

Ecology and Silviculture of Long-Lived Pioneer Timber
Species in a Bolivian Tropical Forest

By

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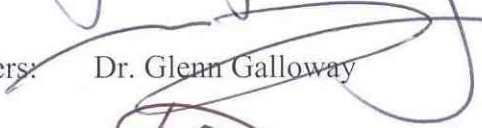



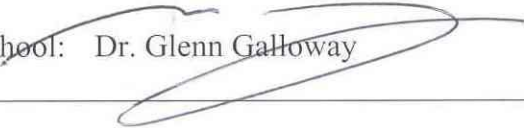
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To my wife Norma Cascante

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BIOGRAPHY

Lincoln Quevedo was born in Santa Cruz, Bolivia. He obtained his BSc in forestry at the Universidade Federal de Vicosa, Brazil, in 1981, and his MSc in forest management at CATIE, Costa Rica, in 1986.

His professional experience is in sustainable forestry development, tropical forest ecology, silviculture and forest management with national and international non-government organizations, as well as with Bolivian government agencies. He is a faculty member of the Forestry School at the Universidad Autónoma Gabriel René Moreno, in Santa Cruz, Bolivia.

He has been engaged in forest management certification since the beginning of the Forest Stewardship Council (FSC) process, serving one term as a member of the Board of Directors of the FSC-International for the environmental southern chamber, and two terms as a member of the Board of Directors of the FSC Bolivian National Initiative, where he worked on the development of national standards for timber and non-timber products management certification.

ABSTRACT

Quevedo, L. 2005. Ecology and silviculture of long-lived pioneer timber species in a Bolivian tropical forest. PhD Thesis, CATIE, Turrialba, Costa Rica.

Key words: Bolivia, Forest ecology, Light requirements, Long-lived pioneer species, Natural regeneration, Silviculture, Topographic effects, tropical rain forests.

The ecology and silviculture of long-lived pioneer species was studied in the plots of the Long-term Silviculture Research Project established in a semi-deciduous tropical forest in Bolivia which was being carried out by the Bolfor Project since 2000 and later on by the Instituto Boliviano de Investigaciones Forestales (IBIF). A random complete block design experiment was used, with three blocks of 800 ha each, and treatments of 27 ha, in which a set of plots of 20 m x 20 m were placed in a 75 m x 75 m grid system. Treatments were Unlogged and Intensive logged. The logged treatment include directional felling; marking future crop trees and seed trees; liana cutting from trees to be harvested, future crop trees and seed trees; skid trails that were previously defined; soil scarification by skidder in places where a tree was harvested but only if there was no advanced regeneration and a seed tree was within the range of seed dispersion; and harvesting about 15 m³/ha which roughly represented two times the normal volume harvested by the logging company.

Several studies have been carried out on gaps and logging effects on natural regeneration, but few on an operational scale like this. For this experiment, eight long-lived pioneer species were chosen, four of which were known to often develop abundant regeneration after disturbances by harvesting (Group A: *Hura crepitans*, *Margaritaria nobilis*, *Schizolobium parahyba*, *Zanthoxylon sprucei*), and four that do not (Group B: *Cariniana estrellensis*, *Cariniana ianeirensis*, *Sweetia fruticosa*, *Ceiba pentandra*). All the plants of the selected species ≥ 0.5 m height were measured in the sample plots. Four studies were carried out that are described in the following paragraphs.

In the first study, the effect of the topography on the species distribution, data from “Unlogged” and “Intensive logging” treatments were combined to obtain the largest possible sample population. The low abundance of some species may have affected the strength of the tests, mainly for trees with dbh ≥ 5 cm, which reflected the condition of rarity of light-demanding species in the tropics and the difficulties to study them. Only one species, *M. nobilis* was statistically related with the topographic position. However, all species expected to develop

abundant regeneration after logging were associated with gentle slope classes. All these species were the most light demanding, probably the fastest growing and had the highest demand for water resources, which would explain why they are associated with gentle slopes, where higher moisture is expected. No pattern was found regarding rarity or commonness and topographic habitat preference.

In the second study, about species regeneration and light environment relationship, the Unlogged treatment was used. Only one individual of *C. pentandra* was found and no individuals of *S. parahyba*, so these species were not included in the analysis. When the species and forest light distribution for sapling and pole sizes were compared, only *Z. sprucei* had a different distribution for crown illumination for dbh < 5.0 cm (saplings), presenting higher illumination. For pole size (dbh 5.0-9.9 cm), we only had data for four species, and three of them differed from the forest distribution. Lateral light entrance proved to be the most important source of light for saplings. The multivariate analysis confirmed that *Z. sprucei* was the most light demanding species of the group, in an intermediate level were *M. nobilis*, *H. crepitans*, *C. ianeirensis* and *S. fruticosa*, and *C. estrellensis* was the least demanding. Three out of eight species (*C. estrellensis*, *S. parahyba*, and *C. pentandra*) were classified as locally rare in the undisturbed forest. We concluded that long-lived pioneer species are able to develop some degree of regeneration under canopy, but larger trees were scarce.

The third study, on seed dispersal, was developed for four species: *M. nobilis*, *Z. sprucei*, *S. parahyba*, and *H. crepitans*. From these, *M. nobilis* and *Z. sprucei* had the shorter seed dispersion (4 m). *S. parahyba* dispersed seeds at least 38 m.

In the fourth study, the effect of logging on regeneration species, responses were better observed in diameter sizes dbh < 5.0 cm. The hypothesis that the group of species expected to respond well to harvesting (group A) developed abundant regeneration after logging was accepted. Also, logging provided more light to natural regeneration. Increase of crown illumination was clear for *C. ianeirensis*, *H. crepitans*, *S. parahyba* and *Z. sprucei*. The test for canopy openness and the regeneration phase in seedling size resulted in that all species showed an increase of light with the exception of *C. estrellensis* (*C. pentandra* did not show enough individuals for any statistical test). Two species, *Z. sprucei* and *S. parahyba*, responded better to canopy openness. The three species that were considered as locally rare in the undisturbed forest, *C. estrellensis* and *C. pentandra* did not show any benefit on abundance from logging disturbances and silviculture treatments, while *S. parahyba* –the most light-demanding of all species- clearly increased its abundance through logging.

The experiment on species responses to skid trails resulted in *S. parahyba* and *Z. sprucei* being statistically different from the other species, showing their distribution skewed toward the soil disturbance caused by skidder movement.

We concluded that harvesting and treatments can increase the abundance of some locally rare species –at least at the regeneration level- and that some abundant species, such as *H. crepitans*, can become even more abundant with planned harvesting. However, some locally rare species may remain rare (*C. estrellensis*, and *C. pentandra*), which would require special attention during harvesting planning. We argued that planned logging together with silviculture treatments can promote natural regeneration recruitment for most species, but this does not necessarily mean that individuals will become harvestable trees. Therefore, treatments after logging may be necessary to ensure that a number of seedlings and saplings will become pole and larger trees. Otherwise, the sustainability of the harvesting species may not be achieved. More studies are encouraged regarding the levels of harvesting and logging damages, ecology and conservation strategies of rare species, seed trees, monitoring species regeneration responses to logging, and the adoption of the adaptive management approach to permanently learn and improve forest management practices.

RESUMEN

Quevedo, L. 2005. Ecología y silvicultura de especies heliófitas maderables de larga vida en un bosque húmedo tropical boliviano. Tesis de PhD, CATIE, Turrialba, Costa Rica.

Palabras claves: Bolivia, Ecología forestal, Requerimientos de luz, Especies heliófitas de larga vida, Regeneración natural, Silvicultura, Efectos de topografía, Bosques naturales tropicales.

En este trabajo se estudió la ecología y silvicultura de especies heliófitas maderables de larga vida en las parcelas del Proyecto de Investigación Silvicultural de Largo Plazo establecido en un bosque tropical semidecídúo en Bolivia, e implementado por el Proyecto Bolfor desde 2000 y posteriormente por el Instituto Boliviano de Investigaciones Forestales (IBIF). Se usó un diseño de bloques completos al azar, con tres bloques de 800 ha cada uno y tratamientos de 27 ha en cuyo interior se instalaron parcelas de muestreo de 20 m x 20 m, en un sistema de malla de 75 m x 75 m. Los tratamientos fueron “Aprovechamiento intensivo” y “Testigo” (no aprovechado). El tratamiento de aprovechamiento incluyó tala dirigida, marcado de árboles de futura cosecha y semilleros, corta de lianas en árboles aprovechables, de futura cosecha y árboles semilleros, pistas de arrastre cuidadosamente planificadas, escarificación del suelo mediante skidder en sitios donde no existía regeneración y dentro del rango de dispersión de semillas de un árbol semillero, y aprovechamiento de alrededor de 15 m³/ha, lo cual representa aproximadamente dos veces el volumen normalmente aprovechado por la compañía.

Muchos estudios se han llevado a cabo en claros y efectos del aprovechamiento sobre la regeneración natural, pero pocos en este nivel de escala operacional. Para este experimento, se seleccionaron ocho especies que usualmente desarrollan abundante regeneración natural después del aprovechamiento (Grupo A: *Hura crepitans*, *Margaritaria nobilis*, *Schizolobium parahyba*, *Zanthoxylon sprucei*), y cuatro que no lo hacen (Grupo B: *Cariniana estrellensis*, *Cariniana ianeirensis*, *Sweetia fruticosa*, *Ceiba pentandra*). En las parcelas de muestreo se midieron todas las especies ≥ 0.5 m de altura. Se llevaron a cabo cuatro estudios que se describen a continuación.

En el primer estudio, el efecto de la topografía sobre la distribución de las especies, se fusionaron los datos de los tratamientos “Testigo” y “Aprovechado” para obtener la mayor cantidad de población muestreada posible. La baja abundancia de algunas especies puede haber afectado el poder de las pruebas estadísticas, especialmente para árboles con diámetro a la altura

del pecho (dap) ≥ 5 cm, aspecto que refleja la condición de rareza de las especies heliófitas en los trópicos y la dificultad de estudiarlas. Sólo una especie, *M. nobilis*, fue estadísticamente relacionada con posición topográfica. Sin embargo, todas las especies que se esperaba desarrollen abundante regeneración después del aprovechamiento estuvieron asociadas con pendientes suaves. Todas estas especies fueron las más demandantes de luz y probablemente las de más rápido crecimiento y más demandantes de agua, lo cual podría explicar porqué están asociadas con pendientes suaves, que es donde mayor humedad se espera. No se encontró ningún patrón acerca de rareza o abundancia y preferencias de hábitats de topografía.

En el segundo estudio, sobre regeneración de especies y sus relaciones con ambientes lumínicos, se usó el tratamiento testigo. Se encontró sólo un individuo de *C. pentandra* y ninguno de *S. parahyba*, de tal forma que estas especies no fueron incluidas en el análisis. Cuando se comparó la distribución de luz de las especies y el bosque para latizales y fustales, sólo *Z. sprucei* tenía una distribución de iluminación de copa diferente para dap < 5.0 cm (latizales), presentando alta iluminación. Para la clase dap 5.0-9.9 cm (fustales), tuvimos datos para sólo cuatro especies, de las cuales tres presentaron una iluminación de copa diferente a la del bosque. Se encontró que la luz lateral fue la fuente de luz más importante para brinzales. El análisis multivariado confirmó que *Z. sprucei* fue la especie más demandante de luz del grupo, mientras que en un estado intermedio estuvieron *M. nobilis*, *H. crepitans*, *C. ianeirensis* y *S. fruticosa*, y como la menor demandante estuvo *C. estrellensis*. De las ocho especies del estudio, tres fueron clasificadas como raras in el bosque no intervenido (*C. estrellensis*, *S. parahyba*, y *C. pentandra*). Se concluyó que las especies heliófitas de larga vida pueden establecer cierto grado de regeneración bajo el dosel, aunque los individuos de mayor tamaño fueron escasos.

El tercer estudio, sobre dispersión de semillas, fue llevado a cabo para cuatro especies: *M. nobilis*, *Z. sprucei*, *S. parahyba* y *H. crepitans*. De este grupo, *M. nobilis* y *Z. sprucei* tuvieron la dispersión de semillas más corta (4 m). *S. Parahyba* dispersó sus semillas hasta 38 m.

En el cuarto estudio, sobre el efecto del aprovechamiento en la regeneración natural, las respuestas fueron mejor observadas en las clases de tamaño dap < 5.0 cm. La hipótesis sobre el grupo de especies que se esperaba desarrollen abundante regeneración después del aprovechamiento (Grupo A) fue aceptada. Además, el aprovechamiento proporcionó mayor iluminación a la regeneración. El incremento de iluminación de copa fue claro para *C. ianeirensis*, *H. crepitans*, *S. parahyba* y *Z. sprucei*. La prueba para apertura de dosel y fase de regeneración para latizales mostró que todas las especies tuvieron un incremento de luz, con la

excepción de *C. estrellensis*. La especie *C. pentandra* no presentó suficientes individuos que permitan realizar pruebas estadísticas. Dos especies, *Z. sprucei* y *S. parahyba*, fueron las que respondieron mejor a la apertura de dosel. De las tres especies que fueron consideradas raras en el bosque no intervenido, *C. estrellensis* y *C. pentandra* no mostraron beneficios en abundancia debido al aprovechamiento y los tratamientos silviculturales, mientras que *S. parahyba* –la especie más demandante de luz en el estudio- tuvo un claro incremento de su abundancia con el aprovechamiento.

El experimento sobre las respuestas de las especies al paso del skidder mostró que *S. parahyba* y *Z. sprucei* tuvieron diferencias estadísticas con el resto de las especies, presentando una distribución orientada hacia los suelos disturbados por el paso del skidder.

Se concluyó que el aprovechamiento y tratamientos silviculturales pueden incrementar la abundancia de algunas especies localmente raras –por lo menos a nivel de regeneración- y que algunas especies abundantes como *H. crepitans* pueden convertirse aún más abundantes mediante el aprovechamiento planificado. Sin embargo, otras especies localmente raras pueden mantenerse raras (*C. estrellensis* y *C. pentandra*), por lo que requieren de especial atención durante la planificación del aprovechamiento. Concluimos que el aprovechamiento planificado junto con tratamientos silviculturales puede promover el reclutamiento de regeneración para la mayoría de las especies, pero esto no necesariamente significa que dicha regeneración se convertirá en árboles aprovechables. Por lo tanto, probablemente se requerirán tratamientos post aprovechamiento para asegurar que un cierto número de plántulas y latizales se conviertan en fustales y árboles grandes. Caso contrario, el aprovechamiento sostenible podría no ser logrado. Se sugieren más estudios sobre volúmenes máximos cosechables y daños del aprovechamiento, ecología y estrategias de conservación de especies raras, árboles semilleros, monitoreo de las respuestas de la regeneración al aprovechamiento, y la adopción del enfoque del manejo adaptativo para aprender y mejorar de forma permanente las prácticas de manejo.

TABLE OF CONTENTS

DISSERTATION APPROVAL FORM	ii
ACKNOWLEDGEMENTS	iv
BIOGRAPHY	v
ABSTRACT	vi
RESUMEN	ix
LIST OF TABLES	xiv
CHAPTER 4	xiv
LIST OF FIGURES	xv
CHAPTER 1. GENERAL INTRODUCTION	1
1. Problem statement	1
2. Objectives	6
3. Hypothesis	7
4. Species studied	8
References	12
CHAPTER 2. PAPER I. EFFECT OF TOPOGRAPHY VARIATION ON LONG-LIVED PIONEER SPECIES DISTRIBUTION IN A BOLIVIAN TROPICAL FOREST	18
Abstract	18
1. Introduction	19
2. Methods	22
2.1 <i>Study site</i>	22
2.2 <i>Study species and sampling</i>	23
3. Results	26
4. Discussion	29
Acknowledgments	32
References	32
CHAPTER 3. PAPER II. LIGHT ENVIRONMENT, SEED DISPERSION AND THE NATURAL REGENERATION OF LONG-LIVED PIONEER TIMBER SPECIES IN AN UNDISTURBED BOLIVIAN TROPICAL FOREST	36
Abstract	36
1. Introduction	38
2. Methods	41
2.1 <i>Study site</i>	41
2.2 <i>Study species and sampling</i>	41
3. Results	45
4. Discussion	49
Acknowledgments	53
References	53

CHAPTER 4. PAPER III. EFFECT OF LOGGING ON NATURAL REGENERATION OF LONG-LIVED PIONEER SPECIES IN A BOLIVIAN TROPICAL FOREST: RESULTS OF AN OPERATIONAL-SCALE EXPERIMENT	58
Abstract.....	58
1. Introduction	60
2. Methods	63
2.1 <i>Study site</i>	63
2.2 <i>Study design</i>	63
3. Results	66
4. Discussion.....	72
Acknowledgments	76
References	76
CHAPTER 5. GENERAL RESULTS, CONCLUSIONS AND RECOMMENDATIONS.....	80

LIST OF TABLES

Chapter 1

Table 1. Possible causes for rarity of long-lived pioneer tree species.....	5
Table 2. Example of tropical timber species guilds	6

Chapter 2

Table 1. List of selected long-lived pioneer species.....	23
Table 2. Species' abundance (per ha) for size classes (unlogged + logged plots)	26
Table 3. Mean abundance (No/ha) \pm standard deviation per size classes and topographic position for size classes.	27
Table 4. Mean abundance (No/ha) \pm standard deviation per size classes and percent slope for size classes.	28

Chapter 3

Table 1. List of selected long-lived pioneer species.....	42
Table 2. Species' abundance (total in 5.68 ha, and mean per ha) for three size classes found in 3 27-ha plots in an undisturbed forest.	45
Table 3. Contingency table (Chi-square) to compare the distribution of crown illumination index (observed distribution) of plants of seven long-lived pioneer timber species and the distribution of crown illumination index in the forest (expected distribution) for sapling and pole sizes.	46
Table 4. Contingency table (Chi-square) to compare the distribution of canopy openness index (observed distribution) of plants of seven long-lived pioneer timber species and the distribution of canopy openness index in the forest (expected distribution) for sapling size and pole sizes.....	47
Table 5. Contingency table (Chi-square) to compare the distribution of regeneration phase index (observed distribution) of plants of seven long-lived pioneer timber species and the distribution of regeneration phase index in the forest (expected distribution) for sapling size and pole sizes.....	47

Chapter 4

Table 1. List of selected long-lived pioneer species and density in the La Chonta forest concession, Santa Cruz, Bolivia	64
Table 2. Total number of individuals found in unlogged and logged treatments in all sample plots (5.68 ha and 5.56 ha for unlogged and logged treatments, respectively).....	66
Table 3. Contingency table for pair of species distribution differences for soil skidder disturbance for sapling size.....	71

LIST OF FIGURES

Chapter 2

- Figure 1. Diagram of the plots of the Long-term Silvicultural Research Project established in La Chonta concession. 24
- Figure 2. 3-D topographic map of a 27 ha treatment plot. 25

Chapter 3

- Figure 1. Histogram comparing *C. ianeirensis* and *Z. sprucei* with forest distributions for crown illumination classes, $dbh \leq 5.0$ cm. 46
- Figure 2 Cluster analysis for species considering crown illumination, canopy openness and regeneration phase variables ($dbh < 5.0$ cm)..... 48
- Figure 3. Multivariate analysis of principal coordinates utilizing crown illumination, canopy openness and regeneration phase ($dbh < 5.0$ cm)..... 48

Chapter 4

- Figure 1. Logging and silviculture effect (No/ha, ± 1 SE) on species density for sapling (a) and pole (b) sizes (ANOVA test). 67
- Figure 2. Mann-Whitney test comparing unlogged and logged treatments for crown illumination, for (a) sapling and (b) pole sizes 68
- Figure 3. Mann-Whitney test comparing unlogged and logged treatments for canopy openness, for (a) sapling and (b) pole sizes 69
- Figure 4. Mann-Whitney test comparing unlogged and logged treatments for regeneration phase, for (a) sapling and (b) pole sizes 70

CHAPTER 1. GENERAL INTRODUCTION

This dissertation is based on three papers included as chapters 2, 3 and 4 and referred to (in the order of the chapters) by their Roman numerals, e.g. Paper I.

1. Problem statement

In the neo-tropics, the most valuable timber species are under pressure from logging and forest conversion. Under this scenario, sustainable forest management has become an efficient tool for conservation purposes if compared with other land uses such as agriculture, grazing, or shifting cultivation (but see Rice *et al.*, 1997; Reid and Rice, 1997; Bowles *et al.*, 1998). However, if the forests are unsustainably managed, forest management may in turn contribute towards deforestation and, eventually, to the genetic erosion of timber species (Buschbacher, 1990). As a result of unsustainable logging, commercial long-lived pioneer species -the focus of this research- are most vulnerable to losing their genetic diversity and the possible impacts are: (a) population bottlenecks (the genetic variability is reduced and contained in a few individuals, caused by a population reduction, and “genetic drift”, i.e. the random gene frequency changes in a small population), (b) dysgenic selection (poor quality of the majority of the residual population, caused by the removal of the best individuals), and (c) inbreeding (mating between close relatives, caused by the reduction of population size and the creation of excessive distances between individuals for reproduction (Jennings *et al.*, 2001). Species in general can become local or globally extinct because of natural evolutionary processes or by anthropogenic activities, such as deforestation or unsustainable harvesting (Meffe and Carrol, 1997).

The design and implementation of sustainable forest management plans are essential in order to achieve a sustained yield and to conserve the biodiversity in forests managed for production. To avoid damage and to make harvesting more efficient, reduced impact logging is encouraged in the tropics, which has proved to be beneficial for maintaining forest structure and conserving species (Pinard *et al.*, 1995). For example, in the Brazilian Amazon the appropriate planning of harvesting resulted in a reduction of 25% of the area affected by harvesting, while liana cutting two years before harvesting has reduced damage to the remaining trees by 30% during logging

operations, and skidder time was reduced by 20% (Uhl *et al.*, 1997). In Costa Rica, controlled selective logging damaged only 17% of the residual forest (Webb, 1997).

Even with the application of careful logging systems, harvesting will always cause a certain degree of impact or disturbance on any forest (Putz, 1994). If these disturbances are well planned and controlled, that may stimulate species growth (Finegan and Camacho, 1999; Fredericksen and Mostacedo, 2000). The net volume growth is practically nonexistent in an undisturbed forest (Bertault *et al.*, 1995), while a substantial increase in growth can be obtained if the basal area is maintained below two-thirds of its maximum (Wadsworth, 1997), or it is reduced to 40-50% of its original size (Dawkins, 1958) by harvesting, refinement or thinning operations.

