of seed trees in the surrounding area. Logging gaps selected in this study in the normal and light silviculture treatment plots had also to fulfil the same requirement but they were not scarified. The easiness of treatment application was also evaluated beforehand as the treatment should be applied in 2 – 4 minutes to reduce costs. The average time used for treatment application was 3 minutes per 100 m^2 (Peña-Claros, personal observations).

Table 1. Treatments applied to the LTSRP plots in La Chonta forest concession, Bolivia. (X) Management practice applied, (XX) 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 commercial trees	x	x	x	x
-Lianas cut on harvestable trees 6 months before logging		x	x	x
-Skid trial planning		x	x	x
-Retention of 20% commercial trees as seed trees		x	x	x
-Directional felling		x	x	x
-Merchantable trees harvested according to their minimum cutting diameter (50-70 cm in DBH)		x	x	xx
-Pre-harvest marking of future crop trees (FCTs) > 10 cm in DBH			x	xx
-Lianas cut in FCTs 2-5 months before logging			x	xx
-Post-harvest liberation of FCTs from overtopping non-commercial trees by girdling			x	xx
-Soil scarification in felling gaps during logging				x
-Post-harvest girdling of non-commercial trees > 40 cm DBH.				x

For this study, 30 scarified logging gaps were selected in each block in the intensive silviculture plots, making a total of 90 gaps. Additionally 90 non-scarified logging gaps were also selected in the normal and light silviculture plots (15 per treatment and per block). In each selected gap a 5 x 5 m plot was established right after logging (180 plots in total, covering 0.45 ha). Control treatment plot was excluded from the study because the objective was to analyze the effects of soil scarification application only in logging gaps. Plots in normal and light silviculture treatment were considered together as “non-scarified plots treatment” in this study because we assumed no differences between both treatments in scarification parcels. In summary, two different treatments are considered in this study to make comparisons: “non-scarified plots”, in the normal and low light silviculture treatments and “scarified plots” in the intensive silvicultural treatment. The plots in the two treatments considered in this study had no other differences apart of the soil scarification application. A schematic view of the design is provided in ANNEX 2.

Plots were evaluated as average 0, 4, 12 (range between plots 10-14), 27 (range 25-28) and 71 (range 69-72) months after treatment application. The last measurements in blocks 1 and 2 were done in 2007 by IBIF researchers. For this study the plots established in block 3 were re-measured in 2008 (6 years after treatment application).

2.2.2. Data collection

Commercial species have been classified in different groups depending on their regeneration strategy. The following classification have been done for the 25 commercial species being considered by the company: 2 of them are shade-tolerant, 8 are partially shade-tolerant and 15 are long-lived pioneers (based on Justiniano et al., 2004; Poorter et al., 2006). A table of the 25 commercial species studied and the classification of them according to their ecological guild and seed dispersal is provided in Table 2.

Table 2. Characteristics of commercial tree species sampled at La Chonta, Bolivia. Functional group: LLP, long-lived pioneer; PST, partial shade-tolerant; ST, shade tolerant. MCD; minimum cutting diameter. Seed production: G, good (> 1000 sound seeds / tree); F, fair (200-1000 seeds / tree); P, poor (< 200 seeds / tree). Dispersal mode: W, wind; A, animal; G, gravity, G^c in *H. crepitans*, gravity is aided by explosive dispersal.

Scientific name	Family	Functional group	Commercial value	MDC	Seed production	Dispersal mode
Ampelocera ruizii	*Ulmaceae*	ST	Potential	50	G	A
Aspidosperma cylindrocarpon	*Apocynaceae*	PST	Potential	50	G	W
Caesalpinia pluviosa	*Caesalpiniacae*	LLP	Potential	50	G	G
Calycophyllum spruceanum	*Rubiaceae*	LLP	Potential	50	G	W
Cariniana domestica	*Lecythidaceae*	LLP	Current	50	G	W
Cariniana estrellensis	*Lecythidaceae*	LLP	Current	50	G	W
Cariniana ianeirensis	*Lecythidaceae*	PST	Current	50	G	W
Cedrela fissilis	*Meliaceae*	LLP	Current	50	G	W
Ceiba pentandra	*Bombaceae*	LLP	Potential	50	G	W
Centrolobium microchaete	*Fabaceae*	LLP	Current	50	P	W
Batocarpus amazonicus	*Moraceae*	PST	Potential	50	G	A
Cordia alliodora	*Boraginaceae*	LLP	Current	50	G	W
Ficus boliviana	*Moraceae*	LLP	Current	70	G	A
Gallesia integrifolia	*Phytolaccaceae*	LLP	Potential	50	G	W
Hura crepitants	*Euphorbiaceae*	PST	Current	70	G^c	G
Hymenaea courbaril	*Caesalpiniaceae*	PST	Current	50	F	A
Maclura tinctoria	*Moraceae*	LLP	Current	50	G	A
Pouteria nemorosa	*Sapotaceae*	PST	Current	50	F	A/G
Pseudolmedia laevis	*Moraceae*	ST	Potential	50	GE	G
Pterogyne nitens	*Caesalpiniaceae*	LLP	Potencial	50	F	W
Schizolobium amazonocum	*Caesalpiniaceae*	LLP	Current	50	G	W
Spondias mombin	*Anacardiaceae*	LLP	Current	50	G	A
Sweetia fruticosa	*Fabaceae*	LLP	Potential	50	P	W
Swietenia macrophylla	*Meliaceae*	PST	Current	50	G	W
Tabebuia serratifolia	*Bignoniaceae*	LLP	Current	50	G	W
Terminalia oblonga	*Combretaceae*	PST	Current	50	G	W

The following biotic factors were measured at the plot level during each census in all the blocks: area covered by herbaceous vegetation (in %), area covered by lianas (in %) and height of the 10 tallest individuals (commercial or not) present in the plot. The tallest individuals had their height measured using a fibber glass extension pole (until 13.5 m height), were identified to species and assigned to crown position classes. The area covered by litter (in %) and the area covered by woody debris (in %) were evaluated right after treatment application (block 1 and block 3) and six years after treatment application (block 3).

Average light availability was measured with a densitometer right after treatment application (block 1 and block 3) and 6 years after harvesting (in all blocks). The measurement was done at the centre of each plot in four different positions, which were then averaged to get the canopy openness (in %).

Soil compaction was determined by taking three samples in three points in each plot, one in the centre and two in the extremes using a bore of known volume. A composite sample per plot was created and dried in an oven at 70 ºC for 3 days. Then samples were weighted by using an electronic balance and the volume per weight was calculated. This measurement was done only in blocks 2 and 3 and only after six years of logging.

Individual tree data was collected in all 180 plots, during each of the four censuses. All individuals of each commercial species present in the plot were counted. From those individuals one to three plants were selected and tagged per plot in the first census. All tagged plants had the following variables evaluated each census: status of the plant (alive, dead, disappeared), total height and diameter for plants > 1.5 m tall, crown position index modified after 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) and origin (seed, re-sprout, advanced regeneration). Plants that were newly recruited were also recorded and a proportion of them (maximum of three plants per species and per plot) were also tagged and evaluated as mentioned before.

Height of commercial species that were < 1.5 m tall was measured with a tape measure, while bigger individuals were measured with an extension pole. The height measurement was done from the basis of the tree following the last point of the stem of the plant. The diameter was measured with a caliper for small trees and with a diameter tape for large ones. All data was recorded in three field forms (see ANNEX 3)

2.2.3. Data analysis

The three first research questions deal with the response of the environmental factors to the treatment application. Since variables were not measured in all censuses and for all plots, different analyses have been carried out depending on the available data (Table 3). Arcsine transformation has been applied to all the variables measured in percentage. The normality and the variability of the data were also tested for all variables.