The application of silviculture treatments is also advocated by foresters to obtain sustainability (e.g. Fredericksen *et al.*, 2003). For decades tropical foresters and ecologists have debated two main approaches: (1) enrichment planting and (2) natural regeneration. Enrichment systems have resulted in more failures than successes (but see Flores, 2002) favoring, in recent years, systems based on natural regeneration (Bertault *et al.*, 1995). The great advantage of natural regeneration systems, compared to enrichment planting or agro-forestry systems is that they tend to maintain the forest cover and its ecological function. However, in natural regeneration systems, the impact of operations depends upon the nature of the system itself: monocyclic systems removing all harvestable trees in one harvesting operation while polycyclic systems extract only a portion of the trees at each intervention (Lamprecht, 1989). For polycyclical systems, the key factors are the correct definition of the cutting cycle, the reduction of damage to advanced regeneration, and the growth of natural regeneration into larger diameter classes. In the neo-tropics, monocyclic systems are rarely used.

Silviculture treatments can be applied to meet multiple objectives, but in general in the neo-tropics they attempt to increase timber (or non-timber) production and the quality of the forest stand. A silviculture system generally involves harvesting, followed by treatments to promote natural regeneration, increase tree growth rates and improve the quality of the residual commercial trees. Its application in terms of timing and intensity makes up a silviculture system (see Baur, 1964; Lamprecht, 1989 for a comprehensive description of silviculture systems).

Logging in Bolivia has typically been selective (1-2 trees/ha, 2-5 m³/ha) but unnecessarily destructive, causing negative impacts on forest ecosystems and the remaining valuable timber species such as *Swietenia macrophylla*, *Amburana cearensis*, and *Cedrela* spp. Unfortunately, there has been degradation caused by high-grading valuable timber species (Gullison *et al.*, 1996), and logging has favored shifting cultivation by opening roads to dense forest areas. The promulgation of a new Forestry Law in 1996 resulted in the reduction of legally harvested areas from 21 million ha to 5.8 million ha (Kaimowitz *et al.*, 1999), but has increased the area actually being well managed. Despite the improvements in harvesting practices in Bolivia, forest management sustainability is still a challenge and needs to embrace silviculture treatments in addition to the current planned logging practices (Fredericksen *et al.*, 2003). Most species have a low natural regeneration explained by the high rate of seed predation or poor seed germination, insufficient size of gaps, irregular or poor seed production, and low natural growth rates (Mostacedo and Fredericksen, 1999).

An understanding of the ecology of harvested species is essential in any silviculture system or forest management plan. Canopy opening is one of the key objectives in silviculture operations in forest management (Pinard *et al.*, 1999) which affects species according to their ecological requirements. Light-demanding species will react better to disturbances than shade-tolerant species and, therefore, some treatments aim to work with ecological species groups. It is desirable to open the canopy enough to promote the growth of valuable species -but not to the degree that lianas and grasses infest the stand (Buschbacher, 1990). The timing and intensity of the disturbances can be decisive in regeneration in gaps: recruitment will be affected by the quality and quantity of seeds in the soil bank, period of fruiting, dormancy, and dispersion (Hartshorn, 1980). Harvesting should not be carried out before fructification and seed fall, and the gaps should be in order to provide opportunities for species with poor dispersion. Many times species may fail to reach sites that can be colonized because of limited seed dispersion (Harper, 1981).

The understanding of species' habitats and microsite requirements for regeneration and plant development is necessary to promote the regeneration of species of interest. For example, the topographic position will affect water availability, soil richness, gap dynamics, and size of the trees, amongst others (Clark *et al.*, 1998; Clark, 2002). Species can be specialists or generalists regarding topographic position; therefore it is possible to predict species' composition along catenas (Gourlet-Fleury and Picard, 2004). Tree species physiologically better adapted to

particular soil conditions will increase their growth faster than their neighbors, and will have greater possibilities of reaching maturity, while those lesser adapted will be smaller, slow growing and lesser competitive (Gartlan *et al.*, 1986).

It is difficult to analyze the influence of microsites and habitats on the abundance and distribution of long-lived pioneer tree species without understanding the nature of rarity and commonness. Species can be naturally rare or common, but a defined number per area unit does not exist in order to classify a species as “rare”, “common” or “abundant” (Reveal, 1981). Rarity is “the state of having low abundance and/or small range size” (Gaston, 1994). Rabinowitz *et al.* (1986) claim that all species can be classified in accordance to three characteristics: *geographic range*, where species may have wide or narrow range; *habitat specificity*, where species may possess broad or restricted habitat requirements; and *local population size*, where species may be present in large or small populations. Based on the cited traits, Rabinowitz (1981) developed seven classes of rarity.

Rarity is a common phenomenon in tropical rainforests (Bawa and Ashton, 1991), which makes their study difficult because of the lack of enough individuals needed to make statistical inferences. This is particularly true for light-demanding tree species in a mature tropical forest, because the number and size of colonizable gaps are limited (Hubbell and Foster, 1986). Basically, species may be rare because available favorable habitats are too small, too few, too ephemeral or too far from seed sources and regenerative individuals (Harper, 1981), or have too high inter-species competition. There are several factors that may cause rarity for long-lived pioneer species, which are summarized in Table 1. If we accept light as the most important factor affecting this guild, then size, number and duration of favorable habitable sites (i.e. canopy openness), may be the most determinant. Habitat distance from seed trees could be crucial for species with low seed dispersal capacity; therefore, forest fragmentation may also cause species rarity. In this research a species is considered rare if abundance is less than 1 individual/ha (dbh \geq 10 cm), following the threshold used by Clark and Clark's (1992) in Costa Rica, and Pitman *et al.*'s (1999) in the Amazon.

Table 1. Possible causes for rarity of long-lived pioneer tree species, summarized from Harper (1981), Rabinowitz (1981), Hubbell and Foster (1986), Bawa and Ashton (1991), Barrett and Kohn (1991), Gaston (1994), and Harms *et al.* (2001).

Causes for rarity	Comments
Spatial and sampling effects.	This is an artificial case of rarity, since rarity could be caused simply because sampling may have been done on small spatial scales or because species have been overlooked or because of limited sampling they were not measured.
Small size of habitable sites	The population size could be restricted by the size of habitable sites, which would limit the reproduction of specialist species.
Few habitable sites	Habitable sites could be large in size, but few in number. This would lead to a species being locally abundant, but rare in terms of range distribution.
Short time duration of site availability	Sites may be available for only a short period of time, for example, following a disturbance, where species may not successfully colonize because of the short period of time. They may be excluded quickly by other faster growing colonizing species.
Distance between available sites	Species with dispersal limitation will fail to colonize a site if it is too far away, even though such available site was habitable.
Effects of predators and pathogens	Predators or pathogens could limit the population of species on a site (e.g. <i>Swietenia macrophylla</i> in the neo-tropics, Chestnut Blight in North America), or even exclude the species altogether.
Establishment ability and Life history	Species may have ecological traits that favor their establishment and dissemination such as those showed by invasive species. Some rare species simply may not have those abilities and fail in the competition with others.
Size and persistence of individuals or seeds	Species exhibit different life strategies such as allocating more or less resources to seed production, size, or seed dormancy, as well as to size or persistence of the individuals. These traits will affect the condition of species rarity.
Immigration	Some species may be rare because they have only recently initiated the colonization of a given site or region.
Escape	Some species like <i>S. macrophylla</i> may be rare due to an escaping strategy from predators or herbivores.

Recognizing the limitations that the study of rare species implies and the possible bias to focus on abundant species, Clark (2002) warns researchers that if they do so, knowledge on rare species will not be developed. When facing this type of inherent difficulty, which would make it logistically impossible to carry out a rigorous sampling, Hall *et al.* (1998) suggest establishing as many plots as possible.

Species guilds have interested researchers mainly for ecological and management objectives. In La Selva, Costa Rica, Clark *et al.* (1993) distinguished four guilds, but they preferred to assign letters instead of functional names: Group A (species that develop under a mature forest), Group B (species with steady size-dependent increases in crown position and growth rates), Group C (species closely related with disturbances during the germination and establishment phase), Group D (pioneers, with highest crown light dependency). Finegan *et al.* (1999), also in Costa Rica, grouped tree species also into four guilds: (a) Short-lived pioneer, (b) Long-lived pioneer, (c) Intermediate, and (d) Shade-tolerant. Finegan's classification system is applied in this

research. From Table 2 it is seen that several valuable timber species that belong to the “Long-lived pioneer” guild are commonly harvested in the Latin American region. Sustainable forest management should ideally base its practices on species ecology (Fredericksen and Peralta, 2001), and this is why ecological studies and classification of species in guilds are of interest to ecologists and silviculturalists. This guild is the focus of our research.

Table 2. Example of tropical timber species guilds

Short-lived pioneer	Long-lived pioneer	Intermediate	Shade-tolerant
<i>Cecropia</i>	<i>Cedrela spp.</i>	<i>Terminalia amazonia</i>	<i>Carapa guianensis</i>
<i>Ochroma</i>	<i>Ceiba pentandra</i>	<i>Pterocarpus hayesii</i>	<i>Minquartia guianensis</i>
<i>Croton</i>	<i>Hieronyma alchorneoides</i>	<i>Humiriastrum diguense</i>	<i>Pouteria campechiana</i>
	<i>Vitex cooperi</i>	<i>Qualea paraense</i>	<i>Virola koschnyii</i>
	<i>Simarouba amara</i>		<i>Virola sebifera</i>
	<i>Vochysia ferruginea</i>		<i>Pentaclethra macroloba</i>
	<i>Cordia spp.</i>		
	<i>Laetia procera</i>		
	<i>Rollinia microsepala</i>		

Source: Finegan *et al.* (1999)

In this research, long-lived pioneer species were selected, four of which usually develop abundant regeneration after logging and four that do not. This research aims to understand the effect of topography on species distribution, light, forest and soil disturbance, and seed dispersion. We try to answer questions such as: Why do some species develop abundant regeneration after logging while others do not? Are the species of interest generalists or specialists? Are they rare or common species and how do they respond to logging?

This research faced some limitations due to the experimental material, the same as mentioned by Clark (2002): the low abundance of many of tropical timber species. Despite the large number and size of the sampling plots, it was difficult to make meaningful statistical inferences for most species in the larger size classes. In addition, the natural high variability of species in disturbed environments resulted in additional statistical constraints. Nevertheless, useful results that were relevant for forest management and policy-making were generated for the Bolivian and regional context.

2. Objectives

The general objective was to contribute knowledge for biodiversity conservation and sustainable management of long-lived timber species. The specific objectives were:

- (a) Determine the effect of topography on the abundance and population structure of long-lived pioneer timber species;
- (b) Determine the relationship between natural regeneration abundance and the light environment found in an undisturbed forest;
- (c) Determine the natural regeneration responses to logging disturbances;
- (d) Characterize seed dispersion of species studied in an undisturbed forest; and,
- (e) Provide recommendations for species conservation and sustainable management of long-lived pioneer species.

The present research focuses on the ecology and silviculture of long-lived pioneer species in a Bolivian tropical forest. Paper I focuses on the effect of the topography on long-lived pioneer timber species distribution. Paper II examines the relationship between natural regeneration and light environment of selected species in an undisturbed forest, and Paper III aims to understand the effect of logging on natural regeneration of the species studied.

This study forms part of a large-scale experiment and a multi-dimensional research initiative on forest ecology and silviculture, including factors that affect species' natural regeneration. Sampling plots were not placed on particular microsites (e.g. gaps vs. non-gaps); instead, attention was directed towards the entire forest and then the species' microsites were characterized.

3. Hypothesis

The following hypotheses were tested:

- (a) Topography position and slope influence distribution of long-lived pioneer timber species;
- (b) Species distribution differs from the expected with regard to crown illumination, regeneration phase, and canopy openness;
- (c) Increasing the harvesting intensity promotes natural regeneration in different magnitudes according to a given species ecological requirements; and,
- (d) Disturbances by skidder movement promote natural regeneration.

4. Species studied

Eight long-lived pioneer timber species were selected for this research, four of which develop abundant regeneration after logging (*Hura crepitans*, *Schizolobium parahyba*, *Margaritaria nobilis* and *Zanthoxylon sprucei*) and four that do not (*Cariniana estrellensis*, *Cariniana ianeirensis*, *Ceiba pentandra* and *Sweetia fruticosa*). Some species are rare and some abundant, and most are economically valuable.

Hura crepitans L. (Euphorbiaceae)

H. crepitans is a neo-tropical species; its range includes the Antilles from Cuba and Jamaica to Trinidad and Tobago. In the Americas it ranges from Costa Rica to Brazil and Bolivia (Salazar and Soihet, 2001). This is an upper canopy co-dominant and dominant species, with height between 25-40 m, cylindrical bole and dbh of mature trees up to 100 cm. It has a large crown that can cover up to a quarter of ha (Justiniano and Fredericksen, 2000). Trees can reach up to 45 m in height and dbh up to 3 m (Hartshorn, 1983). In the Amazon, it is found on young soils of alluvial origin, and develops well in deep clayed fertile soils in flooded or riparian regimes, or terraces, and has the capacity to regenerate in a variety of microsites, including shade, natural gaps, gaps created by harvesting, skid trails (Justiniano and Fredericksen, 2000), but it is commonly seen in valleys, flat terrain and mild slopes (Vargas, 1993a). It is monoecious and seeds can germinate under shade and seedlings can grow under a canopy, but need direct light to continue growing and survive (Justiniano and Fredericksen, 2000). Flowers are pollinated by bats; fruit is a compressed capsule which disseminates seeds mainly by explosion (ballistic); there are about 12-15 seeds per fruit of about 1.5-2 cm each in diameter (Justiniano and Fredericksen, 2000) and about 360-1,000 seeds per kg (Salazar and Soihet, 2001).

It is a fast-growing and light-demanding species (Salazar and Soihet, 2001, Justiniano and Fredericksen, 2000). This species has been classified as a pioneer that develops well either in mature or secondary forests and that it may be light-demanding or partially shade-tolerant (Justiniano and Fredericksen, 2000).

Schizolobium parahyba (Vell.) S.F. Blake (Caesalpinaceae)

This is a species restricted to the neo-tropics, from southern Mexico to southern Brazil (Holdridge *et al.*, 1997), and Bolivia. It is an upper canopy co-dominant species (Justiniano *et al.*, 2001), that can reach 35 m in height (Centurion, 1993). It has a cylindrical and well-formed stem without early ramifications; the crown is not dense and it drops its leaves in the dry season (Justiniano *et al.*, 2001).

S. parahyba develops well in secondary forests and in disturbed natural forests. It responds well and rapidly to disturbances created by harvesting, such as in gaps formed by tree fall gaps, roads, and skid trails. Natural regeneration will not occur without direct light; in an undisturbed forest the species has very low abundance, but it increases with any kind of disturbance (Justiniano *et al.*, 2001). Its abundance can be up to four times higher in forests with soils scarified by skidders (Jackson *et al.*, 2002) and even 10-fold (Fredericksen and Pariona, 2002). This species can colonize a wide range of habitats, such as areas well or poor drained, and rich or poor soils, but it may demand favorable edaphic conditions to reach its potential growth. Once the seedlings are established, they grow very fast reaching in short time a vertical position that ensures their survival. It is an efficient competitor, commonly outgrowing other tree species and vines (Putz, 1984; Justiniano *et al.*, 2001).

The main pollinators are bees and butterflies. Fruiting occurs during the dry season (Justiniano *et al.* (2001). The fruit is a single seeded samara legume (Peña-Claros and de Boo, 2002). Seeds are wind-dispersed. Seeds show properties of long latency and this allows them to respond to canopy openings and develop natural regeneration even without seed trees near (Justiniano *et al.*, 2001). Larvae of the Lepidoptera attack its terminal branches causing severe damage during the early stages of development. The apical branches exude a sticky compound, which traps and kills a number of small insects that try to reach the terminal leaves (personal observation). Its fruits are eaten by macaws and parrots, but depredation does not seem to affect the species' capacity for regeneration (Justiniano *et al.*, 2001). It is a fast-growing very light-demanding species (Justiniano *et al.*, 2001), reported by Peña-Claros and de Boo (2002) as being a pioneer.

Margaritaria nobilis L.f. (Euphorbiaceae)

This is a species that is widely distributed throughout the neo-tropics, including the Caribbean (Little *et al.*, 1967). Trees are medium sized, up to 20 m in height. It is adapted to moist forests in valleys, semi-deciduous, flooded or well-drained riparian zones, and it is found in mature and secondary forests (Vargas, 1993b). It is a dioecious species with abundant regeneration along riparian areas, moist and rich soils (Fuentes *et al.*, 2003) and deciduous at the end of the dry season (Croat, 1978). It has a bright-colored mimetic fruit, probably to deceive fruit-eating birds since they are not fleshy (Croat, 1978), that is dispersed by animals and gravity (Zugliani and Oliveira-Filho, 2004). The male flowers are less than 3 mm long, female flowers 1.6 mm, seeds 3 mm long (Little *et al.*, 1967). It is a light-demanding species (Zugliani and Oliveira-Filho, 2004).

Zanthoxylon sprucei Engler (Rutaceae)

There is little information about this species. It is found in moist forests (Guillén, 1993), it reaches up to 18 m in height and develops abundant regeneration in disturbed habitats. It grows in deciduous forests, develops in well-drained soils and humid valleys. Seed dispersion is by animals (Fuentes *et al.*, 2003). This genera is dioecious, its fruit usually has several follicles and shiny seeds (Croat, 1978). It is a light-demanding species (Fuentes *et al.*, 2003). Most species are pollinated by insects (Ribeiro *et al.*, 1999) and the fruits are predated by birds (Sherry, 1983).

Cariniana estrellensis (Raddi) Kuntze (Lecythidaceae)

C. estrellensis it is found in South America between 9°S and 27°40', specifically in Brazil, northeastern Paraguay, and Bolivia (Salazar and Soihet, 2001). It is an emergent tree reaching up to 50 m and dbh of 150 cm, it is deciduous and is distributed along lowland humid and sub-humid deciduous forests (Mostacedo *et al.*, 2001). The species develops well in drained deep and fertile soils (Mostacedo *et al.*, 2001; Salazar and Soihet, 2001). It does not tolerate sandy or poorly drained soils, but it can tolerate low fertility soils (Salazar and Soihet, 2001).

Its fruits are in pixidio (Quevedo, 1993), and the seeds suffer high rates of predation and show poor germination (Mostacedo and Fredericksen, 1999). Seeds fall from the tree before the fruiting; they are 3-4 cm long, 9,300-32,000 seeds/kg (Salazar and Soihet, 2001). Seeds are wind-

dispersed (Zugliani and Oliveira-Filho, 2004). The species is partially light-demanding (Mostacedo *et al.*, 2001).

Cariniana ianeirensis R. Knuth (Lecythidaceae)

This species' range includes the Atlantic forest of Brazil, the State of Matto Grosso (Brazil) and central-eastern Bolivia. Mature trees are found in the upper canopy, they can reach up to 37 m in height and dbh 130 cm. The stem is cylindrical and well formed. In the dry forest of Bolivia it has adapted to pluvial valley and riparian areas, but in more humid regions it develops on slopes as well. Its distribution is driven by the availability of moisture influenced by the combination of topography-precipitation-soil (Justiniano and Fredericksen, 1999).

C. ianeirensis is a deciduous species; it drops its leaves during the dry season (Justiniano, 1998). Flower production is highly synchronic, beginning with the rainy season; pollination occurs mainly by insects of the Hymenoptera genera; its fruits are very important for macaws and monkeys. During low seeding periods, predation can be as high as 70-85%. Fruit is a dehiscent siliqua, which contains an average of 24 winged-seeds. Seeds are liberated from the fruits during the dry season while they are still on the tree, which facilitates its dispersion by the wind. Cotyledons are rich in oil and very palatable for birds and mammals. Germination is as high as 70-90%, but it can also regenerate by sprouting. It is a fast-growing species, which needs medium light levels for germination and development. It can develop seedlings in the understory, but it also can regenerate in disturbed environments, but it seems that openings do not greatly favor its regeneration (Justiniano and Fredericksen, 1999).

Ceiba pentandra (L.) P. Gaertner (Bombacaceae)

This species ranges from southern Mexico to the Amazon, and it is also present in West Africa. *C. pentandra* is a tall, light-demanding species (Baker, 1983). It can reach up to 45-50 m in height and a dbh of 200 cm in Bolivia (Torrice, 1993; Mostacedo *et al.*, 2001), and even up to 60 m in height (Baker, 1983).

It is adapted to moist to dry forests (Holdridge *et al.*, 1997). It is generally found in secondary forests (Foster, 1990), and also in flooded and riparian forests (Mostacedo *et al.*, 2001). It is

deciduous in the dry season, and the leaves are often attacked by phytophagous. It is pollinated by bats. A mature tree can produce up to four thousand fruits, each of them with about two hundred seeds. Seed are embedded in a mass of light fiber, which serves to be disseminated by wind (each seed is about 5 mm in diameter). Seeds have the capacity of dormancy and germinate in a few days if there is sufficient moisture and light (Baker, 1983). This is a rare, long-lived light- demanding species, which needs large gaps to regenerate in natural forests (Hubbell and Foster, 1990).

Sweetia fruticosa Sprengel (Fabaceae)

This is another species about which we have little information. It is distributed in South America (Mabberley, 1987) and poorly studied, it is adapted to moist and deciduous forests (Mostacedo *et al.*, 2001) and it is semi-deciduous (Vargas, 1993a). Trees can reach about 30 m in height and 50 cm in dbh (Mostacedo *et al.*, 2001). It grows in moist bottomlands and in Bolivia it flowers from October to November, depending on the type of forest. Seeds are wind-dispersed (Mostacedo *et al.*, 2001). It is a light-demanding species (Zugliani and Oliveira-Filho, 2004).

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CHAPTER 2. PAPER I. EFFECT OF TOPOGRAPHY VARIATION ON LONG-LIVED PIONEER SPECIES DISTRIBUTION IN A BOLIVIAN TROPICAL FOREST

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Abstract

The effect of topography on the distribution of long-lived pioneer timber species was studied in a large logging experiment in a semi deciduous tropical forest in Bolivia. A random complete block design experiment was used, comparing treatment plots of 27 ha each, in which a set of plots of 20 m x 20 m were placed in a 75 m x 75 m grid system. Eight species were selected: four that usually develop abundant natural regeneration after logging (Group A: *Hura crepitans*, *Margaritaria nobilis*, *Schizolobium parahyba* and *Zanthoxylon sprucei*), and four that usually do not (Group B: *Cariniana estrellensis*, *Cariniana ianeirensis*, *Sweetia fruticosa* and *Ceiba pentandra*). The effect of their topographic position (*base*, *slope*, *ridge*) and slope (*flat*, *moderate*, *steep*) was analysed by means of a variance analysis and Tukey test for multiple comparisons. Abundance/ha was estimated for each topographic category in each of nine 27 ha plots, giving n= 9 for each category for statistical tests.