Table 3. Summary of the measurements made for abiotic and biotic factors, including censuses in which these measurements were taken and the analysis carried out for each variable. Censuses are referred to time after treatment application. Sample size refers to the number of plots in which variables were evaluated

Variable	Censuses	Blocks	Sample size	Statistical analyses	Factors
Herbs	0 months 4 months 1 year 4 years 6 years	1,3 2,3 all all all	118 119 162 155 156	Univariate ANOVA	Time Treatment
Lianas	0 months 4 months 1 year 4 years 6 years	1,3 2,3 all all all	118 119 162 155 156	Unvivariate ANOVA	Time Treatment
Litter	0 months 6 years	1,3 3	111 51	Univariate ANOVA	Time Treatment
Woody debris	0 months 6 years	1,3 3	111 52	Univariate ANOVA	Time Treatment
Light	0 months 6 years	1 and 3 all	118 137	Univariate ANOVA	Time Treatment
Soil compaction	6 years	2 and 3	97	Univariate ANOVA	Treatment

Density was averaged per plot at two different levels to address the hypotheses of the fourth research question. Since the data were not normally distributed, a logarithmic transformation was performed (ln (density +1)). To test for the effect of treatment application on total density through time (hypothesis 1), repeated-measures ANOVA were carried out with time as within subject factor and treatment as between subject factor. Additionally similar repeated-measures ANOVA were carried out for each functional group to determine if they responded differently to treatment through time (hypothesis 2). For doing so density was averaged per plot and functional group. Time was considered as within subject factor and treatment and functional group as between subject factor. A Greenhouse-Geisser correction was taken for not normal data. Some plots were unintentionally destroyed during trail maintenance in the 27 ha plots, and therefore, these 5 x 5 m plots were excluded from the analysis, so that a total of 149 plots of the 180 initials were included. Density per species was not analyzed but a table summarizes the relative density abundance as well as a density ratio between the scarified and non-scarified plots in each of the censuses. This information gives an idea of which species regeneration was higher or lower in each of the treatments.

Absolute growth rates were calculated as the slope of the linear regression between height growth data and time (censuses in which height was measured). This way of calculating growth rate was preferred because it provides a better idea of the evolution of the growth during the six years of monitoring and takes also into account the four measurements done during the six years since treatment application. Afterwards an average per plot was taken. During the data analysis it was found that 57% of the plants had reduced in height through time or at a given census due to external factors, like herbivory, drought and mechanical damage. Consequently, growth rates were calculated in two ways. One way included only plants that did not suffer any damage in any of the measurements; this growth rate was called “potential growth”. The other way was by including all the measurements, negative and positive growth rates (taking out measurement mistakes); this growth rate was called “real growth”. The real growth provided lower averages per plot than the potential growth but there were no large differences between both measurements. Consequently, I decided to use the potential growth rate for the rest of the analyses. Since the data was not normally distributed due to the high variability on growth data between species and functional groups, it was ln-transformed (ln (growth +1)). Then growth rate data was analyzed for each species to test for normality of the data. All species presented a normal distribution except *Schizolobium parahyba* and *Terminalia oblonga*

The responses of commercial species to treatment in terms of growth rate have been assessed at three levels. To test for the effect of treatment application on total growth rate of commercial species (hypothesis 5.1) an Univariate ANOVA analysis was done. Treatment was considered as factor. To test the differences on the growth rate per functional group between treatments (hypothesis 5.2) an Univariate ANOVA analysis was also carried out. Treatment and functional group were considered as fixed factors. To test for the influence of the treatment on species growth rates (hypothesis 5.3) an Univariate ANOVA analysis was performed per specie (normally distributed). For those that were not normally distributed, *Schizolobium parahyba* and *Terminalia oblonga*, a non-parametric test was applied. Species having a sample size fewer than 4 cases per treatment were excluded from the analysis. Only 12 species were tested of the initial 25 species for address this hypothesis. Finally, to assess the effect of soil compaction six years after logging on the total growth rate, a linear regression was used taking soil compaction as the independent variable and average growth rate of commercial species as dependent variable. The same regression was also made for each of the three functional groups to test if soil compaction affected growth rates of functional groups differently.

To explore species-environment associations a Principal Component Analysis (PCA) was carried out to summarize all the environmental variables measured at each of the census in two orthogonal components. Secondly multiple forward regression analyses were carried out to evaluate correlations between environmental factors and total density in each of the censuses.

All statistical analyses were made with the software SPSS 15.0. Differences were considered significant at p values < 0.05.

3. RESULTS

3.1. Effect of soil scarification on environmental variables (research questions 1, 2 and 3).

Overall herb cover varied with time and treatment (Table 4). The effect of treatment varied with time (Table 4). Herb cover increased through time in all plots but increased more in the non- scarified than in the scarified plots during the first four years after treatment application (Fig. 1A). However, six years after treatment application total herb cover was higher in scarified than in non-scarified plots (ANOVA for treatment: $F_{1;\,154} = 4.9$; $p = 0.028$). Overall lianas cover also varied with time and treatment (Table 4). Lianas cover increased faster in non-scarified than in scarified plots (Fig. 1B). This difference was still visible even six years after treatment application (ANOVA for treatment: $F_{1;\,154} = 5.3$, $p = 0.02$).

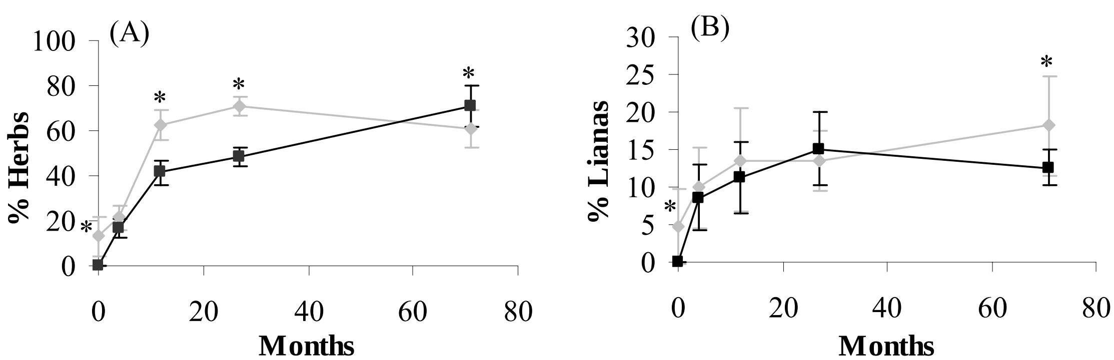

Fig.1. Changes in total herb (A) and liana cover (B) in scarified and non-scarified plots through time in a tropical moist forest, Bolivia. Grey line in the graph represents non-scarified plots and black line scarified plots. Data are back transformed data (mean ± SD). Measurements with * indicate significant differences between treatments at that moment in time.

Table 4: Results of the ANOVA analysis for herb and liana cover evaluated in a tropical moist forest, Bolivia.

Variable	Factors	df	F	p
Herbs	Treatment	1	68.5	< 0.001
	Time	1	233.8	< 0.001
	Treatment x time	1	19.4	< 0.001
Lianas	Treatment	1	16.1	< 0.001
	Time	1	38.3	< 0.001
	Treatment x time	1	5.5	< 0.001

Overall litter cover was higher in non-scarified than in scarified plots (Table 5) but the effect of treatment varied with time (Table 5). Litter cover was significantly reduced in scarified plots at the time of plot establishment but after six years of treatment application differences between treatments had disappeared (Fig. 2A). Similar responses were obtained for overall woody debris cover (Table 5; Fig. 2B). Overall light availability did not vary with treatment (Table 5; Fig. 2C). As time passed light availability decreased in both, scarified and non-scarified plots, so the interaction between treatment and time was not significant (Table 5; Fig. 2C). After six years light availability had decreased significantly faster in non-scarified than in scarified gaps (ANOVA: $F_{1,135} = 7.7$: $p = 0.006$). Finally soil compaction was significantly higher in scarified than in non-scarified plots (Table 5; Fig. 2D).

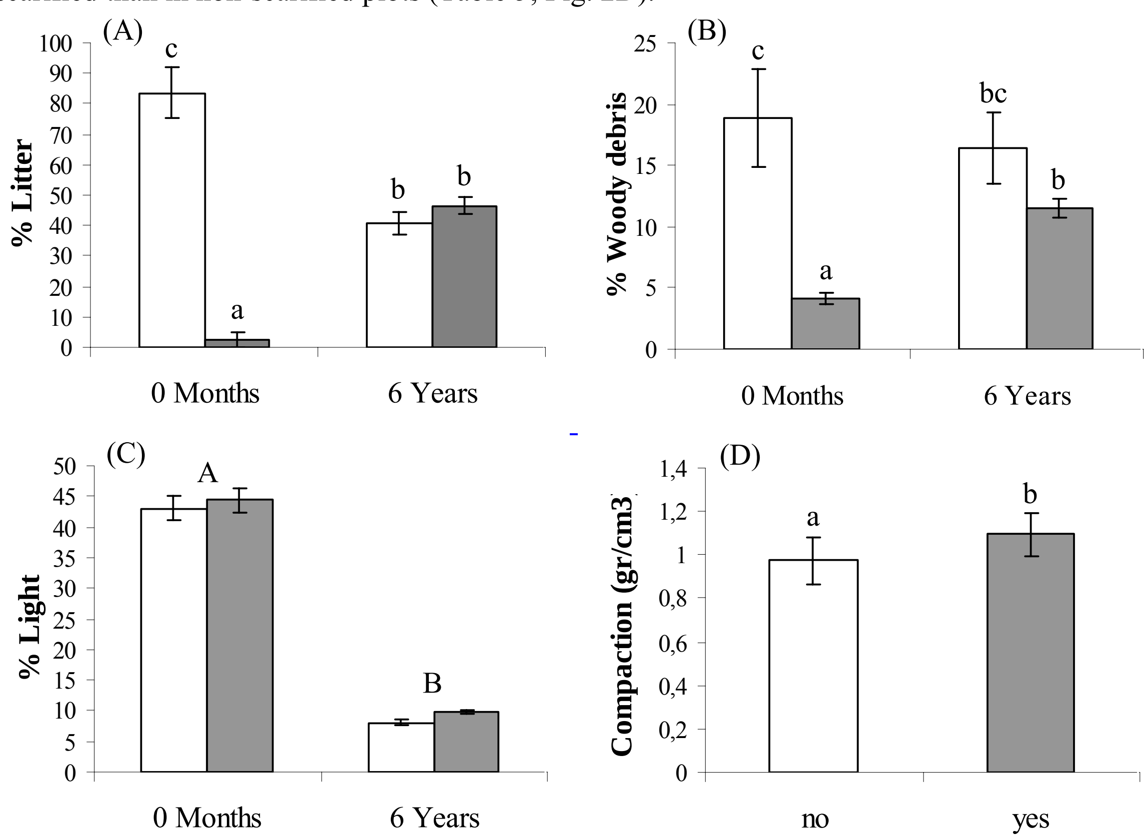

Fig. 2. Differences in total litter cover (A), total woody debris (B) and total light availability (C) per plot between scarified and non-scarified plots evaluated 0 moths and 6 years after treatment application. Differences in total soil compaction (gr cm^{-3}) between treatments after 6 years of treatment application (D). Different capital letters represent significant differences among years after treatment application. Lower case letters represent significant differences

among treatments through time. Data are back transformed data (mean ± SD). Tukey post hoc test for multiple comparisons was used when the interaction between time x treatment was significant.

Table 5: Results of the ANOVA analysis for environmental variables evaluated in a tropical moist forest, Bolivia.

Variable	Factors	df	F	p
Litter	Treatment	1	162.5	< 0.001
	Time	1	3.7	0.057
	Treatment x time	1	204.7	< 0.001
Woody debris	Treatment	1	41.7	< 0.001
	Time	1	4.9	0.028
	Treatment x time	1	12.7	< 0.001
Light	Treatment	1	2.5	ns
	Time	1	949.1	< 0.001
	Treatment x time	1	0.3	ns
Compaction	Treatment	1	32.6	< 0.001

3.2. Effect of soil scarification in the response of commercial species

3.2.1. Effect of soil scarification on density of commercial species regeneration (research question 4)

Total density of commercial species increased through time for the first four years in scarified and non-scarified plots and decreased in the last two years (Table 6; Fig. 3A). Total density varied through time among functional group (Table 6). It was also affected by scarification treatment (Table 6). Total density was significantly higher in scarified than in non-scarified gaps during the whole evaluation period. Even 6 years after treatment application, there was a positive effect of treatment on density in scarified plots that was almost double than in non-scarified plots (Figure 3A).

Table 6: Results of repeated measures ANOVA for total density as dependent variable and time as within factor, treatment and functional group as between factor.

	Factors	df	F	p
Within Subjects Effects	Time	1	22,24	< 0.001
	Time x treatment	1	9,04	0,003
	Time x functional group	2	22,11	< 0.001
	Time x treatment x functional group	2	9,26	< 0.001
Between Subject Effects	Treatment	1	9,34	0,002
	Functional group	2	23,91	< 0.001
	Treatment x functional group	2	10,27	< 0.001

The effect of treatment varied with functional group (Table 6). Long-lived pioneer species density increased through time during the first four years after treatment application in both treatments but increased significantly more in scarified than in non-scarified plots (Fig. 3B). Six years after treatment application long-lived pioneer densities had decreased in both treatments but still was significantly higher in scarified than in non- scarified plots (Table 7; Fig. 3B). Partially shade-tolerant regeneration increased faster in non- scarified than in scarified plots but after six years of treatment application differences in density were not significant between treatments (Table 7; Fig. 3C). Shade-tolerant species density increased faster in non-scarified than in scarified plots the first four years of treatment application. However, after six years shade-tolerant density decreased in non-scarified plots, while highly increased in scarified plots (Table 7; Fig. 3D).