Species varied widely in abundance (height ≥ 0.5 m) from 52.4 individuals/ha in the most abundant (*H. crepitans*) and 0.53 individuals/ha (*C. pentandra*) in the least abundant. These results illustrate the rarity of light-demanding species in the tropics and the difficulties to study them. Most statistical significances appeared at the sapling size, where sufficient individuals were found for statistical inferences.

Species group A showed a generalist pattern regarding topographic position, with the exception of *M. nobilis*, which was statistically related to its *Slope* and *Ridge* position. However, this species group showed a preference for either *Flat* or *Moderate* slope classes, where better moisture and fertility are presumed to exist. In general, species that develop abundant regeneration after logging were generalists with respect to their topographic position and specialists regarding steepness of slope. Since this is a semi-deciduous forest where water availability may be a constraint during the dry season, we hypothesized that higher water availability in gentle slope microhabitats may influence this pattern, which should be considered when managing these species.

Key words: Bolivia; Forest ecology; Long-lived pioneer species; Topographic effects; Tropical forest; Silviculture

1. Introduction

Sustainable forest management and tree species conservation face several challenges in the tropics. One immediate problem when we enter the forest is the identification of the species itself, so the first question is *what species is this?* Species diversity is, on one hand, an opportunity for humanity, but on the other hand it is a management constraint, at least for now, because it implies the need for specific ecological knowledge on hundreds of timber and non-timber species existing in the neo-tropics (Gentry, 1986, 1988; Steege *et al.*, 2003).

Despite the well-known advantages of biodiversity for human beings, species richness raises a practical question about management: How does one deal with this species diversity, including their differences in ecological and microsite requirements? This research focuses on the effect topography has on tree species' distribution and seeks to contribute towards partially answering the previous question. Specifically, it focuses on the ecology of the long-lived pioneer tree species guild, which contains several valuable timber species that are widely harvested in the neo-tropics (Whitmore, 1989), and seeks understand the effect topography has on species' distribution in a Bolivian tropical forest.

A plant species can be associated with a particular environment for several reasons. Amongst these reasons are the dispersal or colonization patterns, anthropogenic impact, competition, the effect of predators, and habitat specialization or habitat-related competitive advantages (Harms *et al.*, 2001). In the case of the topography, substantial evidence suggests that the topography influences the species' distribution in different ways. In the Yasuny National Park, Ecuadorian Amazon, the vegetation zones were distinguished as valley, mid-slope and upper-ridge topographic positions. The basal area and tree size and abundance was higher on the upper-ridge, intermediate on the mid-slope, and lowest in the valley (Valencia *et al.*, 2004). Topography can affect species differently, depending on the tree size, as reported in Indonesia in a study on the habitat association of trees and seedling species (Webb and Peart, 2000). Seedlings' (≥ 5 cm tall to $\text{dbh} \leq 1$ cm) and adults' ($\text{dbh} \geq 10$ cm) density were compared with three physiographic habitats (plateau with deep humus layer; sharp ridges and upper slopes; gullies and lower slopes near permanent streams). Adults' association with the habitat was more evident than the seedlings'.

Water availability can be affected by topographic position; therefore, it can affect species' distribution, as found in Suriname by Gourlet-Fleury and Picard (2004), where the increase in diameter after logging was higher in the bottomlands, probably because of greater water availability during the dry season. The effect of the topographic gradient on the water availability has been also reported by Olivera-Filho *et al.* (1998) as affecting species' distribution in a dry forest, in Brazil, as well as in a Panamanian seasonal forest (Harms *et al.*, 2001).

In addition to water, there are other changes related to the topography, such as gap formation dynamics, canopy height, and edaphic conditions (Clark *et al.*, 1998; Clark 2002). The main edaphic factors modified by topographic gradients are pH, soil nutrients, moisture and texture (Clark, 2002). Nutrient content variations due to the topographic position have been reported by Silver *et al.* (1994), and forest structure and edaphic condition relationships along "catenas" by Magalhães *et al.* (1998). In a 43-km transect in the Peruvian Amazon, the soil texture and cation exchangeable content varied in relation to the topographic position and floristic patterns reflected the differences in the soil along a catena (Tuomisto *et al.*, 2003). Similarly, in Japan, Kubota *et al.* (2004) found that species-specific habitat preferences revealed spatial variation in tree species' abundance distribution, as was also seen in Borneo, where heterogeneity of habitats, such as soil type, or topography, contributes to species' diversity on a landscape scale (Webb and Peart, 2000).

Long-lived pioneer tree species' distribution is most often studied in relation to their light requirements, but studies on substrate conditions are needed to better understand species ecology (Herrera and Finegan, 1997). In La Selva, Costa Rica, Clark *et al.* (1998) studied a species group –two pioneers (*Cecropia obtusifolia* and *Cecropia insignis*), and seven non-pioneers (*Simarouba amara*, *Hyeronima alchorneoides*, *Pithecellobium elegans*, *Dipterix panamensis*, *Hymenolobium mesoamericanum*, *Lecythis ampla*, and *Minquartia guianensis*), and found that 6 out of 9 species (dbh >4 cm) were significantly associated with some type of topographic position (flat terrace/ridgetop, upper slope, mid-slope, and base of slope). Four species were also associated with some type of slope angle (flat, gentle, moderate, and steep), including one pioneer; and seven species (including one pioneer) were associated with some soil type (old alluvial, residual, stream valley). Tree species and topographic position associations have been found in Puerto Rico (Basnet, 1992), and in Bolivia in a seasonal tropical forest (Guzmán, 1997).

When studying long-lived pioneer species habitats, such as the topography, researchers usually face limitations for statistical inferences because of small sample size (Clark, 2002). Low abundance is a common phenomenon in the tropical tree species, making statistical inferences in ecological studies difficult. Species can be rare or common. In general, tree species in tropical forests are less abundant per unit area than in a temperate forest, where the number of species is much lower and the abundance much higher per unit area (Bawa and Ashton, 1991). Therefore, the meaning of rarity differs for tree species in a tropical forest as opposed to a temperate forest. Species scarcity in the tropics has been noted by several authors, such as Clark *et al.* (1999) in La Selva, Costa Rica, who found that 56 species out of a total of 267 were represented by only one individual/ha, and 74% showed ≤ 1 individual/ha (dbh ≥ 10 cm) and were therefore classified as rare species. Similarly, Pitman *et al.* (1999) found in the Amazon that 88% of the species presented less than 1 individual/ha (dbh ≥ 10 cm) and that 253 species and morphospecies out of 829 were represented by a single individual in 36 ha sampled. In BCI, Panamá, 47 species out of 239 (dbh ≥ 1.0 cm) were classified as rare (Hubbell and Foster, 1986), and in Ecuador nearly 40% of the 1104 species identified in a 25-ha plot were represented by ≤ 1 individual/ha (dbh ≥ 1.0 cm) (Valencia *et al.* (2004). In Costa Rica, the official criteria and indicators for forest management consider a species to be rare if it has less than ≤ 0.30 individuals/ha ≥ 30 cm dbh. In this study, we consider a species to be rare when abundance is less than 1 individual/ha (dbh ≥ 10 cm), in accordance to Clark and Clark's (1992) threshold for Costa Rica, and Pitman *et al.*'s (1999) for the Amazon. We expected to find common and rare species, and predicted that common ones would be generalists with respect to the topography, while the rare species would be specialists. Similarly, we expected that species that develop abundant regeneration after logging would also be generalists and those that do not, would be specialists.

This study forms part of a broad research regarding long-lived pioneer tree species' ecology and silviculture, which includes studies on their natural regeneration, light requirements, responses to disturbance, and microhabitat effect. The objective of this research was to determine the abundance and distribution of selected species in relation to their topographic variables. We tested the hypothesis that the topographic position and slope habitats influence species' distribution according to their ecological characteristics.

2. Methods

2.1 Study site

This study was developed in the Guarayos Region, Department of Santa Cruz, in eastern Bolivia. The forest is a transition between dry and moist Amazonian forest (La Chonta, 1998). The natural vegetation of the area is classified as Sub-tropical Humid Forest according to Holdridge's system (Unzueta, 1975). Geologically the region is a continuation of the Crystalline Brazilian Shield with low fertility soils belonging to the orders of Oxisols, Inceptisols and Ultisols (La Chonta, 1998). In general, the study site presents black and brown probably anthropogenic soils, the organic soil is shallow (1-3 cm), and its texture is dominated by silt and fine sand; a high concentration of iron is found (Vroomans, 2003). The annual mean precipitation is 1,562 mm, with an annual mean temperature of 24.5°C, with a maximum of 28.9°C and a minimum of 10°C (La Chonta, 1998). Fire is an ecological factor in the region, and is very likely to occur during the six months of the dry season.

Specifically, the study was carried out in the La Chonta forest concession (15°47'S, 62°55'W). The total area of the concession is 100,000 ha. The site has about 125 tree species dbh > 10 cm (Instituto Boliviano de Investigación Forestal -IBIF, unpublished data), but only 17 were harvested in 2004, and of these, only 7 species were harvested in quantities greater than 100 m³ in all (La Chonta company, unpublished data). *Swietenia macrophylla* was heavily harvested in the past, but is now scarce.

The cutting cycle is 30 years, the annual logging compartments are about 2400 ha, within which only 2-3 trees/ha are harvested resulting in the extraction of 5-7 m³/ha (La Chonta, 1998). This qualifies as a low intensity harvesting system. The Company's management plan was certified by the Forest Stewardship Council in 1998. The forest canopy is about 25 m high; the emergent tree species include *Hura crepitans*, *Cariniana* spp., *Pseudolmedia laevis*, *Terminalia oblonga*, and *Ficus boliviana*, which are the most common species.

The landscape of the treatments where the plots were established varies from flat to moderate slopes, with occasional very steep sites. Soils are generally well drained, with no permanent flooding, and with occasional superficial flat rocks (Vroomans, 2003).

2.2 Study species and sampling

Eight long-lived pioneer species that vary widely in abundance were selected for study. Four species usually develop abundant regeneration after harvesting, while four of them do not (Table 1).

Table 1. List of selected long-lived pioneer species

Species	Family	Abundance/ha (dbh \geq 10 cm)	Dispersion mode	Expected regeneration after logging
<i>Hura crepitans</i>	Euphorbiaceae	8.5	Ballistic	High
<i>Margaritaria nobilis</i>	Euphorbiaceae	2.4	Animal, gravity	High
<i>Schizolobium parahyba</i>	Caesalpiniaceae	1.1	Wind	High
<i>Zanthoxylon sprucei</i>	Rutaceae	0.7	Animal	High
<i>Cariniana ianeirensis</i>	Lecythidaceae	2.8	Wind	Low
<i>Sweetia fruticosa</i>	Fabaceae	2.4	Wind	Low
<i>Cariniana estrellensis</i>	Lecythidaceae	1.1	Wind	Low
<i>Ceiba pentandra</i>	Bombacaceae	0.25	Wind	Low

Source for abundance data: IBIF (Unpublished data)

The study was conducted in the Long-Term Silviculture Research Project (LTSRP) being implemented by IBIF in different forests of Bolivia. In the La Chonta forest concession there have established 3 blocks of LTSRP, each block consisting of four 27 ha plots (Figure 1). Elevation varied from 293 m.a.s.l. to 394 m.a.s.l. (Vroomans, 2003). One of four treatments is applied to each plot. Treatments represent a gradient of harvesting and silviculture intensity, ranging from a control plot (unlogged, no silviculture), to an intensive treatment (roughly twice the normal harvesting, plus a group of silviculture treatments). Each block is 800 ha, and the distance from block to block ranges between 1.5 to 5.5 km, and the distances are not less than 500 m between treatment plots inside the blocks. The experiment was established in the year 2000 as a randomized complete block design, avoiding areas affected by fire. For more detail on the experimental design see www.ibifbolivia.org.bo.

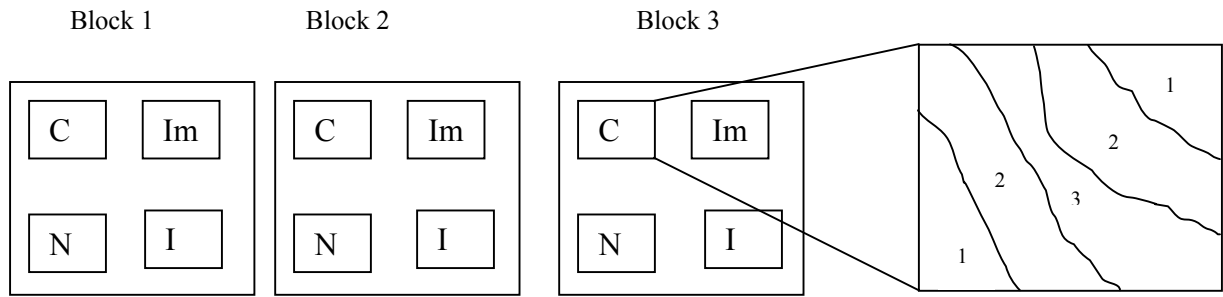


Figure 1. Diagram of the plots of the Long-term Silviculture Research Project established in the La Chonta concession. This research used “Control -C” and “Intensive harvesting -I” treatments to analyze the effect of the topographic position and slope. The magnified plot illustrates the hypothetical topographic variation (1=Base, 2= Slope, 3= Ridge). C=Control, N=Normal, Im=Improved, I=Intensive treatments. Figure not to scale.

Because of the variable nature and the heterogeneous responses of natural regeneration in logged forests, high variances were inevitable. To increase the sample size, data was taking from both unlogged and logged treatments after checking that both unlogged and logged treatment populations responded similarly to the topography. In addition, in an attempt to increase statistical power, the data was analysed using 20 m x 20 m plots as replicas. However, the approach led to even higher variances (data not shown) due to the high variability among the plots. It was concluded that 20 m x 20 m plots were too small to be used as replicas, so the approach was rejected.

Data was taken using a 75 m x 75 m grid system, following a design recommended by Clark *et al.* (1999). Plots of 20 m x 20 m were placed in the intersections of each grid line (to avoid plots overlapping with existing trials, some plots were moved 10 m). Ninety-two plots were established in Block 1, 93 in Block 2, and 96 in Block 3, resulting in 281 plots of 400 m² each, for a total sample area of 11.24 ha within the total area of 162 ha. In each plot all the individuals of the selected species that were ≥ 0.5 m in height were registered, and their height and dbh measured.

The topographic position of each 20 m x 20 m plot was assigned to one of the following categories: 1=Base; 2=Slope; 3=Ridge. Each topographic position was characterized by using 3-D maps (Fig. 2) developed by Vroomans (2003) and verified during the field work. The slope was measured with a Suunto clinometer in the direction of the greatest slope at a fixed distance of two meters. Slope gradient was grouped into three classes for analysis: 1=Flat (<10.0% slope); 2=Moderate (10.0-19.9%); 3= Steep ($\geq 20.0\%$).

For the statistical analysis, data from the 20 m x 20 m plots were converted to means per ha for each topographic and slope category in each treatment plot, giving three estimates (since there were three replications = three blocks) per category (topographic and slope position) per treatment plot. The assumptions for a parametric analysis were first tested and data was log transformed to obtain a normal distribution. A one-way ANOVA was carried out to compare species' abundance among the topographic types of positions and slopes, and one two-way ANOVA was carried out to detect the interaction among types of topographic positions and slopes and abundance in three diameter classes: saplings (dbh <5.0 cm), pole (dbh 5.0-9.9 cm), and trees (dbh ≥10.0 cm). A Tukey's test was used for multiple comparisons. For all the analyses, alpha was 0.05.

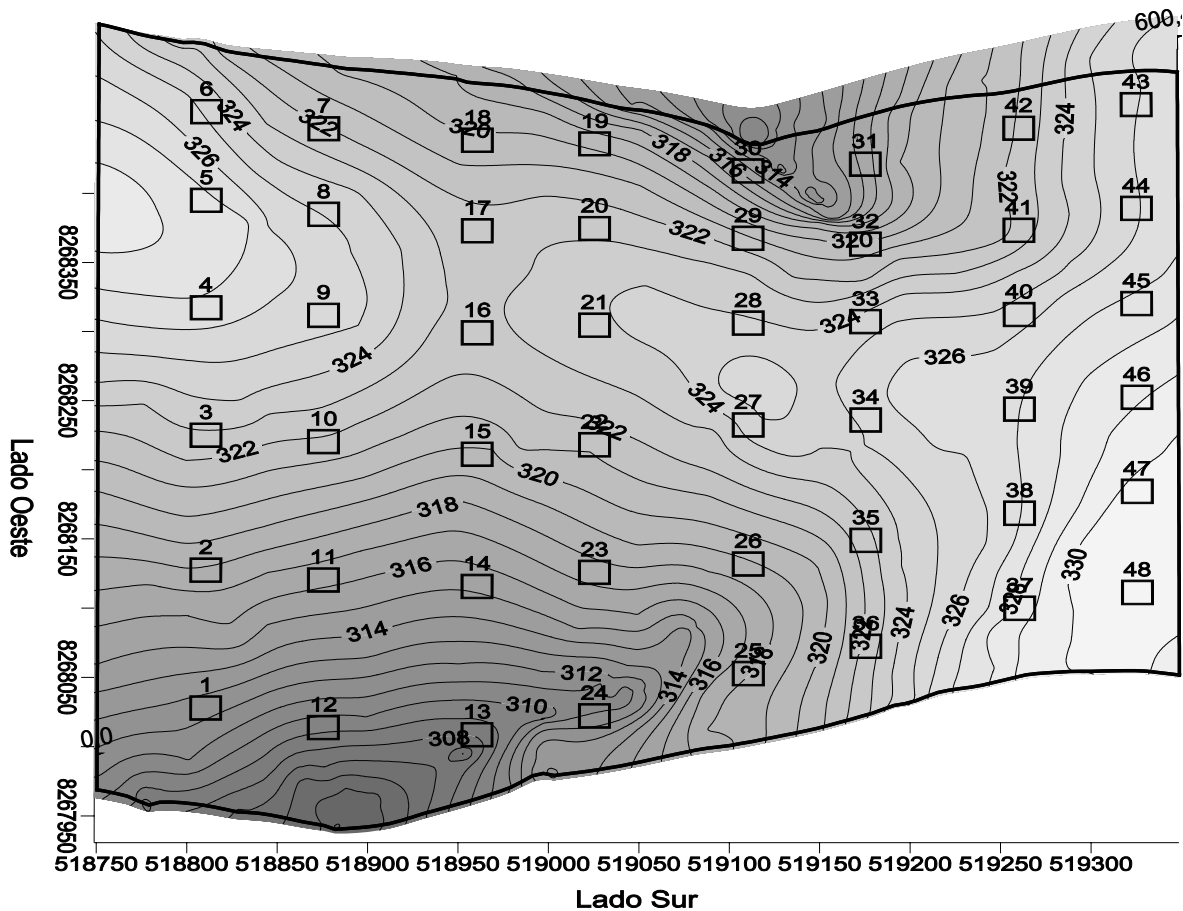


Figure 2. 3-D topographic map of a 27 ha treatment plot with a 75 m x 75 m grid with 48 20 m x 20 m sample plots placed at the intersections of the grid. Transects of plots were sometimes moved 10 m to avoid overlapping with the trail system installed in the plots. Contour lines are drawn at 1 m intervals. Map base taken from Vroomans (2003).

3. Results

As pointed out by Clark (2002) among others, tree species in the tropics are often extremely rare, as we found in this research. *C. pentandra* accounted for only 6 individuals ≥ 0.5 m height, and was eliminated from the analysis because of the lack of sufficient individuals for statistical inferences. The most abundant species was *H. crepitans* with 6.9 individuals/ha (dbh ≥ 10 cm). The least abundant, considered rare, were *S. parahyba*, *C. estrellensis*, and *C. pentandra*, with less than 1 individual/ha (dbh ≥ 10 cm) (Table 2).

Table 2. Species' abundance (per ha) for size classes (unlogged + logged plots)

Species	Classes of individual sizes (N/ha)			Common / rare
	≥ 0.5 m height	≥ 5.0 cm dbh	≥ 10 cm dbh	
<i>H. crepitans</i>	52,4	9,6	6,9	Common
<i>Z. sprucei</i>	38,7	2,1	1,1	Common
<i>M. nobilis</i>	20,2	2	1,5	Common
<i>C. ianeirensis</i>	11,5	2,9	1,8	Common
<i>S. fruticosa</i>	7,7	3,8	2,5	Common
<i>S. parahyba</i>	12	2,2	0,9	Rare
<i>C. estrellensis</i>	4,2	0,9	0,8	Rare
<i>C. pentandra</i>	0,5	0,1	0	Rare
Total	147,2	23,7	15,5	

The one-way ANOVA results for all individuals ≥ 0.5 m height (Table 3a), showed that only *M. nobilis* was dependently distributed amongst the classes of topographic positions, having a significantly higher distribution in (i.e. preference for) Slope and Ridge positions. In addition, it is possible to observe a tendency for significance for *H. crepitans* ($P= 0.0747$), with its greatest abundance in the Slope position. High variability was observed for most species.

The results for the two-way ANOVA, considering diameter classes, confirmed *M. nobilis* as the only species associated with topographic positions (Slope and Ridge) for ddh < 5.0 cm (saplings, Table 3b). For poles (dbh 5.0-9.0 cm, Table 3c) *S. parahyba* showed a trend to favor the Base position ($P= 0.0564$). No one species was associated with topography when examining tree sizes (dbh 5.0-9.9 cm, Table 3d), this may be due to the low sampling size.

Table 3. Mean abundance (No/ha) \pm standard deviation per size classes and topographic position for size classes (a) ≥ 0.50 m height (One-way ANOVA), (b) saplings, (c) pole, (d) trees (Two-way ANOVA). Means within species with the same letter are not significantly different.