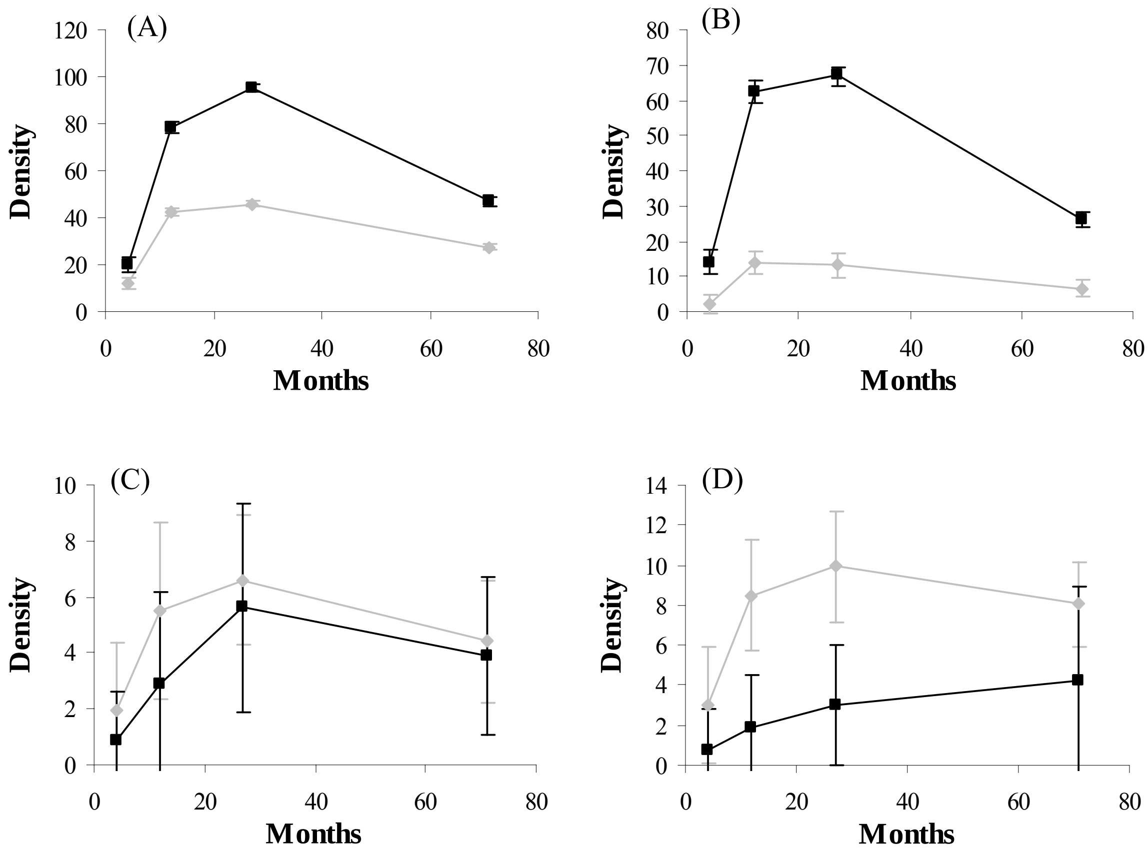

Fig. 3. Changes in density of commercial species through time. Data are back transformed data (mean ± SD). Density is presented in number of individuals per 100 m^2 (A) = total density, (B) = long-lived pioneer species density, (C) = partially shade-tolerant species density and (D) = shade tolerant species density. Black line represents scarified plots and grey line non-scarified plots.

Table 7: Results of repeated measures ANOVA for density per functional group as dependent variable, time as within factor and treatment as between factor. Density is expressed as number of individuals per 100 m^2.

	Within subject factor				Between subject factor	
	Time		Time x treatment		Treatment	
	F	p	F	p	F	p
Density ST	26.9	< 0.001	3.9	0,014	21.6	< 0.001
Density PST	29.8	< 0.001	2.6	ns	3.8	0.052
Density LLP	71.5	< 0.001	1.3	ns	70.2	< 0.001

For tagged individuals, total density of seedlings (< 1.3 m height) dominated the plots in the first years after treatment application while poles (> 1.3 m height) were more abundant between the fourth and sixth year after treatment application (see ANEXX 4).

For tagged individuals, the number of commercial dead stems per plot varied widely. On average, mortality measured in the first year was low for all functional groups but it highly increased for long-lived pioneer species after four years, and increased faster in non-scarified than in scarified plots. After six years long-lived pioneer species accounted for the highest levels of mortality in both treatments, while partially shade-tolerant mortality had the lowest levels. Shade-tolerant mortality increased in scarified plots more than in non-scarified plots in all censuses. In general terms, long-lived pioneer mortality was higher in non-scarified plots. Partially shade-tolerant maintained almost the same levels in both treatments and shade-tolerant mortality had higher levels in scarified than in non-scarified plots (see ANNEX 5).

In general terms the most abundant regeneration species in the plots were *Calycophyllum spruceanum, Gallesia integrifolia, Maclura tinctoria*, mainly in scarified plots, and *Ampelocera ruizii,* mainly in non-scarified plots (Table 8). The least abundant regeneration species were *Pterogyne nintens*, *Hymenaea courbaril, Cedrela fissilis, Caesalpinia pluviosa, Cariniana spp.* and *Swetenia macrophylla.* Most species benefited from the treatment application in terms of density except for *Ampelocera ruizii, Aspidosperma cylindrocarpon, Hura crepitants, Pouteria nemorosa, Cariniana spp.* and *Swetenia macrophylla* which regenerate better in non-scarified plots. *Pseudolmelia laevis* presented more regeneration abundance in non-scarified plots but after six years it had increased six times in scarified than in non-scarified plots. *Terminalia oblonga* regeneration was observed in both treatments.

Table 8. Relative density abundance per species after 4 months (Density 1), 12 months (Density 2), 4 years (Density 3) and 6 years (Density 4) of treatment application. Ratio S/NS is between scarified and non-scarified plots. Values > 1 represent higher densities in scarified plots and values < 1 represent higher densities in non-scarified plots.

	Density 1		Density 2		Density 3		Density 4	
Species	Abundance	S/NS	Abundance	S/NS	Abundance	S/NS	Abundance	S/N
Ampelocera ruizii	9.4	0.1	6.3	0.3	9.1	0.3	10	0.5
Aspidosperma cylindrocarpon	0.3	0.0	0.1	0.0	0.1	0.0	0.2	0
Batocarpus amazonicus	5.5	0.6	2.1	1.2	2.8	0.9	3.2	0.9
Caesalpinia pluviosa	0.0	0.0	0.0	0.0	0.1	2.0	0.3	3
Calycophyllum spruceanum	17.9	117.0	28.8	9.7	17.1	12.6	9.5	16
Cariniana domestica	0.0	0.0	0.1	0.0	0.1	0.0	0.2	0
Cariniana estrellensis	0.6	1.0	0.6	0.9	0.8	0.5	0.5	0.4
Cariniana ianeirensis	0.3	0.0	0.4	0.7	0.3	0.4	0.5	0.3
Cedrela fissilis	0.3	1.0	0.1	2.0	0.1	1.0	0	0
Ceiba pentandra	0.3	0.0	0.6	1.0	0.2	0.3	0.2	1
Centrolobium microchaete	4.8	2.4	1.9	5.9	1.6	16.0	1.3	7
Cordia alliodora	0.3	0.0	0.2	1.5	0.5	2.0	0.5	2.5
Ficus boliviana	2.1	13.0	2.4	1.1	1.4	1.1	0.2	2
Gallesia integrifolia	1.5	0.8	24.5	8.1	30.1	3.8	16.5	3
Hura crepitants	2.1	0.4	0.8	0.4	0.9	0.5	1.9	0.8
Hymenaea courbaril	0.0	0.0	0.0	0.0	0.0	0.0	0.2	1
Maclura tinctoria	12.7	1.8	8.7	2.5	10.4	2.1	12.5	2.9
Pouteria nemorosa	2.7	0.2	1.1	0.2	1.4	0.3	2.1	0.7
Pseudolmedia laevis	10.0	0.8	4.6	0.5	5.4	0.7	29.2	5.7
Pterogyne nitens	0.0	0.0	0.0	0.0	0.1	1.0	0	0
Schizolobium amazonicum	21.2	6.0	5.7	2.4	3.6	2.9	2.2	1.2
Spondias mombin	7.6	8.8	4.2	1.8	5.1	1.0	1.4	1.1
Sweetia fruticosa	0.3	0.0	0.6	1.3	0.3	1.0	0.5	1.5
Swietenia macrophylla	0.3	0.0	0.1	0.0	0.1	0.0	0.2	0
Terminalia oblonga	0.9	0.5	6.0	0.6	8.4	3.4	6.8	2.4
Total	100	2.0	100.0	2.6	100.0	2.1	100	2.5

3.2.2. Effect of soil scarification on the growth of commercial species regeneration (Research question 5).

Overall absolute growth rate was higher in non-scarified plots (20.3 cm year $^{-1}$ on average) than in scarified plots (18.6 cm year $^{-1}$ on average) (ANOVA, $F_{1, 345} = 6.0$; $p = 0.015$). There was a strong effect of the functional group in growth rates (ANOVA, $F_{2, 345} = 37.2$; $p < 0.001$). Long-lived pioneer species had higher overall growth rate than partially shade-tolerant and shade-tolerant species having long-lived pioneer species the highest and shade-tolerant species the lowest growth rates. The combined effect of functional group and treatment was not significant (ANOVA, $F_{2, 345} = 2.7$; $p = 0.064$), which means that each group did not respond differently to treatment.

A separate analysis made per each functional group indicated that the effect of the treatment was only significant for shade-tolerant species (ANOVA, $F_{1,101} = 9.7$; $p = 0.002$).

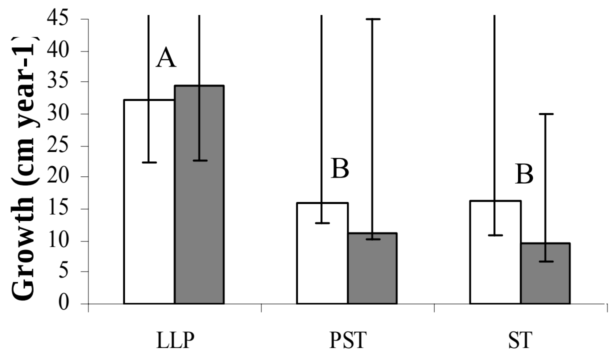

Figure 4. Differences in total growth rate (cm year $^{-1}$) (6 years after post-treatment) of commercial species per functional group. LLP = Long-lived pioneer species, PST = partially shade-tolerant species and ST = shade tolerant species. Data are backtransformed data (mean ± SD). Significant differences in growth rates between treatments are shown with a lower case letter.

Growth rates had great variability among species. The treatment did not have an effect in growth rates of all commercial species except for *Calycophyllum spruceanum*, which presented a significant higher growth rate in scarified than in non-scarified plots. Differences among species growth rate are shown in Tables 9 and 10).

Table 9. Growth rates ratio between scarified and non-scarified plots. Values > 1 represent higher growth rates in scarified plots and values < 1 represent higher growth rates in non-scarified plots. Mann-Whitney U test results of the average growth rate (cm y $^{-1}$) of commercial tree species in two different treatments 6 years after treatment application. NS = Non-scarified and S = Scarified plots. Data are back transformed based on trees sampled in different plots. Significant differences in growth rates between treatments are shown with a lower case letter

Species	Growth rate Ratio S/NS	Sample size S	Sample size NS	χ^2	p
Schizolobium parahyba	1.06	73	38	1.3	ns
Terminalia oblonga	0.51	42	28	0.1	ns

Table 10. Growth rates ratio between scarified and non-scarified plots. Values > 1 represent higher growth rates in scarified plots and values < 1 represent higher growth rates in non-scarified plots. ANOVA analysis results of the average growth rate (cm y^{-1}) of commercial tree species in two different treatments 6 years after treatment application. NS = Non-scarified and S = Scarified plots. The analysis was done only for species with a sample size larger than 4 per treatment. Data are back transformed based on trees sampled in different plots. Significant differences in growth rates between treatments are shown with a lower case letter

Species	Ratio	Sample size		F	p
	S / NS	S	NS		
Ampelocera ruizii	0.72	38	128	3.4	ns
Aspidosperma cylindrocarpon		0	3		
Batocarpus amazonicus	1.55	39	38	3.7	ns
Caesalpinia pluviosa		1	0		
Calycophyllum spruceanum	1.87a	84	24	5.8	0.018
Cariniana domestica		0	4		
Cariniana estrellensis	2.47	4	4		
Cariniana ianeirensis	0.94	4	5		
Cedrela fissilis	1.02	3	1		
Ceiba petandra	2.16	3	4		
Centrolobium microchaete	0.62	46	3		
Cordia alliodora	0.29	9	3		
Ficus boliviana	2.75	25	7	3.6	ns
Gallesia integrifolia	0.64	61	29	2.5	ns
Hura crepitans	0.71	11	25	0.9	ns
Hymenaea courbaril		1	0		
Maclura tinctoria	0.89	138	65	0.3	ns
Pseudolmedia laevis	0.75	43	62	1.6	ns
Pterogyne nitens		0	1		
Pouteria nemorosa	1.75	10	33	1.9	ns
Spondias mombin	0.86	38	27	0.2	ns
Sweetia fruticosa	1.12	4	6		
Swietenia macrophylla		0	3		

There was not a relationship between overall growth rate of commercial species and soil compaction (Regression analysis $F_{1, 93} = 1.3$; $r^2 = 0.014$; $p = 0.257$). Similar results were found for each functional group separately (regression analysis for long-lived pioneers: $F_{1, 82} = 0.06$; $r^2 = 0.001$; $p = 0.803$, for partially shade-tolerant: $F_{1, 68} = 0.07$; $r^2 = 0.001$; $p = 0.794$ and for shade-tolerant: $F_{1, 59} = 0.12$; $r^2 = 0.002$; $p = 0.728$).

3.2.3. Main environmental factors explaining density of commercial species.

The PCA extracted two axes of variation from the different environmental variables measured in each census; the axes accounted for different % of variation of the data set in each of the census (Table 10). Vegetation cover variables explained 55% of the variation in the data set just after treatment application, while light variable, associated with the second axis, explained only 18 %. Similar correlation trends were observed 12 and 27 months after treatment application (Table 10).

Table 10. Correlations between environmental variables with two orthogonal axes extracted with a PCA per census and percentage of explained variation of the data in each of the axes.

Months since treatment application	Variables	Correlation	
		Axis 1	Axis 2
0	area escarified 1	-.971	-.003
	herb1	.753	-.307
	liana 1	.662	.344
	litter 1	.897	-.085
	woody debris 1	.738	.254
	light 1	-.120	.915
	Explained variance	55.1	18.7
12	herb 3	-.798	.081
	liana 3	.801	-.010
	dominant height 3	.072	.996
	Explained variance	42.8	33.3
27	herb 4	-.861	.019
	liana 4	.749	-.497
	dominant height 4	.454	.857
	Explained variance	50.2	32.7

Total density after six years was correlated with the first axis of initial conditions (0 months) ($r^2 = 0.143$; $p < 0.001$). Density increased as vegetation cover and litter decreased. Similar results were found for long-lived pioneer species after six years ($r^2 = 0.300$; $p < 0.001$). On the other hand no relation between partially shade-tolerant species and any of the axes included in the model was found. Finally, shade-tolerant species were correlated with the second axis of the initial conditions but the relation was very slight ($r^2 = 0.044$; $p = 0.042$). It means that the higher light conditions at the beginning the lower density of shade-tolerant species.