(a)				
Species	Height ≥ 0.5 m			P-value
	Base	Slope	Ridge	
<i>C. estrellensis</i>	1.42 \pm 0.41 a	1.70 \pm 0.34 a	1.08 \pm 0.81 a	0.3079
<i>C. ianeirensis</i>	2.32 \pm 1.03 a	3.57 \pm 1.80 a	5.65 \pm 3.79 a	0.1555
<i>H. crepitans</i>	16.27 \pm 1.97 a	22.55 \pm 7.72 a	13.48 \pm 3.31 a	0.0747
<i>M. nobilis</i>	3.58 \pm 4.12 b	9.31 \pm 9.94 a	7.43 \pm 8.71 a	0.0028
<i>S. parahyba</i>	3.02 \pm 1.51 a	6.17 \pm 5.13 a	2.72 \pm 2.77 a	0.4430
<i>S. fruticosa</i>	2.84 \pm 0.83 a	2.77 \pm 1.34 a	2.15 \pm 0.74 a	0.5318
<i>Z. sprucei</i>	12.35 \pm 14.49 a	22.37 \pm 11.93 a	4.18 \pm 1.39 a	0.1776

(b)				
Species	dbh < 5 cm			P-value
	Base	Slope	Ridge	
<i>C. estrellensis</i>	0.98 \pm 0.32 a	1.43 \pm 0.44 a	0.90 \pm 0.68 a	0.3031
<i>C. ianeirensis</i>	1.87 \pm 0.97 a	2.59 \pm 1.54 a	4.13 \pm 2.87 a	0.3637
<i>H. crepitans</i>	13.37 \pm 1.81 a	18.93 \pm 6.93 a	10.47 \pm 2.08 a	0.1144
<i>M. nobilis</i>	3.04 \pm 3.90 a	8.34 \pm 9.66 a	6.98 \pm 7.93 a	0.0833
<i>S. parahyba</i>	2.13 \pm 1.15 a	5.46 \pm 4.86 a	2.10 \pm 2.56 a	0.3953
<i>S. fruticosa</i>	1.34 \pm 0.55 a	1.61 \pm 1.64 a	0.98 \pm 0.17 a	0.8256
<i>Z. sprucei</i>	11.82 \pm 14.27 a	21.56 \pm 10.99 a	3.38 \pm 1.53 a	0.1746

(c)				
Species	dbh 5.0 - 9.9 cm			P-value
	Base	Slope	Ridge	
<i>C. estrellensis</i>	0.00 \pm 0.0 a	0.00 \pm 0.00 a	0.09 \pm 0.16 a	0.4444
<i>C. ianeirensis</i>	0.18 \pm 0.15 a	0.27 \pm 0.47 a	0.72 \pm 0.62 a	0.7378
<i>H. crepitans</i>	0.36 \pm 0.31 a	1.16 \pm 0.43 a	1.14 \pm 0.82 a	0.2928
<i>M. nobilis</i>	0.18 \pm 0.31 a	0.09 \pm 0.16 a	0.18 \pm 0.31 a	0.9837
<i>S. parahyba</i>	0.80 \pm 0.54 a	0.44 \pm 0.15 a	0.09 \pm 0.15 a	0.0564
<i>S. fruticosa</i>	0.53 \pm 0.46 a	0.35 \pm 0.40 a	0.45 \pm 0.41 a	0.9754
<i>Z. sprucei</i>	0.18 \pm 0.16 a	0.45 \pm 0.57 a	0.45 \pm 0.32 a	0.3394

(d)				
Species	dbh ≥ 10 cm			P-value
	Base	Slope	Ridge	
<i>C. estrellensis</i>	0.44 \pm 0.15 a	0.27 \pm 0.27 a	0.09 \pm 0.16 a	0.3509
<i>C. ianeirensis</i>	0.27 \pm 0.27 a	0.70 \pm 0.54 a	0.80 \pm 0.81 a	0.6600
<i>H. crepitans</i>	2.56 \pm 1.58 a	2.47 \pm 1.82 a	1.87 \pm 1.07 a	0.6680
<i>M. nobilis</i>	0.36 \pm 0.41 a	0.89 \pm 0.55 a	0.27 \pm 0.47 a	0.1886
<i>S. parahyba</i>	0.10 \pm 0.16 a	0.26 \pm 0.26 a	0.54 \pm 0.27 a	0.3228
<i>S. fruticosa</i>	0.97 \pm 0.53 a	0.81 \pm 0.72 a	0.71 \pm 0.17 a	0.8379
<i>Z. sprucei</i>	0.35 \pm 0.31 a	0.36 \pm 0.42 a	0.36 \pm 0.41 a	0.9984

The One-way ANOVA for percent slope (population ≥ 0.5 m height, Table 4a) resulted in three species statistically associated with Flat and Moderate slopes: *M. nobilis*, *S. parahyba* and *Z. sprucei*.

The results of the two-way ANOVA (Table 4b) for percent slope for sizes dbh < 5.0 cm, showed a similar pattern, presenting the same species associated with Flat and Moderate slopes (*M. nobilis*, *S. parahyba*, and *Z. sprucei*). Similar to the pattern found for the topographic positions,

there were no statistically significant differences at dbh sizes 5.0-9.9 cm (Table 4c), except for *Z. sprucei*, which showed a tendency to favor Flat slopes (P=0.0754). For larger trees (dbh \geq 10.0 cm, Table 4d) only the *H. crepitans* showed a significant preference for Flat and Moderate slopes, while the *M. nobilis* favored Flat slopes (P=0.0729).

Table 4. Mean abundance (No/ha) \pm standard deviation per size classes and percent slope for size classes (a) \geq 0.5 m height (One-way ANOVA), (b) saplings, (c) pole, (d) trees (Two-way ANOVA). Means within species with the same letter are not significantly different.

(a)

Species	Height \geq 0.5 m			P-value
	Flat	Moderate	Steep	
<i>C. estrellensis</i>	2,03 \pm 1,56 a	1,44 \pm 1,23 a	0,72 \pm 0,62 a	0,6069
<i>C. ianeirensis</i>	3,55 \pm 1,50 a	5,56 \pm 3,54 a	2,42 \pm 2,21 a	0,2592
<i>H. crepitans</i>	25,14 \pm 14,44 a	21,51 \pm 7,82 a	5,66 \pm 4,35 a	0,1081
<i>M. nobilis</i>	10,53 \pm 12,82 a	9,06 \pm 9,93 a	0,72 \pm 0,62 b	0,0495
<i>S. parahyba</i>	6,84 \pm 7,16 a	4,71 \pm 1,13 a	0,36 \pm 0,42 b	0,0495
<i>S. fruticosa</i>	3,55 \pm 0,98 a	3,03 \pm 0,71 a	1,17 \pm 1,21 a	0,1677
<i>Z. sprucei</i>	16,32 \pm 3,97 a	21,15 \pm 10,06 a	1,44 \pm 0,97 b	0,0008

(b)

Species	dbh $<$ 5 cm			P-value
	Flat	Moderate	Steep	
<i>C. estrellensis</i>	1,50 \pm 1,11 a	1,26 \pm 1,10 a	0,54 \pm 0,47 a	0,5387
<i>C. ianeirensis</i>	2,32 \pm 1,03 a	4,48 \pm 2,47 a	1,79 \pm 1,79 a	0,1093
<i>H. crepitans</i>	20,82 \pm 11,71 a	17,61 \pm 7,70 a	4,32 \pm 3,89 a	0,1905
<i>M. nobilis</i>	9,56 \pm 12,24 a	8,25 \pm 9,15 ab	0,54 \pm 0,47 b	0,0367
<i>S. parahyba</i>	5,96 \pm 6,59 a	3,55 \pm 1,13 a	0,18 \pm 0,31 b	0,0227
<i>S. fruticosa</i>	1,52 \pm 1,02 a	1,69 \pm 0,43 a	0,72 \pm 0,82 a	0,1656
<i>Z. sprucei</i>	15,33 \pm 3,91 a	20,25 \pm 9,49 a	1,17 \pm 0,96 b	0,0017

(c)

Species	dbh 5.0 - 9.9, cm			P-value
	Flat	Moderate	Steep	
<i>C. estrellensis</i>	0,09 \pm 0,16 a	0,0	0,0	0,4444
<i>C. ianeirensis</i>	0,27 \pm 0,27 a	0,54 \pm 0,47 a	0,36 \pm 0,16 a	0,6278
<i>H. crepitans</i>	1,14 \pm 0,82 a	1,16 \pm 0,42 a	0,36 \pm 0,31 a	0,2672
<i>M. nobilis</i>	0,0 a	0,36 \pm 0,31 a	0,09 \pm 0,16 a	0,1812
<i>S. parahyba</i>	0,79 \pm 0,78 a	0,54 \pm 0,47 a	0,0 a	0,3307
<i>S. fruticosa</i>	0,79 \pm 0,70 a	0,36 \pm 0,41 a	0,18 \pm 0,31 a	0,6639
<i>Z. sprucei</i>	0,72 \pm 0,79 a	0,36 \pm 0,31 a	0,0 a	0,0754

(d)

Species	dbh \geq 10 cm			P-value
	Flat	Moderate	Steep	
<i>C. estrellensis</i>	0,44 \pm 0,40 a	0,18 \pm 0,16 a	0,18 \pm 0,16 a	0,8134
<i>C. ianeirensis</i>	0,96 \pm 1,05 a	0,54 \pm 0,71 a	0,27 \pm 0,27 a	0,8143
<i>H. crepitans</i>	3,17 \pm 3,17 a	2,74 \pm 1,91 ab	0,98 \pm 0,67 b	0,0293
<i>M. nobilis</i>	0,98 \pm 0,67 a	0,45 \pm 0,56 a	0,09 \pm 0,16 a	0,0729
<i>S. parahyba</i>	0,09 \pm 0,16 a	0,62 \pm 0,39 a	0,18 \pm 0,16 a	0,1527
<i>S. fruticosa</i>	1,24 \pm 0,61 a	0,98 \pm 0,33 a	0,27 \pm 0,47 a	0,1558
<i>Z. sprucei</i>	0,27 \pm 0,27 a	0,54 \pm 0,28 a	0,27 \pm 0,01 a	0,4697

4. Discussion

Despite the large area covered by the sample plots, we found few individuals for some species, which reduced the power for testing the hypothesis. Species were classified as locally rare having ≤ 1 individual/ha (dbh ≥ 10 cm); they were consistently rare or common when using the results from both the unlogged treatment (Paper II) and unlogged + logged (this paper). Since low sampling size may affect statistical power of the tests (Steidl *et al.*, 1997; Underwood, 1997), we suggested characterizing the results for class size dbh ≥ 5.0 cm as preliminary.

Despite our expectations, no clear pattern was found for rare or abundant species. However, all species that presented some degree of association with the topography belonged to the species group known to develop abundant regeneration after logging. These species are considered to be the most light-demanding. *M. nobilis* was associated with slope and ridge topographic positions and with flat and moderate slopes. No species showed any significant preference for steep slopes, perhaps due to the low sample size as steep slopes are uncommon in the plots. *H. crepitans* was the only other species associated with a slope topographic position, being more prevalent on gentle slopes in larger dbh classes, confirming its ecological preference for flat terrain (Justiniano and Fredericksen, 2000; Vroomans, 2003). *S. parahyba* and *Z. sprucei*, the most light-demanding species of the group, favoured gentle topography positions in all cases.

Among the species that were statistically associated with topographic classes, one was considered rare (*S. parahyba*) and three were common (*M. nobilis*, *Z. sprucei*, and *H. crepitans*), so no clear pattern was found coinciding with Harms *et al.* (2001). However, a clear pattern of association was found for species that belong to the group that is known to respond well to disturbances. Therefore, we concluded that species that often respond well to disturbances were specialists regarding topography and those that do not develop abundant regeneration after logging were generalists.

Several factors might explain why certain species may be influenced by topography. Soil condition changes with topography and slope could be one explanation, as found by other researchers. Clark *et al.* (1998) found in La Selva, Costa Rica, that the rank of the factors affecting species distribution was soil type > topographic position > slope angle. In a tropical semi-deciduous forest in Brazil, Martins *et al.* (2003) found significant correlations among

species distribution and topographic gradient, soil fertility and texture: soil fertility increased from ridge to bottoms, explained by processes of erosion and deposition. Soil aluminum content was found to increase as one moved from lower to upper slopes as the soil became more acidic. In Costa Rica, Herrera and Finegan (1997) found that distribution of two long-lived pioneer species was clearly related to topography and soil fertility: *Vochysia ferruginia* was found on steeper slopes with higher acidity and lesser Mn and *Cordia alliodora* on flatter topography with lower acidity and higher Mn.

Disturbance changes along topographical gradients may be another reason for species distribution patterns. Increase of slope angles usually results in an increase in frequency and size of tree fall (Poorter *et al.*, 1994; Gale, 2000) and confirmed by a model developed by Robert (2003). Similarly, in Puerto Rico and Costa Rica, it was also found that higher species diversity was a result of higher tree fall frequency (Denslow, 1995). In our case, species favored Flat and Moderate slopes, not Steep ones, so if harvesting triggers species regeneration, a hypothetical non-random harvesting favoring flat and moderate slopes could influence species responses in these habitats.

Soil moisture is another factor that often influences species distribution, and we suggest that this may be the main factor in our case since the La Chonta concession is a semi-deciduous forest, where water availability might become a limiting factor. In the dry season in Panama, the water potential was always higher in bottom slope sites (-25 kPa) than plateau sites (-550 kPa) (Daws *et al.* 2002), confirming Becker *et al.* (1988)'s findings that slope bottom sites are more moist (during the dry season) than mid-slope and plateau sites, which could be critical for moisture-demanding species during the dry season. Also in Panama, drought-sensitive species were associated with slopes and stream banks, finding that seedling survival was higher in these habitats because of the higher water availability during the dry season compared to plateau sites (Harms *et al.*, 2001). In another study, uprooting was more common in poorly drained bottom lands and on steep slopes- up to three times higher than in the valley (Gale and Barfo, 1999). In the Colombian Amazon, the highest tree species richness was found in well-drained upland soils with a total of 668 species, and the lowest was found in poorly-drained flood plains only 90 species (Duivenvoorden, 1996). In Japan, Kubota *et al.* (2004) claim that the non-random spatial distribution might also reflect species' susceptibility to water limitations along topographic catena.

As already indicated, moisture may be the factor driving our species distribution in relation to topography. Higher water content in the flat/moderate microsites may be the predominant factor influencing species distribution in our study area, since water is the primary limiting factor in forests where water is not abundant. Our study site is a semi-deciduous forest, and water may be a limiting factor, as found by Oliveira-Filho *et al.*'s (1998) in a dry forest in Brazil and Harm *et al.* (2001). Vroomans (2003) also reached similar conclusions on our study site, finding a greater abundance of *H. crepitans* (dbh \geq 40 cm) in valleys, but no associations for *S. parahyba* and *C. ianeirensis*. Although moisture seems to be an important factor affecting species' distribution, a question remains: how can species' distribution be significantly associated with slope, but have no significant relationship with topographic position? We hypothesize that slope percent reflects better species habitats than topographic position, because the % of declination was measured for each tree, while the topographic position was assigned for the entire 400 m² plot.

There is another question pending for consideration, why did species that developed abundant regeneration after logging favour specific topographic conditions, while the remaining species behaved more as generalists with regard to topography? The first group of species belong to the most light-demanding, and although we do not have data about growth, we speculate that this group of species may be faster-growing, which would make them highly-demanding of water resources, more available in gentle and flat slopes. However, the relationship between the degrees of light-demanding, growing and water requirements still need to be studied. Interestingly, *M. nobilis*, one of the high light-demanding species, was found to be associated with the slope and ridge topographic position classes, as well as to gentle slopes. This fact adds another level of complexity, which may be explained by a combination of soil properties and moisture requirements. For silviculture purposes, our results suggest paying attention to species that develop abundant regeneration after logging on gentle slope sites, since these microsites seem to be their best habitat and therefore, where they may be more likely to respond better to silviculture treatments.

Although in the La Chonta concession moisture may play a key role for seedlings growing in diverse topographic conditions, there may be other even more critical factors affecting regeneration survival, such as light availability, especially for small seedlings. Most species have

few individuals in medium and large diameter classes, which mean that silviculture treatments should focus not only on seedlings, but also on saplings and poles.

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CHAPTER 3. PAPER II. LIGHT ENVIRONMENT, SEED DISPERSION AND THE NATURAL REGENERATION OF LONG-LIVED PIONEER TIMBER SPECIES IN AN UNDISTURBED BOLIVIAN TROPICAL FOREST

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Abstract

Progress towards understanding of tropical forest stand dynamics requires an objective characterization of the regeneration niches of tree species. In an operational scale logging experiment in a semi-deciduous tropical forest in eastern Bolivia, we studied the light environment and microsites of long-lived pioneer species in an undisturbed forest and determined their seed dispersal distance. Eight species were selected: four that often develop abundant regeneration after logging (*Hura crepitans*, *Margaritaria nobilis*, *Schizolobium parahyba*, *Zanthoxylon sprucei*), and four that do not (*Cariniana estrellensis*, *Cariniana ianeirensis*, *Sweetia fruticosa*, *Ceiba pentandra*). Individuals ≥ 0.5 m in height were sampled in three undisturbed plots of 27 ha each, using sample plots of 20 m x 20 m placed in a 75 m x 75 m grid. An expected distribution was built based on independent samples taken in the forest and compared with the distribution of species regeneration. Only one individual of *C. pentandra* was found and *S. parahyba* was absent, therefore we only had data for six species.

The hypothesis tested was that species distribution (“observed” distribution) differed from the forest distribution (“expected” distribution) regarding crown illumination, regeneration phase, and canopy openness and that species differed among themselves. Only *Z. sprucei* showed a higher crown illumination index than the forest (expected) distribution (saplings, dbh < 5.0 cm). For pole size (dbh 5.0-9.9 cm), we only had data for four species, and three them differed from the forest distribution. For canopy openness only *Z. sprucei* (for saplings) was different from the forest distribution, with high abundance in the large opening class. However, for the regeneration phase all species had similar distributions as the forest. Low abundance of some species may have affected the statistical power of the tests, so we suggest that these results be taken with caution, especially for pole size.

The multivariate analysis confirmed that *Z. sprucei* was the most light-demanding species and *C. estrellensis* the least. This analysis allowed us to define three groups of species: (1) *Z. sprucei* as the most light-demanding, (2) *M. nobilis*, *H. crepitans*, *S. fruticosa* and *C. ianeirensis* as intermediate and (3) *C. estrellensis* as the least light-demanding.

The experiment on seed rain for four species showed the following dispersal distance: *S. parahyba*: 38 m, *H. crepitans*: 10 m, *M. nobilis*: 4 m, *Z. sprucei*: 4 m.

As a conclusion, the distribution of regeneration in relation to microsites vary within the same subjectively delimited guild. Some long-lived pioneer timber species were able to develop some degree of regeneration in the shade, at least for some time. Large trees are scarce in these forests, suggesting that silviculture should aim not only at small individuals, but also at larger individuals to ensure future crop trees. Coinciding with other findings, canopy opening through intensive well-planned harvesting systems is suggested as the direction to promote long-lived pioneer species recruitment and development.

Key words: Bolivia, Light, Long-lived pioneer, Natural regeneration, Species guild, Tropical forest

1. Introduction

Light has been recognized as the most important factor for the success of natural regeneration (e.g. Clark and Clark, 1992; Clark *et al.*, 1993), and it is known that tree falls provide a critical entrance of light for gap-dependent species. Many attempts have been made to explain tropical forest dynamics in relation to gaps (see Hartshorn, 1980; Denslow, 1980; Brokaw and Schneider 1989) and to characterize gaps (Brokaw, 1982), but others have pointed out limitations in the use of the gap concept (e.g. Swaine *et al.*, 1987; Liberman *et al.*, 1989; Clark and Clark, 1992), as well as in the classification of species in guilds regarding gaps (Denslow, 1980; Swaine and Whitmore, 1988; Brokaw and Scheine, 1989).

Early studies on regeneration in tropical forests emphasized the importance of gaps. However, some authors (e.g. Clark and Clark, 1987, Lieberman *et al.* 1989) advocated ecologists to focus on light levels from dense shade to full sunlight, and stop comparing gap vs. non-gap. Species light requirements can change in time and with age, be flexible or remain constant (Oldeman and van Dijk, 1991). For all these reasons, the decision was made in the present study to sample the whole forest and focus on the light levels of individual trees, something that few researchers have done. In addition to light levels, one should consider other factors at the microsite level that influence plant development, such as light quality, root competition, nutrients, soil texture and effect of predators and pathogens (Clark and Clark, 1987).

In forests free of recent drastic natural disturbances, the effect of light on regeneration becomes clearer in logged forests because of larger disturbances, and it is in these cases when the species composition could be strongly influenced by controlling gap characteristics (Whitmore, 1998). Therefore, it is important to understand the strengths and limitations of gap and guild concepts. A species guild is defined as a group of species that exploit environmental resources in a similar fashion and have overlapping niche requirements, without considering their taxonomic classification (Root, 1967). Species from the same guild are expected to share key ecological -or biological- characteristics, such as light requirements for regeneration, which is essential to understanding the application of silviculture treatments to promote natural regeneration and growth of selected trees. Silviculturalists have tried to classify species in guilds according to their light requirements to manage them as groups. There are several guild classifications (e.g. Whitmore, 1975; Denslow, 1980; Swaine and Whitmore, 1988; Brokaw and Scheiner, 1989;

Whitmore, 1989; Oldeman and van Dijk, 1991), which vary according to the researcher's approach, objectives, the species considered, and other factors.

Whitmore (1989) and Swaine and Whitmore (1988) proposed to simplify the species guilds in two major groups: pioneer and climax. However, later Whitmore (1991) clarified that this simplification might not work for specific purposes. Working in Costa Rica, Finegan *et al.* (1999) identified four tree species guilds for neo-tropical moist forests: short-lived pioneer, long-lived pioneer, intermediate and shade tolerant. In general, pioneer species have been classified as having common characteristics such as small seeds, disturbance-dependency for germination and growth, low wood density, fast growth, seed dormancy, and wide ecological range (Swaine and Whitmore, 1988).

Most pioneer species rely on seed availability and dispersal to reach and colonize appropriate habitats. Seed dispersal has two objectives: to escape from the density-dependent or distance-dependent mortality near the parent tree, and to increase the probabilities of seed colonization of random disturbances (Augspurger, 1984). Four factors influence seed falling on a unit area: distance and height of mother tree, density of seed trees, dispersability, and dispersal agents (Harper, 1977) including secondary dispersals that act once the seed has reached the soil, such as ants, rodents, and beetles (Dalling, 2002).

In general, short-lived pioneer species produce a large number of seeds frequently, and have small and easily dispersed seeds (Denslow, 1980), mainly by birds, bats and wind (Hartshorn, 1980), while long-lived pioneers have larger seeds and shorter viability (Finegan, 1996). There is no consistent pattern of dispersability within light-demanding species (Dalling *et al.*, 1998). The type of diaspore dispersal is very important for light-demanding species to get seeds from low density sources to colonizable sites (Hartshorn, 1980), specially for those that requires large openings, which are usually scarce in the forest. In our case, four species are wind-dispersed seeds, two by animals and one is ballistic.