4. DISCUSSION

4.1. Response of the environmental factors to soil scarification application

Soil scarification appeared to be an effective control of herbs regeneration over the four years after treatment application (Table 3; Fig. 1B). Herbs were only significantly higher in scarified plots after six years, and probably at that moment commercial species had already become established. Some studies have found an invasion of herbs in logging gaps in the years following harvesting in La Chonta, (Park et al., 2005), mainly Heliconia spp. (Felton et al., 2006). In this study the trend of increasing herbs right after logging was also shown in non-scarified that reached high levels of herb cover in the first years. However, herb cover in scarified plots, although steadily increased, did not seem to suffer an herb invasion at least in the first years. Therefore the treatment effect was enough large on time to make commercial regeneration to have a chance to regenerate with competing advantage. Other study also found that herb cover was higher in non-scarified plots after 13 months (Fredericksen and Pariona, 2002). The effectiveness of the treatment was also tested for lianas proliferation. Although after four months of treatment application scarified and non-scarified plots had almost the same level of lianas, they were significantly lower in scarified than in non-scarified plots after six years (Table 3; Fig. 1B). A study carried out in La Chonta, found that gaps created by trees that had lianas cut before being fell had significantly higher liana density than control gaps (Alvira et. al., 2004). The results of this study suggest that scarification may be a good tool for dealing with lianas. This finding is important because lianas suppress tree regeneration in logging gaps (Clark and Clark, 1990; Putz, 1984a, 1995; Pinard and Putz, 1994; Vidal et al., 1997; Kennard, 1998; Perez-Salicrup and Barker, 2000) and La Chonta contains one of the highest liana densities of the world (Perez-Salicrup, 1998). The results in this study contrasts with other study in La Chonta that found a significantly higher lianas cover in scarified plots than in non-scarified plots after 13 months (Fredericksen and Pariona, 2002). As expected, litter and woody debris were significantly higher in non-scarified plots right after treatment application but the differences had disappear after six years of treatment application (Table 4; Fig. 2A, 2B). Although no comparisons on time have been possible for litter and woody debris in this study, some studies carried out in La Chonta found similar values of litter cover in control and logged plots after 1-4 years harvesting (Felton et al., 2006) and in scarified and non-scarified areas after 7 months (Fredericksen et al., 2002), suggesting that litter cover levels highly increase after treatment application. A study carried out in La Chonta provided an average of 79% of litter cover in logged gaps after 1-4 years harvesting (Felton et al., 2006), which contrast to the lower averages of litter cover found in this study after six years (between 40-50 % in non-scarified and scarified gaps respectly). Lower litter cover averages could have positive effect on seedling establishment of commercial species regeneration in both treatments.

Light availability was not different between treatments at initial conditions but after six years of treatment application, scarified plots had significantly higher light availability than non-scarified plots (Table 4; Fig. 2C), contrary to the hypothesis. Other studies in La Chonta have found no differences in the canopy cover in gaps 1-4 years after harvesting between unlogged and logged gaps (Felton et al, 2006). The significant higher light availability found in this study was probably because light was measured 1 m aboveground, height at which herbs were very common and dense in non-scarified plots.

Although herb cover was higher in scarified plots after six years, it was observed that herb height was higher in non-scarified plots. Probably no differences in light availability would be found if the same measure would be done at different aboveground height.

As hypothesized, soil compaction levels were higher in scarified plots after six years of treatment application (Table 4; Fig. 2D). Since a measurement of the same variable just before and after treatment application was not available for our study, a comparison through time was not possible. However, it has been found, that non-harvested plots in La Chonta have a mean of 1.01 g/cc bulk density, while bulk density in skid trails averages 1.181 g/cc (Ohlson-Kiehn, 2003). In this study, mean bulk density in scarified plots was 1.09 gr/cc, which is in between the values mentioned earlier, suggesting an acceptable level of compaction for scarified plots. Some studies have reported a negative effect of soil compaction on tree growth rate (Malmer and Grip, 1990; Jusoff and Majid, 1992; Pinard et al., 1996, 2000) but in this study no relation was found between soil compaction and growth rate for any of the functional groups.

4.2. Responses of commercial species to soil scarification application

In Bolivia commercial species regeneration is scarce and it has been suggested that excessive competition with weeds could be one of the probably reasons (Mostacedo and Fredericksen, 1999). Several studies in Bolivia have observed improved recruitment of seedlings and saplings in short term in areas where soil was scarified unintentionally by logging machinery (Fredericksen, 1999, Fredericksen and Mostacedo, 2000, Pariona and Fredericksen, 2002). This study was the first large-scale experiment testing the effects of soil scarification during a long time period. The results obtained indicate strongly that soil scarification had an overall positive effect on commercial density regeneration over the six years monitored (Table 6; Fig. 3A). Similar results were found in La Chonta where commercially valuable species were three times more abundant in scarified plots after 15 months of treatment application (Fredericksen and Pariona, 2002).

According to the hypotheses this effect varied, however, with functional group (Table 7). It was clearly positive for long–lived pioneer species, where density was significantly higher in scarified plots in all the measurements with almost three times more density in scarified plots even after six years of treatment application (Fig. 3B). On the other hand, partially shade-tolerant density seemed not respond to treatment application (Table 7; Fig. 3C), probably because sample sizes were too small and the variability of the data very high which means that statistically no significant differences can be found with these characteristics. The effect was negative for shade-tolerant regeneration in the first years but after six years of treatment application there was a trend of progressive density increase in scarified plots (Table 7; Fig. 3D). In a regeneration study in La Chonta was also found that long-lived pioneer species significantly increased as intensive logging and silviculture practices increased while partially shade-tolerant and shade-tolerant species did not present changes in density, suggesting that these groups of species did not have reaction to increased management practices (Peña-Claros et al., 2008[a]). Following the natural regeneration dynamics (1.2.2) smaller sized long-lived pioneers rapidly colonized the scarified gaps creating high competitive conditions for shade-tolerant species to recruit. In this study the relative importance of long-lived pioneer species in scarified plots diminished over time (Fig. 3B) because of the higher mortality levels of long-lived pioneer species compared to shade-tolerant species (ANNEX 4). Although the initial shade-tolerant regeneration was lower in scarified plots compared to non-scarified plots, it steadily increased in scarified plots while decreased in non-scarified plots during the last two censuses. The highest shade-tolerant species density was found after six years in scarified plots, indicating a later but increased regeneration in scarified plots (Fig. 3D).

At species level, *Ampelocera ruizzi* and *Pseudolmedia laevis* dominated non-scarified plots and *Terminalia oblonga* had high presence in both treatments. Similar results were found in La Chonta (Park, et al., 2005; Fredericksen and Pariona, 2002). However, it is important to point that the regeneration density of *Pseudolmelia laevis* was six times higher in scarified plots than in non-scarified plots after six years of treatment application, suggesting a long-term benefit of the treatment for this specie. On the other hand *Ampelocera ruizzi* semmed not to have any benefit from the disturbed plots contrary to the results found in other studies (Nabe-Nielsen et al., 2005). Both species were between the most abundant after six years of treatment application. Similar results were found in a regeneration study in gaps after 4 years havesting in La Chonta (Peña-Claros et al., 2008[a]), although in this study they had overall lower relative abundance. Surprising low abundance of *Pouteria nemorosa* was found in this study compared to other studies that have pointed this specie regeneration to be between the highest (Nabe-Nielsen et al., 2005;Park, et al.,2005; Peña-Claros et al., 2008[a]). The relative abundance of this specie after 6 years was 2.1 % in this study, which contrast with 10.32 % after 4 years logging reported in Peña-Claros et al., 2008[a]. The same study reported an abundance of 6.28 % of *Sweetia fruticosa* which was much higher than the 0.5 % abundance reported in this study. The treatment had a positive effect on the regeneration of most of the species. Some of them like *Ficus boliviana*, *Schizolobium amazonicum* and *Spondias mombin* have also been found to benefit from scarified or disturbed sites (Fredericksen and Pariona, 2002; Nabe-Nielsen et al., 2005). In this study we found very low density regeneration of some of the most commercially valuable tree species, such as, *Cedrela fissilis, Ficus boliviana*, *Swietenia macrophylla* and *Cariniana spp*. as it also was found in La Chonta (Fredericksen and Pariona, 2002; Park et al. 2005; Peña-Claros, 2008[a]). The failured regeneration was especially acute for *Cedrela fissilis* and *Swietenia macrophylla*. *Cedrela fissilis* was observed to have higher regeneration in scarified plots, especially in the first years. On the other hand, the treatment had a negative effect on *Swietenia macrophylla* and *Cariniana spp.* that presented lower regeneration levels in scarified gaps as it also was found in other studies (Fredericksen and Pariona, 2002; Nabe-Nielsen et al., 2005).