Seed availability is one of the first variables to investigate when natural regeneration is sparse. Shade-tolerant species tend to form "seedling banks" while most pioneers form "soil seed banks" (Whitmore, 1998; Finegan, 1996). On Barro Colorado island (BCI) the seeds of almost all pioneer species studied (short- and long-lived) exhibited dormancy (Dalling *et al.*, 1998) and Putz

and Appanah (1987) found more buried seeds under the canopy in Malaysia than in gaps and that regeneration by sprouting can be a very important mechanism. Under high forest conditions, long-lived pioneer seedlings' and saplings' growth and survival are affected by microclimatic variations, especially light intensity (Whitmore, 1998), although early regeneration does not necessarily reflect later development. According to Augspurger (1983a), on BCI, light caused by gaps enhanced the survival and growth of seedlings at all times, especially during the first year.

This study is part of a multi-dimensional research project on species' ecology and silviculture, including their natural regeneration, light requirements, response to disturbance and diverse microhabitats. We did not focus our sampling on particular microsites, such as gaps; instead, the entire forest area was sampled and microsites were characterized where the species were found. This study contributes through a sampling at an operational scale, characterizing rare species that require large areas for their study. The objective of this research was to determine the relationship between the natural regeneration abundance of selected species and microsites in an undisturbed forest, to determine their light requirements, and also to examine the issue of seed dispersal. We tested the hypothesis that the individuals' distribution ("observed" distribution) of long-lived pioneer timber species was different from the forest distribution ("expected" distribution) regarding crown illumination, regeneration phase, and canopy openness, according to their light requirements.

2. Methods

2.1 Study site

This study was developed in the eastern part of the Department of Santa Cruz, Bolivia, in the La Chonta Concession (15°47'S, 62°55'W). The forest is classified as Sub-tropical Humid Forest according to the Holdridge system (Unzueta, 1975). The mean annual precipitation is 1,562 mm, with a mean annual temperature of 24.5°C, with a maximum of 28.9°C and a minimum of 10°C, and the elevation is 250 m (La Chonta, 1998). The dry season length is 6 months. The total area of the concession is 100,000 ha with a cutting cycle of 30 years. For more details about the study site see Paper I in this volume.

2.2 Study species and sampling

The work was developed on an operational-scale experiment carried out by the Long-term Silviculture Research Project implemented by the Instituto Boliviano de Investigación Forestal (IBIF), which installed large plots in a randomized complete block design experiment. Three blocks of about 800 ha each were installed, within which four treatments were applied over areas of approximately 27 ha. This study was carried out using the Control (unlogged) treatment because we were interested in understanding the relationship between the natural regeneration of long-lived pioneer timber species and the light environment in natural conditions. Data was taken from 20 m x 20 m plots arranged in a 75 m x 75 m grid system, following Clark *et al.* (1999)'s approach. See Paper I for more details about the experimental design and visit www.ibifbolivia.org.bo for more information about the site and the general experiment design.

Eight long-lived pioneer timber species were selected for the study. They differ in abundance at the site (dbh \geq 10 cm), with *Hura crepitans* being the most abundant (8.5 ind/ha) and *Ceiba pentandra* the least abundant (0.3 ind/ha) (Table 1).

Table 1. List of selected long-lived pioneer species

Species	Family	Abundance/ha (dbh \geq 10 cm)	Dispersion mode	Expected regeneration after logging
<i>Hura crepitans</i>	Euphorbiaceae	8.5	Ballistic	High
<i>Margaritaria nobilis</i>	Euphorbiaceae	2.4	Animal	High
<i>Schizolobium parahyba</i>	Caesalpiniaceae	1.1	Wind	High
<i>Zanthoxylon sprucei</i>	Rutaceae	0.7	Animal	High
<i>Cariniana ianeirensis</i>	Lecythidaceae	2.8	Wind	Low
<i>Sweetia fruticosa</i>	Fabaceae	2.4	Wind	Low
<i>Cariniana estrellensis</i>	Lecythidaceae	1.1	Wind	Low
<i>Ceiba pentandra</i>	Bombacaceae	0.3	Wind	Low

Source for abundance data: IBIF (unpublished data)

All individuals \geq 0.5 m in height of the selected species were measured. 44 plots were established in Block 1, 50 in Block 2, and 48 in Block 3, resulting in 142 sample plots within a total area of 81 ha. Variables that were measured included: diameter at breast height (dbh); height (m); crown illumination according to the 7 classes modified from Dawkins by Clark and Clark (1992); regeneration phase (Clark and Clark, 1992): 1= Mature (canopy $>$ 10 m height), 2= Building (canopy 2-10 m height), 3= Gap (canopy $<$ 2 m height); Canopy openness: 1=Closed (no gap), 2=Medium Gap ($<$ 200 m²), 3=Large Gap (\geq 200 m²). Because of the low abundance of most species, crown illumination classes were combined for analysis, resulting in the following three classes: Class 1 (No direct light): the original class 1; Class 2 (Lateral light): original classes 1.5, 2 and 2.5; Class 3 (Vertical light): original classes 3, 4 and 5.

Additionally, we sampled 55 plots systematically distributed in each control plot in order to determine the distribution of microsite conditions within the forest (hereafter referred to as the forest distribution). In these plots the crown illumination index, canopy openness and regeneration phase were measured at three vertical points: 0.75 m, 3 m and 10 m in height, which represents most of the individuals sampled below 10 cm dbh. We assumed that data taken at both 0.75 m and 3 m in height were comparable to data from saplings (dbh $<$ 5 cm), and data at 10 m height comparable to data from poles (dbh 5.0-9.9 cm). We aimed to determine whether the illumination, regeneration phase, and canopy openness associated with the species studied differed from the forest distribution in order to characterize species according to microsite preferences.

For the statistical analysis, the observed species' distribution regarding illumination index, canopy openness and regeneration phase were compared with the forest distribution by means of

a contingency table. All analyses were done for two size classes: saplings (dbh <5.0 cm), and poles (dbh 5.0-9.9 cm), because small sized trees are more sensitive to light changes than larger ones (Bertault *et al.*, 1995). We used a cluster analysis to group species according to their responses to crown illumination, canopy openness and regeneration phase, supported by a multivariate analysis of principal components. SAS and Infostat statistical programs were used to process the data.

Seed dispersion was measured for four species: *H. crepitans*, *S. parahyba*, *M. nobilis*, and *Z. sprucei*. The fruit of *H. crepitans* is a compressed capsule that disseminates seeds by explosion (Justiniano and Fredericksen, 2000). *S. parahyba* fruits are a samara legume, single-seeded and wind dispersed (Peña-Claros and de Boo, 2002). *M. nobilis* has bright-colored mimetic fruits, animal dispersed; probably to attract animals since they are not fleshy (Croat, 1978), while the fruits of *Z. sprucei* contains several follicles with shiny seeds also dispersed by animals (Croat, 1978).

Four to five mature trees of each species were selected and measured; we assured that trees were isolated from other mature trees from the same species to prevent trap contamination. To collect seeds, four transects were established from the base of each tree considering wind direction: NE (45°), SE (135°), SW (225 °), NW (315 °). A set of seed traps using umbrellas of 80 cm in diameter placed upside down were installed in each transect starting from the center of the crown. In each transect, the first trap was placed between the center and the edge of the crown, the second trap in edge of the crown, the third, fourth and fifth traps at 10 m, 20 m, 30 m and 60 m respectively from the edge of the crown. Since crowns differ among species, trap distances also differed: *M. nobilis* and *Z. sprucei* had average 8 m diameter crowns, while *S. parahyba* was 16 m, and *H. crepitans* 20 m. Consequently, trap distances for each species were, for *Z. sprucei*: 2 m, 4 m, 14 m, 34 m, 64 m; for *M. nobilis*: 2 m, 4 m, 14 m, 34 m (because of its short seed dispersion distance traps at 65 m were not installed); for *S. parahyba*: 4 m, 8 m, 18 m, 38 m, 68 m; for *H. crepitans*: 5 m, 10 m, 20 m, 40 m, 70 m.

Seed dispersal was calculated based on means of four trees for each trap at each distance. The initial intention was to take 6 measurements for each species every 15 days. However, the lack of seed production complicated the field work, so there were different seed collection periods: *M.*

nobilis, 6, *Z. sprucei*, 3, *H. crepitans*, 2, and *S. parahyba*, 2 measurements, respectively. Therefore, these results must be taken as preliminary.

3. Results

For most species, tree abundance (N/ha) was low. The most abundant species (dap \geq 10.0 cm, Table 2) was *H. crepitans* (6.3 ind/ha), and the least *C. estrellensis* (0.9 ind/ha). *M. nobilis* and *C. estrellensis* were absent from the diameter class 5.0-9.9 cm. Only one individual was found across all size classes for *C. pentandra*, and no *S. parahyba* trees of any size class were located, a phenomenon of rarity already observed by Clark (2002), Hubbel and Foster (1987) and Primak (1992), among others, who mention that tropical tree species can be extremely rare locally, which may make robust statistical analysis quite difficult. Although no individuals of *S. parahyba* were found in the undisturbed forest it is known that this species becomes abundant in disturbed forests (Justiniano *et al.*, 2001), illustrating how different species' abundance can be in different site conditions.

Table 2. Species' abundance (total in 5.68 ha, and mean per ha) for three size classes found in 3 27-ha plots in an undisturbed forest.

Species	Abundance by size classes						Common / rare
	dbh < 5.0 cm		dbh 5.0-9.9 cm		dbh \geq 10.0 cm		
	N total	N/ha	N total	N/ha	N total	N/ha	
<i>H. crepitans</i>	148	26,1	15	2,6	36	6,3	Common
<i>C. ianeirensis</i>	60	10,6	10	1,8	16	2,8	Common
<i>S. fruticosa</i>	12	2,1	10	1,8	12	2,1	Common
<i>Z. sprucei</i>	20	3,5	7	1,2	7	1,2	Common
<i>M. nobilis</i>	15	2,6	0	0	7	1,2	Common
<i>C. estrellensis</i>	14	2,5	0	0	5	0,9	Rare
<i>C. pentandra</i>	1	0,2	0	0	0	0	Rare
<i>S. parahyba</i>	0	0	0	0	0	0	Rare

Only *Z. sprucei* saplings had a distribution that differed from the forest distribution (sapling size), presenting higher abundance in vertical light and also in no direct. *C. estrellensis* was significantly different at $\alpha=0.1$, presenting higher abundance in the no direct light class (Table 3). For pole size, three species differed statistically from the forest distribution: *H. crepitans*, *S. fruticosa* and *Z. sprucei*. The first two species presented a higher abundance than the forest distribution in the lateral light class, and the third presented all its distribution in the lower illumination classes. Few trees were found in this size, which may have affected the statistical results so we suggest that these results be taken with caution.

Table 3. Contingency table (Chi-square) to compare the distribution of the crown illumination index (observed distribution) of plants of seven long-lived pioneer timber species and the distribution of crown illumination index in the forest (expected distribution) for sapling and pole sizes. For the equivalent of sapling size, Forest crown illumination index was measured at both 0.75 m and 3 m height, and for pole size at 10 m height. Values are given in %.

Species	Classes of crown illumination for saplings (dbh < 5.0 cm)					Classes of crown illumination for poles (dbh 5.0-9.9 cm)				
	No direct light	Lateral light	Vertical light	N	P-value	No direct light	Lateral light	Vertical light	N	P-value
<i>C. estrellensis</i>	21,4	78,6	0,0	14	0,0885	0,0	0,0	0,0	0	-
<i>C. ianeirensis</i>	5,0	86,7	8,3	60	0,5876	0,0	50,0	50,0	10	0,3069
<i>H. crepitans</i>	10,8	80,4	8,8	148	0,3693	6,7	46,7	46,7	15	0,0019
<i>M. nobilis</i>	7,1	64,3	28,6	15	0,1520	0,0	0,0	0,0	0	-
<i>S. fruticosa</i>	0,0	83,3	16,7	12	0,5528	10,0	60,0	30,0	10	< 0,0001
<i>Z. sprucei</i>	25,0	40,0	35,0	20	0,0001	14,3	28,6	57,1	7	< 0,0001
Forest	7,5	81,1	11,4	334	-	0,0	34,1	65,9	167	-

The species most different from the forest distribution was *Z. sprucei*, and the most similar was *C. ianeirensis* (dbh ≤ 5.0 cm). See illustration in Figure 1.

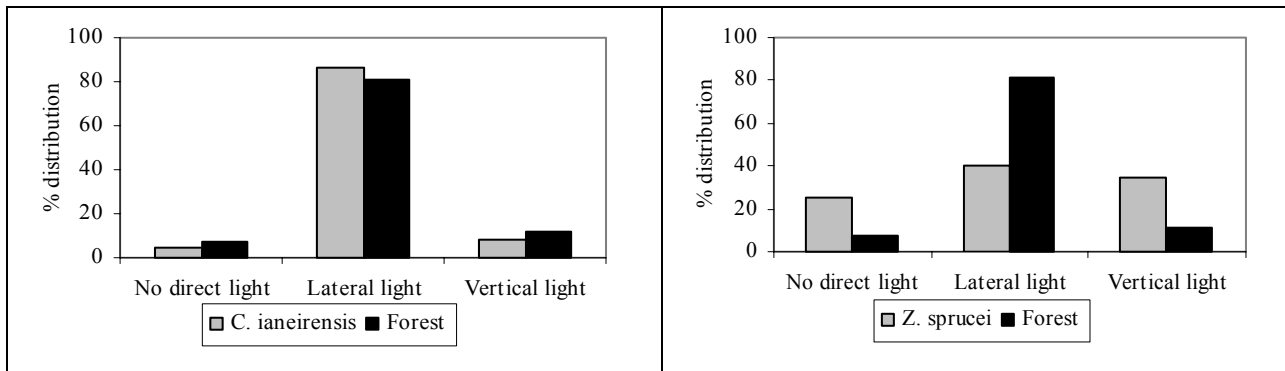


Figure 1. Histogram comparing *C. ianeirensis* and *Z. sprucei* with forest distributions for crown illumination classes, dbh ≤ 5.0 cm (P= 0.5876 and P= 0.0001 respectively)

When each species was tested for its distribution regarding canopy openness for sapling sizes (contingency table), only *Z. sprucei* had a distribution that was different from the forest, with a percentage of distribution in large gaps that was six times higher than the forest distribution (Table 4), following a similar pattern to crown illumination. For pole size, no significances were found; all species followed the forest pattern, concentrating their distribution in the closed canopy, although *Z. sprucei* showed a tendency for concentrating its individuals in the large gap class.

Table 4. Contingency table (Chi-square) to compare the distribution of the canopy openness index (observed distribution) of plants of seven long-lived pioneer timber species and the distribution of canopy openness index in the forest (expected distribution) for sapling size and pole sizes. For the equivalent of sapling size, Forest canopy openness index was measured at 0.75 m and 3 m height, and for pole size at 10 m height. Values are given in %.

Species	Classes of canopy openness for saplings					Classes of canopy openness for poles				
	Closed canopy	Medium gap	Large gap	N total	P-value	Closed canopy	Medium gap	Large gap	N total	P-value
<i>C. estrellensis</i>	85,7	14,3	0,0	14	0.5937	0,0	0,0	0,0	0	-
<i>C. ianeirensis</i>	81,7	15,0	3,3	60	0.6098	60,0	30,0	10,0	10	0.4164
<i>H. crepitans</i>	80,4	17,6	2,0	148	0.1081	60,0	33,3	6,7	15	0.2097
<i>M. nobilis</i>	73,3	26,7	0,0	15	0.3452	0,0	0,0	0,0	0	-
<i>S. fruticosa</i>	91,7	8,3	0,0	12	0.4798	80,0	10,0	10,0	10	0.8355
<i>Z. sprucei</i>	40,0	20,0	40,0	20	< 0.0001	57,1	14,3	28,6	7	0.0941
Forest	77,8	15,6	6,6	334	-	77,8	15,6	6,6	167	-

The results for the regeneration phase were different from the test for crown illumination and canopy openness variables: no species was statistically different from the forest distribution (sapling and pole sizes). All species presented a higher abundance in the most common forest environment: the *mature* regeneration phase (Table 5).

Table 5. Contingency table (Chi-square) to compare the distribution of the regeneration phase index (observed distribution) of plants of seven long-lived pioneer timber species and the distribution of regeneration phase index in the forest (expected distribution) for sapling size and pole sizes. For the equivalent of sapling size, Forest regeneration phase index was measured at 0.75 m and 3 m height, and for pole size at 10 m height. Values are given in %.

Species	Classes of regeneration phase for saplings					Classes of regeneration phase for poles				
	Mature	Building	Gap	N	P-value	Mature	Building	Gap	N	P-value
<i>C. estrellensis</i>	85,7	7,1	7,1	14	0.7362	0,0	0,0	0,0	0	-
<i>C. ianeirensis</i>	81,7	16,7	1,7	60	0.1432	60,0	20,0	20,0	10	0.4276
<i>H. crepitans</i>	80,4	12,8	6,8	148	0.6672	60,0	26,7	13,3	15	0.2880
<i>M. nobilis</i>	73,3	26,7	0,0	15	0.2185	0,0	0,0	0,0	0	-
<i>S. fruticosa</i>	91,7	8,3	0,0	12	0.3738	90,0	0,0	10,0	10	0.4686
<i>Z. sprucei</i>	70,0	25,0	5,0	20	0.3462	71,4	28,6	0,0	7	0.3955
Forest	77,3	13,8	9,0	334	-	77,3	13,2	9,6	167	-

Finally, the groups of species were differentiated on the basis of their light-demanding characteristics by means of multivariate analyses using cluster analysis (minimum linkage method, Euclidean distance) and principal coordinates analysis (minimum spanning trees) for dbh < 5.0 only because here we had the largest number of individuals sampled. Both analyses presented similar results, separating *Z. sprucei* from the other species, it being the most light-demanding species. The cluster analysis (Figure 2) presents the possible species groups based on the combined species responses from the three variables measured: crown illumination, canopy openness and regeneration phase. These results present *Z. sprucei* and the rest of species as the other in opposite groups. Considering the limitations of sample size, we built three species

groups: (1) *Z. sprucei*, as the most light-demanding one, (2) *M. nobilis*, *H. crepitans*, *S. fruticosa* and *C. ianeirensis*, as intermediates, and (3) *C. estrellensis*, as the least light-demanding.

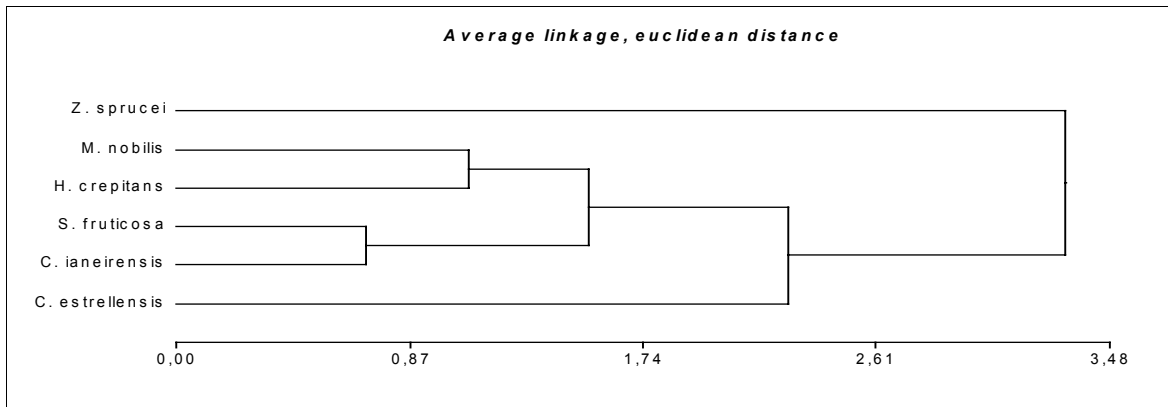


Figure 2 Cluster analysis utilizing crown illumination, canopy openness and regeneration phase variables for the species studied (dbh < 5.0 cm).

These results were consistent with the principal coordinates analysis (Fig. 3). Here, the order of species responses to light from high to low demanding was: *Z. sprucei*, *M. nobilis*, *H. crepitans*, *C. ianeirensis*, *S. fruticosa*, and *C. estrellensis*, which roughly suggests the species' light-demanding gradient.

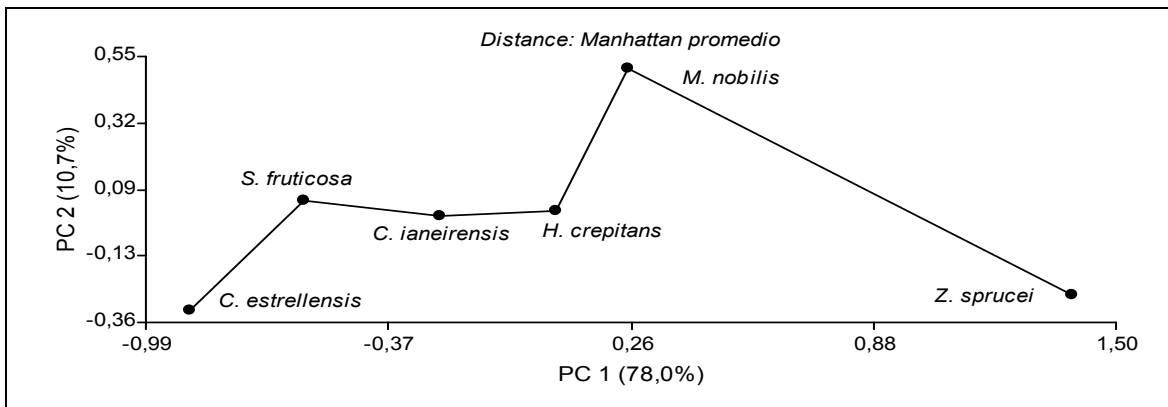


Figure 3. Multivariate analysis of principal coordinates utilizing crown illumination, canopy openness and regeneration phase variables for the species studied (dbh < 5.0 cm).

Regarding dispersal distance, the maximum distance recorded was: *S. parahyba*: 38 m, *H. crepitans*: 10 m, *M. nobilis*: 4 m, and *Z. sprucei*: 4 m.

4. Discussion

Three out of the seven species studied were classified as common. The most abundant one was *H. crepitans* with 6.3 ind/ha and the least were *C. pentandra* and *S. parahyba* which showed no individuals ≥ 10 cm dbh. It was expected that the least light-demanding species presented the highest abundance (Poorter and Arets, 2003), but this expectation was only partially met.

We found that the predominant microsites in the undisturbed forest were those with low light levels, as other authors have found in other forests (e.g. Clark *et al.*, 1993; Diaz, 1995; Guzmán, 1997; Poorter and Arets, 2003). These results led us to question if the species trends were due to species microsite preference, or if it was influenced by the proportion of the forest microsite so that the high abundance of species under canopy would not necessarily mean that these species “prefer” shaded microsites. To find out, the contingency test on crown illumination, canopy openness, and regeneration phases, compared the species’ distribution with the forest distribution. Only *Z. sprucei* proved to present a different distribution, with a high concentration of saplings in more illuminated environments. The species that most concentrated its distribution in a low light environment was *C. estrellensis*.

For pole size, *H. crepitans*’ distribution was different from the forest, with less individuals in the vertical light class and some in the no direct light class, showing the capacity of this species to respond well to large openings and to develop regeneration under canopy as well, as reported by Foster and Brokaw (1996) and Justiniano and Fredericksen (2000). Similarly, *Z. sprucei*, the most light- demanding species of the group, presented higher abundance in lesser-illuminated microsites than forest distribution, like *S. fruticosa* as well, suggesting the ability of seedlings and saplings of pioneer species to survive in the understory, as found by Guariguata (2000). We hypothesize that indirect light and sun flecks play a greater role than suspected in species’ regeneration under canopy.

In all cases individuals increased their crown illumination indexes when passed from sapling to pole size, which suggests that individuals in larger diameter classes are exposed to a higher degree of illumination (Davies *et al.*, 1998; Poorter and Arets, 2003).

Despite the findings that *Z. sprucei* was the most light-demanding species, it was also found in the lower crown illumination class, as well as in the test for canopy openness. This finding was not expected since this species is the most light-demanding one, generally found in well illuminated microsites. What would explain this? A large proportion of *Z. sprucei* was found in large gap microsites, growing below faster growing species like *Cecropia*, so we assume that despite the assigned index 1 (“no direct light”) in these cases, *Z. sprucei* plants were actually growing in microsites with higher temperatures and intensive indirect light under faster-growing, short-lived pioneer species, but this situation was not reflected by the crown illumination index assigned. This suggests that the crown illumination index may need to be modified to reflect the microsite conditions when crown suppression is ephemeral, such as when the crowns of short-lived pioneer species are temporarily above long-lived pioneers.

H. crepitans, a species known to respond well to disturbances (Justiniano and Fredericksen, 2000), was well represented in low illumination classes. This may explain the high abundance of this species in undisturbed as well as disturbed forests due to its capacity to develop abundant regeneration under the canopy and then react to openings. This characteristic may facilitate its development after logging in response to canopy openings.

The results of the test for canopy openness were consistent with the results of crown illumination for sapling size: *Z. sprucei* was the only species different from the forest. However, the test for the regeneration phase showed that *Z. sprucei*, as well as the other species, did not differ from the distribution in the forest. We speculate that the reason for this is because the variable “Mature” phase, where most species’ abundance was found, does not necessarily reflect ground light availability because small vertical or lateral gaps may occur in the mature phase providing light for regeneration, but not reflected by this variable. Therefore, the “mature” regeneration phase might not always be a good surrogate for light canopy penetration, but for the structure of the vegetation. We did not find any pattern between the degree of shade tolerance and the abundance of natural regeneration, as found by Poorter and Arets (2003) in a Bolivian tropical moist forest, and Hartshorn (1980) in Costa Rica.

For those species that had a distribution similar to the forest, we concluded that microsite influence on the distribution of the study species was minimal, and that they were mostly influenced by the common forest environment: low crown illumination, closed canopy, and

mature regeneration phase. It still needs to be determined how long these species can live before a gap is created in order to develop into larger sizes.

The absence of *S. parahyba* and the presence of only one individual of *C. pentandra* in our sample units is probably due to different reasons: *S. parahyba* needs high levels of disturbance to regenerate (Justiniano *et al.*, 2001), a condition not found in an undisturbed forest, and *C. pentandra* is a very rare species and we simply found only one individual. The speculation for *S. parahyba* was tested in Paper III (see Chapter 4 in this volume), finding that this species responds well to harvesting disturbances.

Although all the species studied are considered to be long-lived pioneers, we found that species responded differently to different light conditions and that they were able to germinate and develop regeneration, coinciding with Guariguata (2000), who suggests that species supposedly belonging to the same guild, actually occupy different illumination niches, and that this may contribute towards the species' coexistence (Poorter and Arets, 2003) and richness. The fact that these species were able to regenerate under the canopy challenges their classification as light-demanding, or implies that the concept should be reviewed.

The species' capacity to develop some level of regeneration under canopy may be explained by the fact that they receive, as we found, lateral light, sun flecks and diffused light, which was most common for trees with a dbh < 10 cm (Clark and Clark, 1987). This is why plants' microsites cannot be classified just as gap or non-gap. This is particularly important in a semi-deciduous forest like ours, which can provide a minimum of light through the canopy when most trees lose their leaves for some months, therefore promoting the establishment of seedling banks of light-demanding species. The existence of seedlings and saplings under shade would give these species a certain advantage to respond to canopy openings created by tree falls or logging. However, they may not permanently survive in shaded microsites. Favorable light must be available at crucial periods of the life of each seedling (Clark and Clark, 1987).

The capacity of long-lived pioneer species to develop a limited degree of regeneration in hostile microsites may explain the persistence of rare species in undisturbed forests, which ultimately seems to be a successful regeneration strategy. However, for forest management purposes, this creates a challenge for ecologists and forest managers on how to increase species abundance from

seedlings and pole size to larger diameter classes. Species rarity suggests that their conservation requires large areas (Hubbell and Foster, 1986; Pitman *et al.*, 1999; Bawa and Ashton, 1991). This is why sustainable forest management may become an important and effective tool for species conservation outside protected areas and also landscape-scale approaches that integrate sustainable forest management and protected areas. Rare species, including strong light-demanding ones, are more vulnerable than more common ones (Rabinowitz *et al.*, 1986; Jennings *et al.*, 2001), so we suggest paying special attention to those classified as such.

We support the need for more research on seed ecology. Today, silviculture systems in the neotropics usually fail to consider the ecological requirements of seeds and seed dispersal (Guariguata, 2000). These considerations are particularly important when identifying the seed trees to be left after logging and the timing for harvesting.

The species with the lowest seed dispersion were *M. nobilis* and *Z. sprucei*. However, since these seeds are dispersed by animals, we really do not know their true dispersal distance. These species were found to be the most light-demanding and we speculate that they benefit from animal dispersion to colonize disturbed sites. Rare species like *S. parahyba* may compensate their low abundance by their capacity for long seed dispersal and their reported seed dormancy (Justiniano *et al.*, 2001). *H. crepitans* showed an intermediate dispersion. It seems that the regeneration strategy of this species is based on its capacity for developing abundant regeneration under canopy and at the same time being able to colonize gaps when they occur. Other survival strategies to be considered in further studies are mechanisms to escape predators, fast growth, and the capacity for seed germination in a wider range of substrates and moisture conditions. Considering that our results on seed dispersion are preliminary, we recommend continued research on long-lived pioneer species phenology, seed production, dispersion, predation and germination in undisturbed and disturbed forests.

Our results show that most species presented low abundance. How can their abundance be increased? Light gaps enhance the probability of seedling survival (Augsburger, 1984), therefore canopy openings seem to offer an approach to favor the recruitment and development of light-demanding timber species such as those analyzed in this study, as found by Guariguata (2000) in Costa Rica. He found contrasting patterns of species regeneration despite species belonging to the same guild: some could regenerate under canopy, others needed openings, and others had

intermediate responses, but all responded well to canopy openings. Based on this, he concluded that a monocyclic system would be appropriate for the species studied since they would need “an almost complete canopy removal, either for stimulating seed germination or for sustaining seedling growth and survival”. However, we should be careful when considering monocyclic systems because of its ecological impacts. In the case of Bolivia, we concur with Fredericksen (1998) that intensive polycyclic logging systems may disturb the forest enough to promote the regeneration of light-demanding species.

Seedling recruitment promoted by intensive harvesting may not be enough to ensure the existence of future crop trees; therefore it will probably be necessary to implement silviculture treatments so that seedlings can develop into poles and larger harvestable trees. Surely, the viability of silviculture treatments will depend to a large degree on their economic feasibility.

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CHAPTER 4. PAPER III. EFFECT OF LOGGING ON NATURAL REGENERATION OF LONG-LIVED PIONEER SPECIES IN A BOLIVIAN TROPICAL FOREST: RESULTS OF AN OPERATIONAL-SCALE EXPERIMENT

Lincoln Quevedo, Bryan Finegan, Marielos Peña, Glenn Galloway, José Joaquín Campos

Abstract

The effect of logging on natural regeneration in an operational scale experiment was studied in a 100,000-ha forest concession in a semi-deciduous forest in Santa Cruz, Bolivia. Species responses were evaluated in a random, complete block design experiment, comparing unlogged and logged and silviculturally-treated plots of 27 ha each within blocks of 800 ha, a scale seldom seen in the past. In the logging treatment, about 15m³/ha were harvested, roughly twice the normal harvesting in Bolivia, and a set of silviculture treatments were implemented (directional felling, soil scarification, marking future crop trees and seed trees, and cutting the lianas from trees to be harvested, future crop trees and seed trees). To evaluate the logging effect, eight long-lived pioneer species were selected: *Hura crepitans*, *Margaritaria nobilis*, *Schizolobium parahyba* and *Zanthoxylon sprucei* which are believed to develop abundant regeneration after logging, while *Cariniana estrellensis*, *Cariniana ianeirensis*, *Sweetia fruticosa* and *Ceiba pentandra*, do not. Logging was carried out 2-3 years before sampling.

Species responses were evident in trees dbh < 5.0 cm. The group of species previously believed to respond well to harvesting developed abundant regeneration after logging and silviculture (ANOVA, $\alpha= 0.05$). From the eight species studied, three were considered to be locally rare in the undisturbed forest (*C. estrellensis*, *S. parahyba*, and *C. pentandra*). Of these, *C. estrellensis* and *C. pentandra* did not show any benefit in abundance from logging disturbances and silviculture treatments, while *S. parahyba* was more abundant on logged sites.

The test for light increase after logging (Mann-Whitney test for crown illumination, canopy openness and regeneration phase) also led to the acceptance of the hypothesis that logging increased illumination of regeneration, with the exception of *C. estrellensis* which was the least light- demanding, and *C. pentandra* which had so few individuals that it was not possible to make any statistical inference.

We found that harvesting and silviculture treatments can increase the abundance of regeneration of some locally rare species, and that some abundant species, such as *H. crepitans*, can become even more abundant with planned harvesting. However, some locally rare species

may remain rare, and would require special attention to ensure regeneration if they were harvested.

The species pair-wise test regarding classes of skidder soil disturbance determined that *S. parahyba* and *Z. sprucei* responded positively to soil disturbance caused by skidder movement.

There were few individuals in the pole-size class (dbh 5.0-9.9 cm) in both treatments, and half of the species did not present any in the unlogged treatment. Our findings suggest that silviculture treatments after logging may be necessary to ensure larger individuals. Additional studies on logging damage, levels of harvesting, rare species, seed trees, and monitoring species regeneration responses after logging are recommended.

Key Words: Tropical forest, Species guild, Long-lived pioneer, Natural regeneration, Silviculture, Logging effects, Bolivia

1. Introduction

Bolivia has shown remarkable improvements in forest management over the last ten years. However, despite these achievements, it is still necessary to carry out field experiments to develop and implement silviculture systems to promote species conservation and sustainable forest management (Fredericksen *et al.*, 2003). Forest management has been characterized several times as less profitable in the short term compared with illegal or unsustainable logging (Rice *et al.*, 1997; Reid and Rice, 1997; Bowles *et al.*, 1998). However, this comparison is not fair, since it fails to recognize that unsustainable practices are illegal in any forestry law and no longer accepted by society. Forest management, if implemented well, becomes an effective system for biodiversity conservation in forest lands for consumptive uses (Boot and Gullison, 1995; Jennings *et al.*, 2001) and, in the long-term, contributes towards economic development.

One general concern among ecologists and forest managers in Bolivia is the lack of natural regeneration of the commercial species. Mostacedo and Fredericksen (1999) report that 60% of 68 species do not seem to have adequate natural regeneration (“*poor*”= very little regeneration + “*problematic*”= little regeneration, but it is known how to improve it). In addition, 78% of highly valuable timber species have poor regeneration, and most of the species with regeneration problems require the application of silviculture treatments, considered by Mostacedo and Fredericksen (1999) difficult to implement at an operational scale, such as cleaning, controlled fire, and liberation cuttings. Nevertheless, to make forest management sustainable, silviculture treatments may have to be implemented in logged areas.

Some of the most important commercial timber species of the Bolivian forests are light-demanding, and this is why we are focusing on this guild. Long-lived pioneer species need high levels of light and a suitable substrate to regenerate and grow; harvesting opens the canopy and disturbs the soil (Whitmore, 1998), therefore we need to pay attention to logging as a key silviculture practice (Fredericksen, 1998). Some of the possible silviculture implications of harvesting, soil disturbance and canopy opening relates to how much substrate disturbance is required by different species, how germination and growth is affected by environmental changes in soil moisture and temperature modification, what the appropriate light intensity is for growth of the selected species, and when should disturbances be created to coincide with fruiting and how many seed trees should be left.

Most studies of seedling recruitment have been carried out in relatively undisturbed forests. However, species' responses to light will be more evident in logged forests, especially if the disturbance is intense. If silviculturalists manipulate light intensity appropriately through harvesting or silviculture treatments, it may be possible to trigger the desired responses from species guilds (Pinard *et al.*, 1999). Light is the most important factor (Swaine 1989), and it can be directly influenced by logging or other silviculture treatments, provided that the treatments are implemented at the appropriate time so that the most desirable trees can respond.

Harvesting is the main operation in forest management, and, depending on how it is carried out, it may contribute to the regeneration processes or lead to the unnecessary damage of the forest and alter the functioning of the ecosystem. In the first case, if it is a result of a planned and reduced impact logging system, then it can be considered a silviculture treatment. The second case, where harvesting unnecessarily damages the forest and harms species, is what foresters and loggers should avoid by all means. Planning the logging aims to reduce damage to vegetation, water sources and soil and increase the efficiency of operations (Pinard *et al.*, 1995).

In Bolivia, in addition to the gradual degradation of forest value caused by selective logging, the absence of large disturbances –but not necessarily periodic or catastrophic ones- and the absence of soil disturbance do not favor the regeneration of light-demanding species. Consequently, to promote the appropriate ecological conditions for natural regeneration of these species, it may be necessary to intensify harvesting in forest management systems or use additional silviculture treatments to promote regeneration (Fredericksen, 1998). As part of these silviculture practices, it has been observed that soil scarification enhances seed germination (Fredericksen and Mostacedo, 2000; Fredericksen and Pariona, 2002).

Seed dispersal, seed predation, seed germination, early establishment and seedling growth, and mortality explain the abundance and distribution of pioneer tree species, but seed dispersal and dormancy determine which individual species first colonize gap sites (Dalling *et al.*, 1998). Seedlings established before gap formation, and also sprouts, have more advantages than those established after (Garwood, 1990), having a higher survival rate and a higher probability of successful long-term development.

This study is part of a broad research on long-lived pioneer species' ecology and silviculture. Several studies have been carried out on species regeneration in specific forest microsites (e.g. Hubbell *et al.*, 1999; Park, 2003; van Rheenen *et al.*, 2004) and on logging effects on natural regeneration (Silva *et al.*, 1995; Panfil and Gullison, 1998; Sabogal *et al.*, 2001), but few on a large scale like ours. We focused on the integrated overall impact of treatments on the forest, which includes a set of silviculture treatments such as (a) directional felling, (b) soil scarification, (c) liana cutting from trees to be harvested, future crop trees and seed trees, and (d) marking future crop trees and seed trees. We did not focus on particular microsites –such as gaps- or silviculture treatments –such as soil scarification; instead, we focused on the whole forest.

The objectives of this paper were (a) to determine the responses of long-lived pioneer timber species to logging and silviculture treatments, (b) to compare species' reaction to light in unlogged and logged forest, (c) to provide knowledge for species' conservation and sustainable management. We hypothesized that harvesting operations (a) promotes natural regeneration of long-lived pioneer timber species in different magnitudes according to each species' ecological requirements, (b) increases the level of light as measured by crown illumination, canopy openness and regeneration phase classes, and (c) that disturbances by skidder movement promotes natural regeneration.

2. Methods

2.1 Study site

This study was developed in the Guarayos Region, Department of Santa Cruz, in eastern Bolivia. The forest is classified as a “Subtropical Humid Forest” according to Holdridge’s system, (Unzueta 1975). The annual mean precipitation is 1,562 mm, with an annual mean temperature of 24.5°C with a maximum of 28.9°C and a minimum of 10°C (La Chonta, 1998). The dry season length is 6 months. The experiment was carried out in the "La Chonta" forest concession (15°47'S, 62°55'W), in a total area of 100,000 ha; the elevation is 250 m.

The cutting cycle is 30 years with annual logging compartments of 2400 ha, 2-3 trees/ha are harvested with an average of 5-7 m³/ha (La Chonta 1998). The forest contains about 125 tree species dbh > 10 cm (Instituto Boliviano de Investigación Forestal -IBIF, unpublished data); from these, 17 were harvested in 2004, but only 7 species were harvested in volumes greater than 100 m³. These species were: *Cariniana ianeireneis* (38.9%), *H. crepitans* (26.7%), *Ficus* spp. (18.3%), *Cariniana estrellensis* (7.9%), *Terminalia* spp. (2.8%), *Schizolobium parahyba* (2.6%), and *Ceiba pentandra* (1%) (La Chonta Company, unpublished data). The canopy is about 25 m high, the most prominent tree species being *Hura crepitans*, *Cariniana* spp., *Pseudolmedia laevis*, *Terminalia oblonga*, and *Ficus boliviana*. *Swietenia macrophylla* was the main species harvested in the past, now it is scarce. The Company’s forest management plan is certified by the Forest Stewardship Council. For details on the site, see Chapter III in this volume.

2.2 Study design

The study was carried out in a large-scale logging experiment established by the Bolfor Project in the year 2000 as a randomized, complete block design and which is now operated by the Long-Term Silviculture Research Project (LTSRP) being implemented by IBIF. The experiment consists of three 800 ha blocks, each containing four 27 ha plots. Distances from block to block range from 1.5 to 5.5 km, with distances of not less than 500 m between the treatment plots inside the blocks. For more details see www.ibifbolivia.org.bo and Chapter III in this volume.

The experiment has four treatments, representing a gradient of harvesting and silviculture intensity. These range from a control plot (unlogged, no silviculture), to an intensive treatment plot (roughly twice the normal harvesting + a set of silviculture treatments). Due to the magnitude of the experiment, harvesting was not carried out during the same period, which may have added some error to the experiment among the Blocks and inside Blocks.

The effect of the disturbance on the regeneration of long-lived pioneer species was studied in the control and intensive treatment forest. We selected four species previously believed to develop abundant regeneration after logging and four species believed not to (Table 1). Species' responses in abundance were a result of logging and a set of silviculture treatments.

An average of 15 m³/ha was harvested 2-3 years before sampling (3, 2.5 and 2 years for blocks 1, 2, and 3, respectively), distributed among 11 species in the intensive treatment plots, using skidders for logging. Reduced impact logging techniques involved directional felling, marking future crop trees and seed trees, and cutting the lianas from trees to be harvested, future crop trees and seed trees. Skid trails were carefully planned. Some logging gaps were scarified using the skidder to promote regeneration. Only gaps without advanced regeneration and with seed trees around them were scarified (for specific methodology and results regarding soil scarification see Fredericksen and Pariona, 2002). 108 trees were harvested in all logging plots, with an average of 4 trees/ha and 1.92 m²/ha basal area, creating 168 m/ha of skid trails, and a total gap area of 896 m²/ha on the average; the dbh of harvested trees averaged 79.9 cm (Ohlson-Kiehn *et al.*, 2003).

Table 1. List of selected long-lived pioneer species and density in the La Chonta forest concession, Santa Cruz, Bolivia

Species	Family	Density (N/ha (dbh ≥10 cm))	Dispersion mode	Expected regeneration after logging
<i>Hura crepitans</i>	Euphorbiaceae	8.5	Ballistic	High
<i>Margaritaria nobilis</i>	Euphorbiaceae	2.4	Animal	High
<i>Schizolobium parahyba</i>	Caesalpiniaceae	1.1	Wind	High
<i>Zanthoxylon sprucei</i>	Rutaceae	0.7	Animal	High
<i>Cariniana ianeirensis</i>	Lecythidaceae	2.8	Wind	Low
<i>Sweetia fruticosa</i>	Fabaceae	2.4	Wind	Low
<i>Cariniana estrellensis</i>	Lecythidaceae	1.1	Wind	Low
<i>Ceiba pentandra</i>	Bombacaceae	0.3	Wind	Low

Source for abundance data: IBIF (unpublished data)

The attributes measured on each individual tree were: (a) diameter at breast height; (b) crown illumination according to the seven classes modified from Dawkins by Clark and Clark (1992); (c) regeneration phase (see Clark and Clark 1992): 1= mature (canopy >10 m height), 2= Building (canopy 2-10 m height), 3= gap (canopy <2 m height); (d) canopy openness: 1=closed canopy (no gap), 2=medium Gap (<200 m²), 3=large Gap (≥ 200 m²). Skid trail effect was recorded for each plant as 1: no skidder trail, 2: low trail impact on soil (no visible compaction/disturbance, 3: moderate, 4: high (evident compaction/disturbance, more than 15 cm deep).

Species density was obtained from the 20 m x 20 m plots installed in the unlogged and logged treatments (see Chapter III for more details). Data was converted to means per ha for each replica of each treatment (n= 8), and compared using ANOVA and Tukey test. Data was log-transformed to meet the assumptions for a parametric test. The effect of logging on light variables was tested by comparing species' crown illumination, canopy openness, and regeneration phase using a Mann-Whitney test, having each individual as the sample unit. The skidder trail effect on species' abundance was tested by a contingency table. Analyses were done for two size classes: saplings (dbh <5.0 cm), and poles (dbh 5.0-9.9 cm). For all analysis $\alpha = 0.05$. Data was processed using the SAS and Infostat statistical programs.

3. Results

Effect of logging and silviculture on species' abundance

The abundance of most species studied in the unlogged plots was low. For saplings we found only 1 individual of *C. pentandra* in the unlogged forest and 4 in the logged forest in all sample plots, therefore, it was not possible to carry out statistical tests for this species (see Table 2, the number of individuals for sapling and pole sizes in all sample plots). The most abundant species for dbh \geq 10.0 cm was *H. crepitans* (6.3 ind/ha), while no individuals of *C. pentandra* and *S. parahyba* were found, which, together with *C. estrellensis* (0.9 ind/ha) were considered as rare species (data not shown).