The results in this study reported a significant higher overall growth rates in non-scarified than in scarified plots. However the average growth rates per treatment were not so different. This result contrasts with a regeneration study in La Chonta that found enhancing growth rates in areas with increased intensity of logging and silvicultural treatment application like soil scarification (Peña-Claros et al., 2008). The difference in overall growth rates between treatments in the mentioned study was, however, only significant when comparisons were made between normal intensity of logging and intensive silvicultural treatment plots were compared. In La Chonta, a commercial regeneration study in scarified and control areas during 15 months, found that overall height growth rates were significantly higher in scarified than in control plots

(Fredericksen and Pariona, 2002); however no results were reported per each functional group separately.

The results of the analysis made to test the effect of the treatment in each functional group separately found that the treatment only affected shade-tolerant species. Long-lived pioneer growth rates were higher in scarified plots while growth rates of partially shade-tolerant and shade-tolerant were lower in scarified than in non-scarified plots (Fig. 4). As hypothesized, in all treatments long-lived pioneer species had a significant higher growth rates than partially shade-tolerant and shade-tolerant species. Similar results were found in a regeneration study in La Chonta (Peña-Claros et al., 2008[a]). The same study reported an average of 17 cm year $^{-1}$ growth rate in logging gaps. This value is lower than the 20.2 and 18.6 cm year $^{-1}$ average growth rate in scarified and non-scarified plots in this study, suggesting an overall higher growth rates than in the mentioned study. The negative effect of the treatment in shade-tolerant species growth rates can be explained by two factors. On one hand, the elimination of all vegetation cover increased drought conditions in the gap; on the other hand long-lived pioneers found in scarified gaps the optimal conditions to regenerate. According to Grime's (1977) the most competitive species are the ones that are able to capture and monopolize resources. Scarified gaps were shown to have more density of long-lived pioneer species consequently they became more competitive environment for shade-tolerant species.The highest growth rates of long-lived pioneers makes them to monopolize the resources in the gap. At high densities competition is likely to affect growth rates. Due to the initial light conditions were the same in both treatments, competition could be for the water resources. The results are not suppressive taking into account that shade-tolerant species performs better under moist and higher root competition areas and pioneers do are better adapted to worse conditions in the soil performing with advantage in scarified gaps It seems clear that the application of the treatment reports more profitable results for long-lived pioneer in terms of growth than for the other species suggesting that the complete elimination of litter and debris may not benefit to shade-tolerants as other studies have found (Poorter et al., 2005).

Growth rates also differed at species level. For all of them there are not significant differences between treatments except for *Calycophyllum spruceanum,* which was the most benefited by the treatment application in terms of growth. However it is important to point that for quite higher commercial species densities of some species the growth increased in scarified plots. This the case of some species like *Ficus boliviana* that presented a growth ratio S/NS of 2.78 at around three times more density in scarified plots and *Schizolobium parahyba* with a ratio S/NS of 1.05 with double density in scarified plots.

4.3. Environmental factors explaining density of commercial species

Overall density after six years of treatment application was directly related with the conditions created by soil scarification as it was hypothesized. The higher long-lived pioneer densities were correlated with the absence of litter, woody debris and vegetation cover (Table 10; regression analysis). No correlations were found for partially shade-tolerant species. In contrast the density of shade-tolerant species, with larger seed size, was only little affected by initial light conditions. These results are supported by the theory that long-lived pioneer species with small seed sizes depend for emergence and establishment on areas where roots easily get soil contact (Coomes and Gruub, 2003). Some studies have also found a negative effect of litter density on smaller size commercial species emergence as it is reported in this study (Schiotz, et al., 2006; Dalling and Hubbell, 2002). On the other hand Mabbeerley (1992), Grubb (1996) and Turner (2001) suggest that larger seeds of shade-tolerant species produce bigger seedlings to penetrate a thicker litter layer. Other study carried out in Barro Colorado Island, Panamá, observed that four shade-intolerant species with small seed size reduced seedling establishment under leaf litter compared to bare ground (Mofolsky and Augspurger, 1992). In contrast, the same study showed that non-pioneer species were proportionally much more abundant than pioneers in the litter addition plots and they were less abundant in the litter-free plots.

4.4. Recommendations for forest management.

The results of this study confirm that commercial regeneration is enhanced by soil disturbance although other factors, besides soil scarification, like seed supply, seed dispersal ability and seed predation (Fredericksen and Licona, 2000) are important factors in securing regeneration in logging gaps. These aspects have not been assessed in this study but they should be taken into account for management practices.

Other studies have pointed the importance of gap size, shape and orientation to create suitable microsites for the establishment of specific groups of plants (Brandani et al., 1988; Denslow and Hartshorn, 1994; van der Meer et al., 1998; Brokaw, 1985). Large logging gaps may favor wind-dispersed, shade-intolerant pioneers at the expense of shade-tolerant timber trees that have a competitive advantage in smaller gaps (Denslow, 1987; Bazzaz, 1991). In Bolivia logging gaps have been demonstrated to be larger than natural tree fall because the harvesting of some species, such as *Ficus boliviana*, creates large gaps (Park, et al., 2005). Pioneer species regenerate predominantly in larger gaps (Brokaw, 1985), and in the case of Bolivian forest most of this species are non-commercial. In this context soil scarification at the same time of gap creation by logging may be a useful tool to deal with the non-commercial species invasion in logging gaps and enhance the chances for commercial species establishment.

Before favouring the application of some silvicultural treatments is crucial to consider the ecological requirements of the species being managed (Fredericksen et al., 2003). Based on the results, scarified plots were dominated by commercial regeneration even after six years of treatment application suggesting that the treatment was successful in promoting the regeneration of commercial species. Long-lived pioneer species were the first in regenerate but shade-tolerant species tended to increase their density in scarified plots, which could mean a long-term benefit of the treatment for this group of species. In La Chonta, nearly all the major timber species are long-lived pioneer species (Mostacedo and Fredericksen, 1999). Therefore a forest managed for light-demanding species will require more disturbance than a forest managed for shade tolerant species (Peña-Claros et al., 2008[b]). The application of soil scarification together with additional silvicultural treatments, such as liberation of future crop trees from competition to promote seed production, could be recommendable management practices to help forest management to sustainable yields.