Table 2. Total number of individuals found in unlogged and logged treatments in all sample plots (5.68 ha and 5.56 ha for unlogged and logged treatments, respectively)

Species	Saplings		Poles	
	Unlogged	Logged	Unlogged	Logged
<i>C. estrellensis</i>	14	23	0	1
<i>C. ianeirensis</i>	60	36	10	3
<i>C. pentandra</i>	1	4	0	1
<i>H. crepitans</i>	148	333	15	15
<i>M. nobilis</i>	15	190	0	5
<i>S. fruticosa</i>	12	32	10	5
<i>S. parahyba</i>	0	110	0	15
<i>Z. sprucei</i>	20	391	7	5

Sapling abundance generally increased with the logging treatment in different proportions (Figure 1). For sapling size, the species that showed the highest increase of individuals were *Z. sprucei* (P= 0.0325), *H. crepitans* (P= 0.0429), and *S. parahyba*, which were the species initially expected to respond well to harvesting, as well as *M. nobilis* (P= 0.0752) which showed a large abundance difference between unlogged and logged treatments, but the results were significant only at $\alpha= 0.1$ due to the high variability among plots. *S. fruticosa*, was also nearly significant (P= 0.0622). No statistical test was possible for *S. parahyba* since all the individuals were found in the logged treatment, which is obvious proof of the benefits of logging for this species.

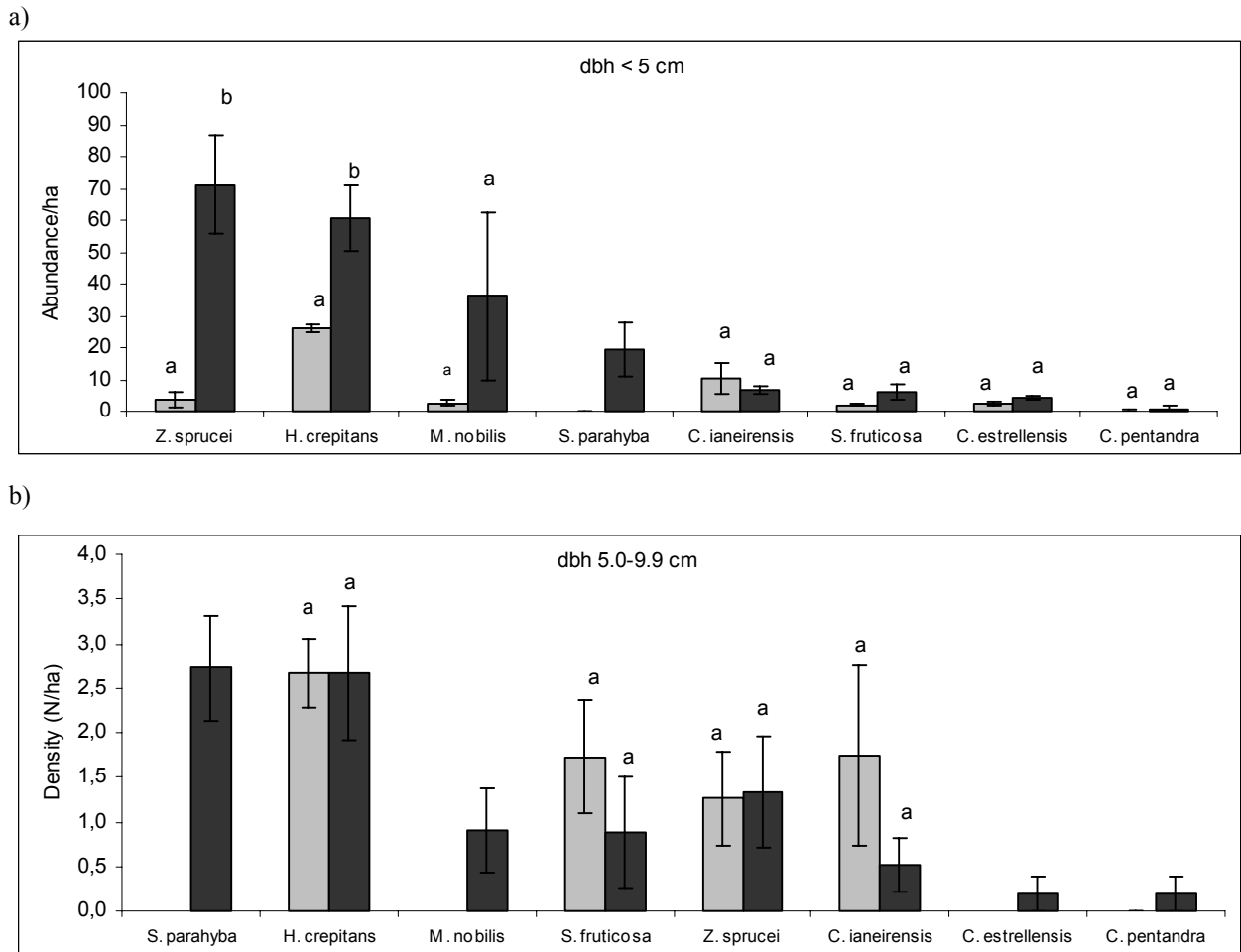


Figure 1. Logging and silviculture effect (No/ha, ± 1 SE) on species density for sapling (a) and pole (b) sizes (ANOVA test). Light shading, control plots; dark shading, intensive treatment plots.

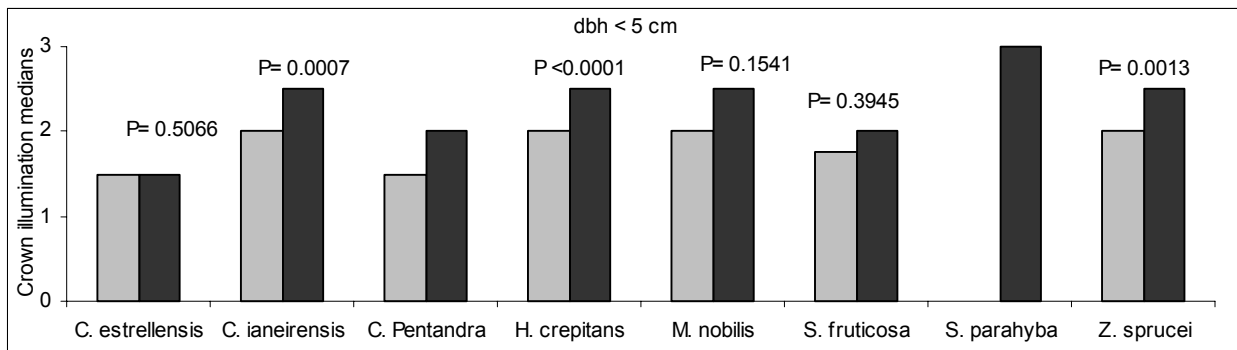
For pole size it was not possible to observe any statistical differences since the population size so soon after intervention was too low and logging treatment was not expected to significantly affect this class size except for those fast-growing species such as *S. parahyba* (Figure 1b). Therefore, these results for this size class should be taken as being preliminary. However, one result needs to be noted for pole size: three species showed no individuals in the unlogged area but did show individuals in the logged one (*S. parahyba*, *M. nobilis*, *C. estrellensis*, *C. pentandra*). We suggest this to be an obvious treatment effect, at least in the case of *S. parahyba* and *M. nobilis*.

In general, the variability of abundances, as evidenced by the standard errors (Figure 1), was higher in the logged plots, which it is attributed to heterogeneous regeneration after logging due to openings by harvesting and the effect of seed trees that colonize sites in the range of their seed dispersal capacity, and perhaps this is also affected by lower population sizes.

Effect of logging on light availability

Logging effects on crown illumination, canopy openness and the regeneration phase were also better observed in class sizes dbh < 5.0 cm. The Mann-Whitney test for crown illumination showed that three species received more light in the logged treatment (*C. ianeirensis*, *H. crepitans* and *Z. sprucei*) at the sapling size (Figure 2a). Similarly, *S. parahyba* benefited most from harvesting, presenting the highest crown illumination index of all species. With the exception of *C. estrellensis*, species had a higher median of crown illumination class in the logged plots than in the unlogged ones, illustrating that the harvesting regime applied resulted in more illuminated sites. For pole size trees, statistical differences were only for *H. crepitans* and *S. parahyba*, which again had the highest crown illumination index (Figure 2b). The number of individuals for each species for sapling and pole sizes is presented in Table 2.

a)



b)

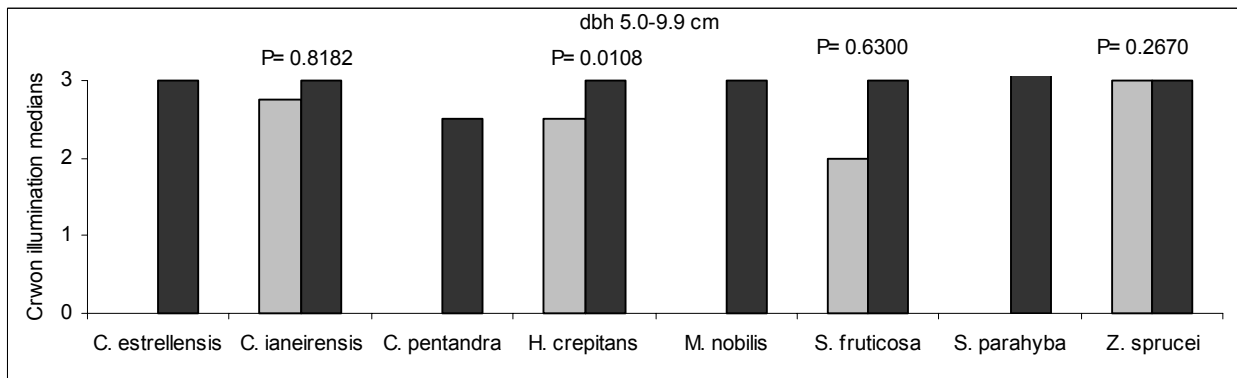
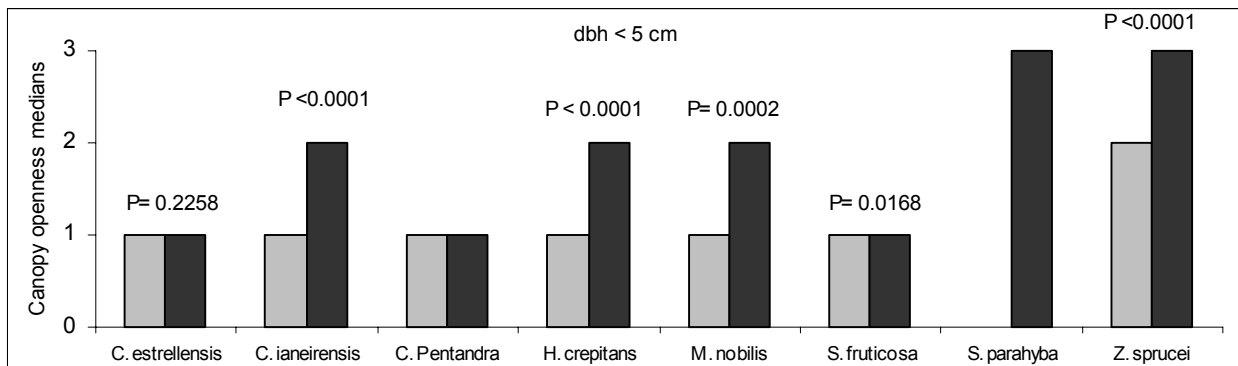


Figure 2. Mann-Whitney test comparing unlogged and logged treatments for crown illumination, for (a) sapling and (b) pole sizes (Medians represent crown illumination indexes, Clark and Clark 1992). Light shading, control plots; dark shading, intensive treatment plots.

The results for canopy openness and the regeneration phase were similar for saplings (Figures 3 and 4); differences were more clearly evident in this size class. *C. ianeirensis*, *H. crepitans*, *M.*

nobilis, *S. fruticosa*, *Z. sprucei*, and *S. parahyba* clearly benefited from logging, showing a significant change to a larger median index from unlogged to logged sites. The exception was *C. estrellensis*, which exhibited medians with no statistical differences. No statistical inferences were possible for *C. pentandra* because of the low number of individuals. *H. crepitans*, *Z. sprucei* and *S. parahyba* benefited from the logging treatment. We concluded that, as expected, logging increases illumination. For pole size, statistical inferences were restricted by low abundance. Despite this, *H. crepitans* and *Z. sprucei* yielded significant statistics for canopy openness and the regeneration phase, respectively. In both cases, *S. parahyba* continued showing large illumination median indexes.

a)



b)

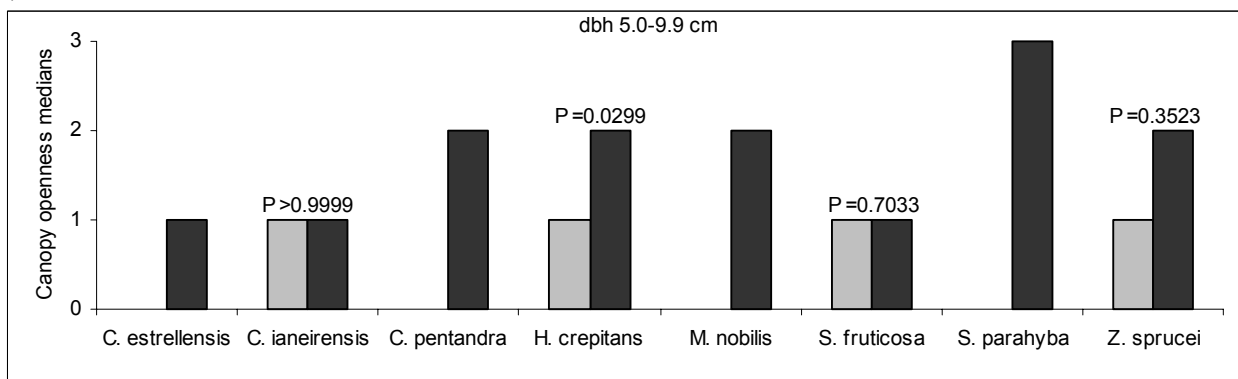


Figure 3. Mann-Whitney test comparing unlogged and logged treatments for canopy openness, for (a) sapling and (b) pole sizes (Median 1= Closed canopy; 2= Medium gap; 3= Large gap). Light shading, control plots; dark shading, intensive treatment plots.

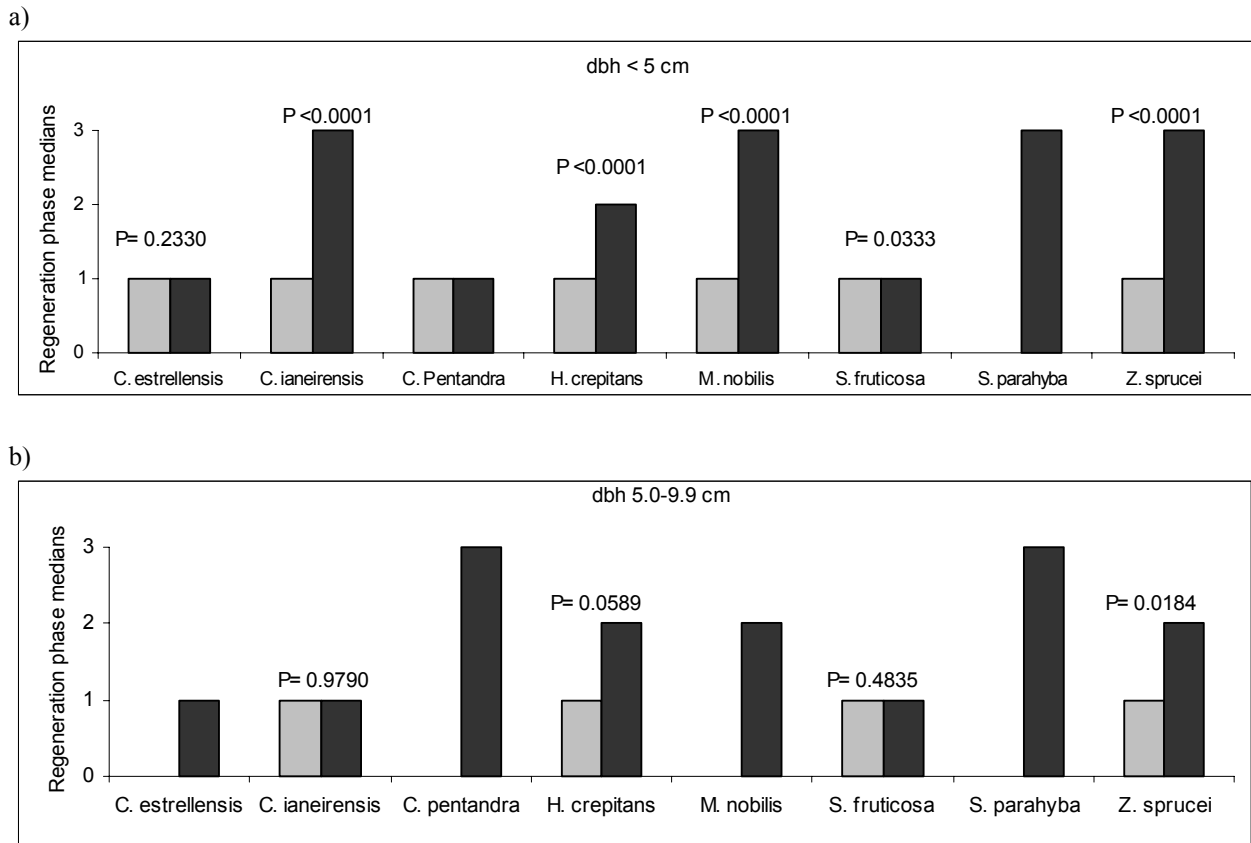


Figure 4. Mann-Whitney test comparing unlogged and logged treatments for regeneration phase, for (a) sapling and (b) pole sizes (Median 1= Mature forest; 2= Building; 3= Gap). Light shading, control plots; dark shading, intensive treatment plots.

Effect of skidder trail disturbance

The effect of skidder soil disturbance could only be detected for dbh < 5.0 cm and upon comparing the strong light-demanders *S. parahyba* and *Z. sprucei* with the other species. *S. parahyba* showed high abundance in the “low” skidder soil disturbance class (the most common disturbance class) and differed from *C. estrellensis*, *H. crepitans*, *M. nobilis*, and *S. fruticosa*, which all had their higher abundance in the “No skidder” disturbance class. *Z. sprucei* differed from *H. crepitans* by also having its higher distribution in the “Low” soil disturbance class (Table 3). The results show that *S. parahyba* and *Z. sprucei* were the species that responded best to skidder soil disturbance, developing more regeneration on skid trails in comparison to the other species. Statistical tests for pole size were not made because, for most species, differences in pole size were not expected to be observed so soon after logging. The exception may be *S. parahyba*, a very fast-growing species in disturbed sites.

Table 3. Contingency table for pair of species distribution differences for soil skidder disturbance for sapling size. Data shows species' frequency distribution (%) by classes of skidder disturbance. Only the results that were significant at $P \leq 0.05$ are presented. Species at pole size did not show any statistical significance.

Species	Classes of skidder disturbance (dbh < 5.0 cm)				N	P-value
	No skidder	Low	Moderate	High		
<i>S. parahyba</i>	65.5	32.7	1.8	0.0	110	0.0478
<i>C. estrellensis</i>	91.3	8.7	0.0	0.0	23	
<i>S. parahyba</i>	65.5	32.7	1.8	0.0	110	<0.0001
<i>H. crepitans</i>	90.1	6.6	2.4	0.9	333	
<i>S. parahyba</i>	65.5	32.7	1.8	0.0	110	0.0004
<i>M. nobilis</i>	79.0	13.9	5.8	1.6	190	
<i>S. parahyba</i>	65.5	32.7	1.8	0.0	110	0.0021
<i>S. fruticosa</i>	96.9	3.1	0.0	0.0	32	
<i>Z. sprucei</i>	72.1	21.5	5.9	0.5	391	<0.0001
<i>H. crepitans</i>	90.1	6.6	2.4	0.9	333	

4. Discussion

The low abundances found in the undisturbed forest plots for most species is consistent with similar findings by Clark (2002), who pointed out how extreme rarity complicates ecological studies and statistical inferences. Species' scarcity in the tropics has been recognized as a problem for ecological studies. Despite the size of the sampling plots in this experiment and the area covered by the field survey, several species showed extremely low abundance, the extreme example being *C. pentandra*. *S. parahyba* represents a different situation. No individuals were found in the unlogged forest, but regeneration was abundant in the logged treatment, confirming its ecological preference for disturbed areas. For size class dbh 5.0-9.9 cm no statistical inferences were possible for three species: *C. estrellensis*, *C. ianeirensis*, and *M. nobilis* because of the small number of individuals.

Our results regarding species rarity are consistent with other studies in the tropics, in which many species are locally rare (see Hubbell and Foster, 1986; Clark *et al.*, 1999; Pitman *et al.*, 1999; Valencia *et al.*, 2004). Acknowledging this problem of rarity in ecological studies in the tropics, Clark (2002) recommends researchers not to stop studying rare species because of abundance constraints. This recommendation is particularly pertinent in the case of rare species that are also commercially valuable.

From our eight species studied, three were considered as locally rare in the undisturbed forest (*C. estrellensis*, *S. parahyba*, and *C. pentandra* (abundance $\leq 1/\text{ha}$, dbh ≥ 10 cm). From these, *C. estrellensis* and *C. pentandra* did not show any benefit from logging disturbances, while *S. parahyba* dramatically increased its abundance through logging. These results concur with Harper's (1981) claims, that some rare species could become more abundant in time, and others remain rare. On the other hand, some abundant species, such as *H. crepitans*, could become even more abundant.

Harvesting in Bolivia is very selective, which results in small gaps which do not favor the regeneration of light-demanding species (e.g. Gullison *et al.*, 1996; Fredericksen, 1998). In the plots of our study, harvesting was about twice the normal harvesting intensity and therefore larger disturbances were expected. The canopy opening represented 1.5 times the damage occurring in normal harvesting (Ohlson-Kiehn *et al.*, 2003), not twice, coinciding with Panfil and Gullison

(1998) who found that disturbances do not follow a linear relationship between the affected area and harvesting intensity in the Chimanes forest, Bolivia.

In our study, the influence of disturbance was clear at the sapling size for two reasons. The survey was done only 2-3 years after logging, therefore, the disturbance effect is visible in the smaller plant sizes, and because the sample size was higher in this size class, so it was possible to make meaningful statistical inferences. Opening the canopy to favor the development of small- and medium- sized trees has already been carried out successfully in other studies (Bertault *et al.*, 1995), but in our study it is too early to reach any conclusions regarding pole and tree sizes. However, we can speculate that with the increase of light there will be an increase of growth and survival, as found by Clark and Clark (1992) and Poorter and Arets (2003).