5. CONCLUSION

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Environmental conditions right after treatment application differed between scarified and non-scarified plots. After six years these differences between treatments had disappeared in litter and woody debris variables. Herb cover was significantly higher in scarified plots while lianas cover was significantly lower in non-scarified plots. Light availability resulted had decreased lower in scarified plots and compaction remained higher in scarified plots. This study confirmed that soil scarification enhance the regeneration of commercial species. Total density regeneration was significantly higher in scarified plots in all censuses and was about double after six years of treatment application. Long-lived pioneer species had the strongest response to treatment in short-term but the results suggested that shade-tolerant species could have a positive response in the long-term with regard to density regeneration. However we cannot assure that growth rates of commercial species are enhanced by treatment application, especially for partially shade-tolerant and shade-tolerant species. Overall density after six years was negative correlated to litter and vegetation cover. The initial absence of vegetation cover allowed commercial species germination and establishment in the first years, especially those of long-lived pioneers with small seed. Therefore, the treatment seemed to be effective against non-commercial species proliferation enhancing the chances for commercial regeneration. The recommendation of this practice will depend on the ecological characteristics of the species being managed. A forest managed for light-demanding species, as it is the case of La Chonta, will require the use of soil scarification and other silvicultural practices that have been proved to enhance commercial regeneration

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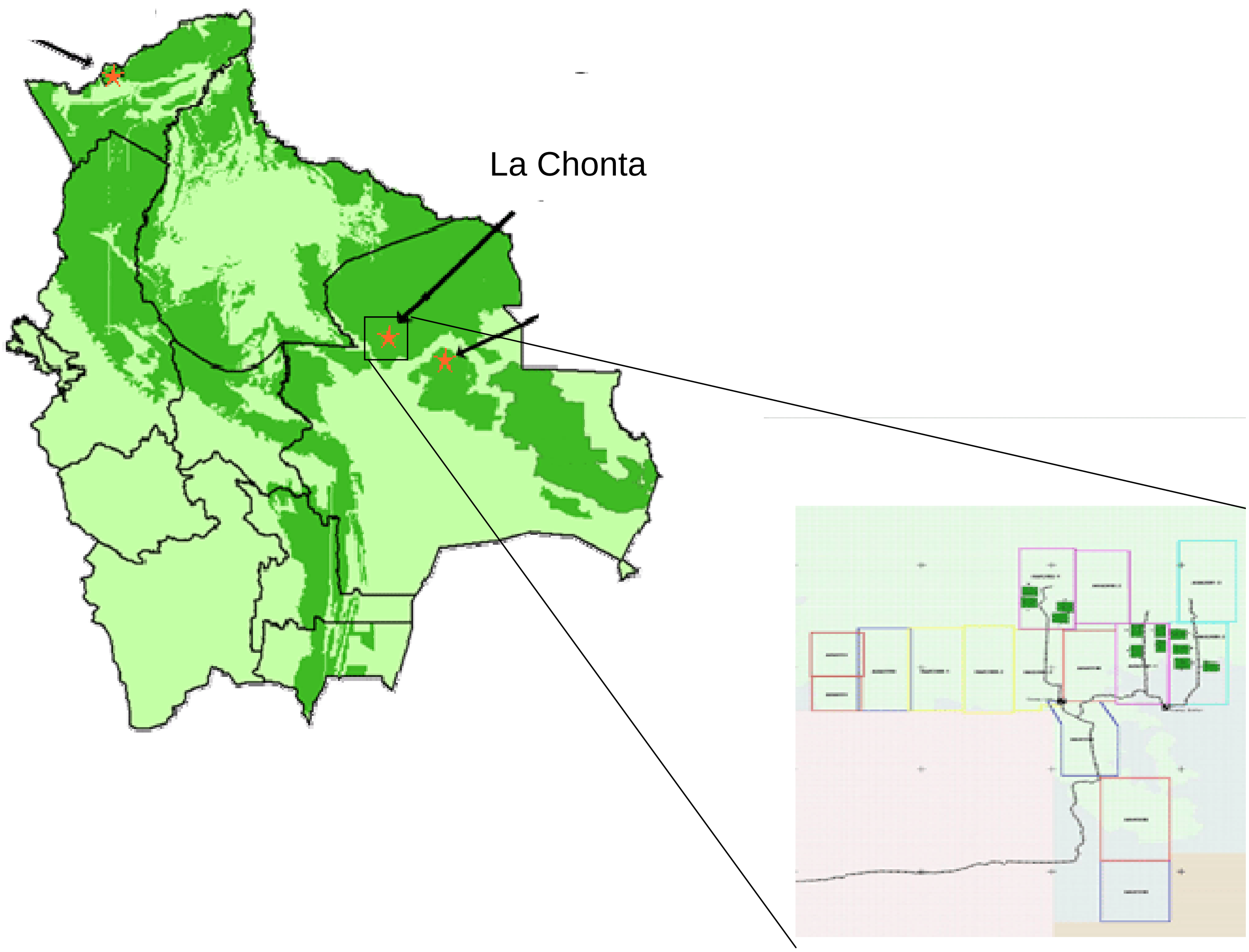
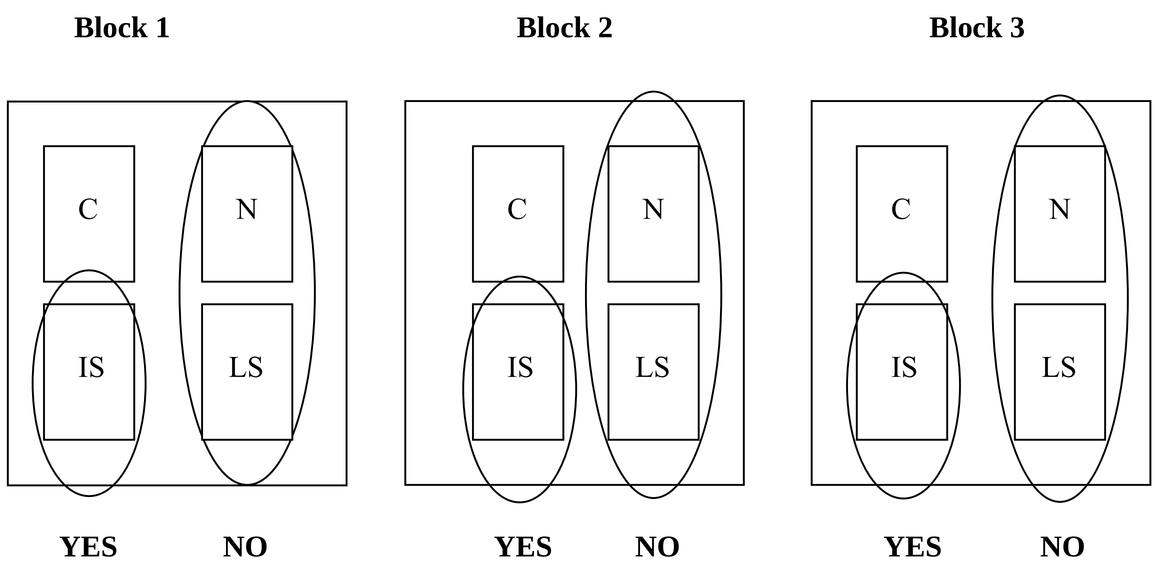
7. ANNEXES

ANNEX 1. Map of the location of La Chonta forestry concession and the permanent plots with different treatment in each of the three blocks.



ANNEX 2. Summarized scheme of the methodology design



The figure below provides an overview of the methodology design:

- Three blocks of plots in different harvesting compartments.
- Plots located in areas of the same environmental conditions in all blocks.
- 180 plots in logging gaps: 90 intensive silviculture (scarified treatment) and 90 normal silviculture and light silviculture, 45 in each, (non-scarified treatment).
- Control plot excluded
- No differences between normal and light silviculture treatment in scarification experimental plots.

ANNEX 3. Worksheets for data collection

- Environmental variables data

Block
Date

Treatment	Plot	% Litter	% Woody debris	% Scarification area	% Herb	% Liana	Light white points (densitometer)				C
							1	2	3	4	

- Individual commercial tree species data

Block
Date

Treatment	Plot	Tag	Sp name	# individuals	Height	Diameter Category	Origin	Comment

- Dominant vegetation data

Block
Date

Treatment	Plot	Sp name	Height	Crown position