Our hypothesis regarding the increase of some species' regeneration abundance after logging was accepted. We found evidence that three out of the four species that were previously supposed to respond well to harvesting, actually benefited from harvesting: *Z. sprucei*, *H. crepitans* and *S. parahyba*. The responses of *M. nobilis* were significant at $\alpha= 0.1$. We note that despite the large mean difference between unlogged and logged treatments for *M. nobilis*, the test was only significant at $\alpha= 0.1$. We attribute this to the high variability among the plots in the logged treatment, as a result of the heterogeneous regeneration after logging due to seed dispersal heterogeneity limitations and colonization restricted to sites near seed trees. *S. fruticosa* (which belongs to the group that does not usually develop abundant regeneration after logging) also showed a tendency to benefit from logging, being significant at $\alpha= 0.1$. Post-harvesting regeneration seems to be a key issue for most species.

The two *Cariniana* spp. did not show any statistically significant responses to disturbance, and *C. pentandra* did not yield any statistical results because it presented only 6 individuals in all the plots. However, one could ask if the lack of significance for the two Carinianas is a real response or if it is affected by the low power of the test. The coefficient of variation of both species was similar to the species that were statistically significant, so this could lead us to conclude that we are not committing a type II error. However, the difference between means is lower, which makes it difficult to detect significant differences (effect size). We recommend more intensive sampling in future studies in order to overcome a possible lack of statistical power.

It is expected that the treatment's effect on the pole class size, where no statistical significances were obtained, will be observable over the next few years, when the regeneration caused as a result of logging should develop into larger size classes.

Our hypothesis on light increases after logging was also accepted. Light increases, a key factor for plant recruitment, could be observed in the median increases for crown illumination, canopy openness and the regeneration phase for all species, with the exception of *C. estrellensis*, which is the least light-demanding of our species. *Z. sprucei* and *S. parahyba* presented the highest species' medians (3= partial vertical light), which confirms that these were the most light-demanding species and that they benefit most from harvesting disturbance, including skid trails. The fact that we found *S. parahyba* only in logged treatments illustrated that this species requires a high degree of canopy opening, and that logging and silviculture promote its regeneration, which is greatly enhanced by skidder soil scarification (Fredericksen and Pariona, 2002; Park 2003).

The positive response to skid trails suggests that forest managers should pay attention to regeneration on these sites for silviculture purposes, monitoring and planning new loggings at the same site, as well as to logging roads where regeneration also develops, as found by Severiche (2002) in the same forest.

Bolivia has taken great strides in planning forest management, but it fails to embrace silviculture practices mainly because silviculture does not bring immediate economic returns and it has a high cost of capital (Fredericksen *et al.*, 2003). Our results suggested that increasing the harvesting intensity together with a package of silviculture treatments may promote the regeneration of some light-demanding timber species, coinciding with Silva *et al.* (1995) in Tapajos, Brazil. We suggest carrying out studies to determine the limits of acceptable damage and disturbance for plant species and the forest. In general, harvesting will necessarily cause changes in the forest's structure, and a certain degree of tolerance to changes in the forest's composition is required in forest management. However, tolerance must not embrace the loss of species and excessive damage to ecosystem processes (Boot and Gullison, 1995), especially in the protection areas within the forest management and buffer zones in protected areas. In addition to timber species and forest structure concerns regarding the reactions to an increase of logging levels, we must

pay attention to the impacts on wildlife, although Fredericksen *et al.* (1999a) concluded that the current level of harvesting neither benefits nor negatively affects wildlife populations because of the “lack of dramatic impacts of the gap size”.

Our results support Panfil and Gullison’s (1998) findings, who argue for more intensive harvesting to promote growth and better regeneration of valuable species. Fredericksen *et al.* (1999b) arrived to similar conclusions for another common genus –*Ficus*– whose regeneration was enhanced by logging disturbances in a seasonal dry forest and at the site of this study. Snook (1996, 2005) concurs with the need for disturbances for another light-demanding species in Mexico, *S. macrophylla*. According to Boot and Gullison (1995) the lack of sufficient disturbance may explain why *S. macrophylla* develops little natural regeneration under low-intensity harvesting in Bolivia.

We conclude by warning that, despite the fact that some rare species in the undisturbed forest increased their abundance with logging and silviculture treatments, others remained rare. Before harvesting rare species, managers should get enough ecological data on the rare species to ensure that their practices do not threaten them. This remains an unanswered question in this research: how to promote the regeneration of rare species like *C. pentandra*? One option would be to carry out heavier harvesting than we did, so more light would be available for seedling recruitment. However, if too much light is provided, there is the risk of invasion of non-commercial species such as lianas. When logging rare species, we recommend making sure that they are protected in the protection zones within the forest management unit and that they are abundant at the landscape scale. Before harvesting rare species, it will be necessary to determine thresholds of acceptable reduction of abundance; if monitoring is too difficult or impossible, rare species should be protected through a precautionary approach during harvesting (Finegan *et al.*, 2004). If no sufficient information is available, the best option, at least from the ecological point of view, is not to harvest them.

Finally, in order to improve forest management in a dynamic manner, it will be necessary to implement a management system that allows a company to learn from their failures and success, and systematically improve it by means of an adaptive management approach requiring permanent learning through monitoring, evaluation, and the opportune adjustment of forest management (Nyberg, 1999).

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CHAPTER 5. GENERAL RESULTS, CONCLUSIONS AND RECOMMENDATIONS

Results presented here come from four studies: (1) the effect of topography on species distribution, (2) the determination of the relationship between species regeneration and light environment in undisturbed forest, (3) seed dispersion, and (4) effect of logging and silviculture on regeneration, including the effect of skidder trails on natural regeneration. To carry out these studies, we chose eight long-lived pioneer species, four of which are known to develop abundant regeneration after disturbances by harvesting (*Hura crepitans*, *Margaritaria nobilis*, *Schizolobium parahyba*, *Zanthoxylon sprucei*), and four that do not (*Cariniana estrellensis*, *Cariniana ianeirensis*, *Sweetia fruticosa*, *Ceiba pentandra*). The selected species had different densities.

Results from the undisturbed forest showed that three species could be classified as locally rare, having an abundance of ≤ 1 individual/ha (dbh ≥ 10 cm), using the Clark and Clark (1992) threshold developed for Costa Rica, and Pitman *et al.* (1999) for the Amazon. These species were: *C. estrellensis*, *C. pentandra*, and *S. parahyba*. However, the Instituto Boliviano de Investigaciones Forestales found a slightly different abundance in the same area (unpublished data), sampled in a larger area (324 ha) not covered by this survey. According to that study the only rare species were *Z. sprucei* and *C. pentandra*.

The phenomenon of rarity of tropical forest species has been pointed out by several authors (Hubbell and Foster, 1986; Bawa and Ashton, 1991; Clark and Clark, 1992; Pitman *et al.*, 1999; Clark *et al.*, 1999; Harms *et al.*, 2001; Clark 2002, Valencia *et al.*, 2004). This common attribute makes ecological studies and statistical inferences difficult (Steidl *et al.*, 1997, Underwood, 1997; Clark, 2002), affecting statistical results, mainly on the power of the tests. The power of a statistical test is influenced by (a) α value, (b) the sample size $-n-$, (c) the intrinsic variability of the population, and (d) the “effect size” -i.e. how large is the difference between the null and the research hypothesis (Steidl *et al.*, 1997; Underwood, 1997).

In our case, we assumed that the low frequency showed in the results -because of species' low abundance- may have reduced the statistical power of the tests, which means there is a problem for statistical inferences and the increased probability to commit a Type II error (i.e. failing to

reject the null hypothesis when it is actually false). This, however, should not prevent us from trying to analyse biological differences, as suggested by Steidl *et al.* (1997).

To increase power, tests were run using the 20 m x 20 m plots as replicas, however, the variance was higher when using this approach because the plots were too small to use as replicas, so that power was not in fact increased. In the logged treatment, high variability was expected. In fact, all species that develop abundant regeneration after logging presented the highest variability within the logged treatment.

We could make inferences for sizes dbh < 5.0 cm, but the statistical constraints were obvious in larger diameter sizes because of small sample sizes. Indeed, some species did not show any individuals in larger dbh size classes. This is why the results discussed in this chapter will focus on trees with a dbh < 5.0 cm, except when otherwise noted. There was another statistical concern that we tried to avoid at the beginning of the study, the problem of the plots' spatial autocorrelation. The main problem when a given sample influences another one because of proximity, i.e. plots are not independent, is that the new observation does not add a full degree of freedom (Legendre, 1993). To avoid this, we placed our sapling plots in a systematic design, which provided an unbiased estimation of the parameters sampled (Fortin *et al.* 1989, Clark 2002), and the plots were separated by long distances (75 m each), since spatial autocorrelation declines with distance (Fortin *et al.*, 1989; Koenig, 1999). We assumed that the most common event that could affect the independence of sampling plots was tree felling and species responses within the resulting gaps. Canopy trees reach 25 m in height, so trees felled from one plot were not expected to affect the neighbouring plot, at a distance of 75 m, even if one tree felled led to another tree being felled.

For our first study, the effect of the topography, we hypothesized that the topographic position (*Base, Slope, Ridge*) and percent slope (*Flat, Moderate, Steep*) affected species' distribution. *C. pentandra* was eliminated from the analysis because it presented too few individuals to yield statistical inferences. We found that species expected to respond well to harvesting were specialists favoring gentle slopes. *M. nobilis* was the only species to be statistically associated with its topographic position. All species associated with topography were the most light-demanding ones, and probably the faster growing and highly moisture demanding ones. Considering that this site is a semi-deciduous forest, with moisture limitations during the dry

season, we hypothesized that water availability in bottom lands and shallower slopes was important for the growth of the light-demanding species, as suggested by Harms *et al.* (2001) for BCI plots. We recommended that silviculture treatments for these species should focus on gentle slopes where the species are expected to respond better, and to develop more studies on the association of species-soil properties.

In the second study regarding species' regeneration and light relationship in an undisturbed forest, we tested the hypothesis that the variables, crown illumination, canopy openness and regeneration phase, would be different for the species studied than in the forest distribution. In other words, we wanted to determine if the species had a particular trend or behaviour regarding light, or it just followed the evident pattern in the forest and was not therefore distinguished from random. Differences were only detected for *Z. sprucei*, as it showed a distinct crown illumination distribution, with a higher abundance in more illuminated classes. *C. estrellensis* showed an opposite trend, with its distribution concentrated in lower crown illumination classes, statistically significant at $\alpha= 0.1$. When analysing pole size, we found individuals of only four species, and three of them differed from the forest distribution.

For canopy openness we found the same results as for crown illumination for sapling size: *Z. sprucei* was the only species differing in distribution from the forest when exposed to well-illuminated sites, suggesting that this species is the most light-demanding one. All the other species roughly followed the forest distribution. No species resulted in being different from the regeneration phase and forest distribution for both size classes, suggesting that all species followed the forest distribution and that all species were similar amongst themselves regarding this variable. However, here we concluded that the regeneration phase is not a good surrogate for light entrance or availability because the "mature" phase niche could contain small gaps in the canopy which provides light for regeneration, not considered when assigning this class for the site.

Three groups of species were recognized regarding the light-demanding gradient: (1) *Z. sprucei*, as the most light-demanding, (2) *M. nobilis*, *H. crepitans*, *S. fruticosa* and *C. ianeirensis*, as intermediate ones, and (3) *C. estrellensis*, as the least light-demanding.

Since most species had distributions similar to the forest, we were cautious when making conclusions about microsite influence on species' distribution: microsite influence on the distribution of the species studied seemed to be minimal. *S. parahyba* and *C. pentandra*, species with reproductive strategies that depend on higher intensity disturbances, were the rarest species in the sampling plots. *H. crepitans*, a species known to respond well to openings by harvesting and the most abundant in all size classes, proved to have the ability to develop natural regeneration in the shaded understory, which partly explains the abundance of this species in both undisturbed and disturbed forests.

All six species in this study, including the more light-demanding, developed some degree of regeneration under the canopy and we speculate that they receive sufficient light from sun flecks and diffused light to persist at least for some time under the canopy. Indeed, all species received most of their light from lateral light (saplings), coinciding with Clark and Clark (1987) regarding the importance of lateral light for trees below 10 cm dbh. We do not know how long this regeneration can persist in the understory, but we speculate that this "seedling bank" of long-lived pioneers, although not abundant, may be an advantage for forest management if harvesting provides sufficient light entrance.

We cautioned silviculturalists and forest managers when harvesting rare species, such as those we found, since rare species are more vulnerable than common ones (Rabinowitz *et al.*, 1986), which include the light-demanding species (Jennings *et al.*, 2001). Since locally rare species need large areas for their conservation, we suggest that sustainable forest management –if properly designed and implemented- could become an efficient tool for species conservation outside protected areas and integrated with the protected areas in a more comprehensive conservation strategy. Therefore, policy-makers need to consider the conservation of rare species on a landscape scale, inside and outside forest management units.

In the third study on seed dispersal, we were interested in determining seed dispersion. Because of the lack of seed production of most of the species during the study, data was collected for only four species: *H. crepitans*, *M. nobilis*, *S. parahyba*, and *Z. sprucei*. We found that *M. nobilis* and *Z. sprucei* had the lowest dispersion distance (both 4 m). However, since these species have their seeds dispersed by vertebrates, we do not know their actual dispersal capacity. *H. crepitans* dispersed its seeds up to 10 m, and these species may compensate its short dispersion by its

capacity of developing regeneration under canopy. *S. parahyba* had the furthest seed dispersal recorded (38 m), which would partly explain this species' ability to be virtually absent in the undisturbed forest (at least in our sampling plots) and be present in openings in harvested forests. It is known that this species presents seed dormancy (Justiniano *et al.*, 2001) and therefore, the seeds remain viable in the soil and germinate when large canopy openings occur. We advise that this result be taken as preliminary because we could not complete all the measurements initially planned.

Our fourth study, regarding the effect of logging and silviculture on species' abundance and light availability at an operational scale, found that all the species that were initially considered responded well to harvesting and increased their abundance with logging and silviculture: *Z. sprucei*, *H. crepitans*, and *S. parahyba*, led to the acceptance of the hypothesis showing a higher regeneration abundance in the logged treatment. The fourth species of this group, *M. nobilis*, also showed higher abundance in the logging treatment, but it was only significant at $\alpha = 0.1$. We attributed the lack of significance at a lower α to its high variance in logging plots as a result of the heterogeneous regeneration in harvested sites. Indeed, most species showed a higher variance in logged treatment. On the other hand, *S. parahyba* was only present in the logged treatment, which illustrated its requirement for larger disturbances. For the other group of species, not expected to develop abundant regeneration after logging, the logging treatment did not show any statistically significant effect on their abundance.

The tests regarding responses to light (crown illumination, canopy openness, and regeneration phase) showed, with the exception of *C. estrellensis*, that the regeneration benefited from harvesting. No conclusions were possible for *C. pentandra* because of the few individuals that were found. We concluded that logging increases illumination and that most species get significant benefits from it, at least in the smaller size classes.

Rarity was an important issue to consider when analyzing the results of logging. As mentioned before, three species were considered to be locally rare in the undisturbed forest (abundance ≤ 1 individual/ha): *C. estrellensis*, *S. parahyba*, and *C. pentandra*. Two species, *C. estrellensis* and *C. pentandra*, did not increase their abundance after the logging disturbances and silviculture treatments. However, *S. parahyba* increased its abundance. We concluded that harvesting and

silviculture treatments increased the regeneration of some locally rare species; some rare species failed to increase their regeneration, and some abundant species could become more abundant (e.g. *H. crepitans*). We recommend paying special attention to the rare species that do not benefit from treatments during harvesting planning. We finalized by encouraging studies on logging damage, levels of harvesting, silviculture for rare species, number of seed trees to be left after logging, and monitoring species' regeneration responses after logging.

Regarding skid trail disturbances, we tested the hypothesis that disturbances by skidder movements promote natural regeneration. We compared all the species against each other, and we found that two species differed: *S. parahyba* and *Z. sprucei*, showed a higher abundance on skid trails than the other species. Therefore, we concluded that these species responded to disturbances caused by skid trails. It must be noted that skidding benefits could not only be a result of soil scarification by wheels, but also the entrance of light caused by the skidder's passing through the vegetation. We are not suggesting to indiscriminately disturb the forest by the widespread use of skidders because damages would more than offset the regeneration gains; we suggest instead, to observe the regeneration on skid trails when planning management practices.

The increase of abundance in the logging treatment must not be assumed to be the result of the sole effect of canopy openness, but also the result of a set of impacts from logging and silviculture treatments. We concluded that this set of treatments were beneficial for the species that were expected to develop abundant regeneration after logging, but failed to promote the regeneration of the other species group. Therefore, more studies are needed to find treatments to promote the regeneration of this group of species. In addition, complementary studies are needed on logging damage when increasing the level of harvesting, and also on seed dispersal, the number of seed trees, fructification and timing for harvesting, and monitoring of the natural regeneration to define adequate silviculture treatments after logging to promote regeneration and survival in different size classes.

Although all species were initially considered to belong to a single guild, we detected a gradient in terms of light requirements and abundances. Some species were more light-demanding than others and responded differently to the logging treatment. The most light-demanding species coincided with the group of species that were expected to respond well to harvesting, so we inferred that canopy opening by harvesting plays a key role in triggering the natural regeneration

of this group. The lesser light-demanding did not develop abundant regeneration after logging, so we speculate that the level of canopy opening in our treatment was either not large enough or these species simply do not react to openings.

In the following paragraphs we summarize the main ecological patterns that we found for each species for dbh < 5.0 cm, except where otherwise stated, since it was in this size class where we found the largest number of individuals for statistical inferences.

S. parahyba was the most light-demanding species. We could not fully compare it to the other species since it was absent in our sample plots in the undisturbed forest, but a multivariate analysis of principal coordinates that combined data from unlogged + logged treatments showed that this species is the most light-demanding (data not shown). Indeed, the fact that it was abundantly found in the logged treatment indicates its preference for large open microsites. This species was associated with gentle slopes. It was another species considered locally rare in the undisturbed forest. It disperses its seeds the farthest. This capacity to disperse seeds over long distances, the ability of seed dormancy, and its capacity to regenerate in disturbed areas and its fast growth explains the abundant presence of this species in the disturbed forests.

Zanthoxylon sprucei was one of the most light-demanding species that responded most vigorously to the logging treatment. This species is a generalist regarding its topographic position, but it is a specialist regarding slope, presenting a higher abundance in flat and moderate slope classes where a higher availability of moisture and better soil fertility are expected. It showed a seed dispersal limitation, but since it is animal dispersed, we did not document its actual dispersal capacity. We hypothesized that this species compensates its low abundance in undisturbed forest by its aggressive capacity to colonize open microsites. This colonizing capacity seems to be very efficient, showing an increased regeneration in the logged treatment. Further studies on seed dormancy would provide more insights into its ecological strategy for regeneration.

Margaritaria nobilis was the third most light-demanding species, which also responded well to harvesting, despite the fact that the results were only statistically significant at $\alpha = 0.1$. However, we have grounds to speculate that this species belongs to the group of species responding well to harvesting as predicted. *M. nobilis* showed a much higher abundance/ha mean in the logged

treatment ($2,7 \pm 1,9$ in the unlogged forest vs. $36,1 \pm 45,8$ in the logged areas). We hypothesized that its capacity for colonizing open microsites explains its high abundance variability. Unlike the other species that responded well to harvesting, it proved to be associated with its topographic position (slope) as well as with gentle slopes, which led us to conclude that this is a specialist species regarding topography associated with moist habitats. Like *Z. sprucei*, we recorded a low seed-dispersal distance, but since it is also dispersed by vertebrates we do not know its real dispersal capacity.

Hura crepitans, also proved to be generalist regarding its topographic position, but a specialist on gentle slopes for $\text{dbh} \geq 10$ cm, which allowed us to confirm previous findings that trees of this species are distributed in flat and poorly drained areas. Like the previous species, it presented seed dispersal limitations, although its maximum dispersal distance seemed to be higher than the *Z. sprucei* and *M. nobilis* because of its larger crown diameter. This species was relatively well-distributed in microsites with all gradients of light, and was able to respond aggressively to disturbances, reflecting its flexibility for a wide gradient of illumination. We concluded that this pattern explains the abundant presence of *H. crepitans* in both undisturbed and disturbed forests. This species was one of the species considered as “common” and it became even more abundant in the logged treatment.

Cariniana ianeirensis was another species considered as “common” in the undisturbed forest, and represented the highest volume harvested in the La Chonta concession (39% of total volume for year 2004). This species was a generalist regarding topography, and failed to increase its abundance with logging; however, it presented statistical evidence of increasing its median for crown illumination, canopy openness and the regeneration phase with logging. It would be interesting to test this species’ responses to larger canopy openings. Seedlings’ survival of this species has been reported as good (43% in one year) in abandoned logging trails (Pereira and Fredericksen, 2002). The principal coordinate analysis ranked this species as less light-demanding than *H. crepitans*. Considering the commercial importance of this species, further ecological and silviculture studies are merited.

Sweetia fruticosa was also considered a common species in the undisturbed forest. It was also a generalist species regarding topography. Like *C. ianeirensis*, its abundance did not increase with

the logging treatment. The principal coordinate analysis ranked this species as less light-demanding than *C. ianeirensis*, and thus, it showed a lesser increase in illumination medians than *C. ianeirensis* in the logging treatment. However, there was significant evidence of benefits derived from crown illumination, canopy openness and regeneration phase variables, so we also advocate for further studies for this species, considering larger canopy openings.

Cariniana estrellensis is the fourth species in terms of commercial importance for the La Chonta forest concession. It is a species that is considered locally rare and it did not increase its regeneration with logging. Since a large portion of mature trees (i.e. seed trees) have been removed from the forest due to logging, we warn that the regeneration of this species could be threatened by harvesting and that it could become even rarer over time. Like *M. nobilis*, we did not find individuals of pole size. The major difference between both species is that in most cases *M. nobilis* responded to logging while *C. estrellensis* did not, which may be explained by the degree of light requirements for each species. *C. estrellensis* did not show any statistical significance when comparing unlogged and logged treatments for crown illumination, canopy openness and the regeneration phase. This is consistent in both multivariate analyses, which showed that this species was the least light-demanding.

C. pentandra was the rarest species and we cannot say much about it since we could not make any statistical inferences, except that logging treatment did not promote its regeneration. This species was very similar to *S. parahyba* in one way: both species were extremely rare and virtually absent in our sample plots in the unlogged forest. The greatest difference between them was that *S. parahyba* developed abundant regeneration after logging disturbances (mean 19.4 individuals/ha), while *C. pentandra* did not (mean 0.8 individuals/ha) (dbh < 5.0 cm). It is known that this species develops in open fields, so it may need larger gaps than those existing in our plots. Since large gaps are often few, seed availability and dispersal restrictions may be a complementary limitation for seedling development. Forest managers must consider the recruitment constraints of this species when planning harvesting so that logging does not threaten this species' conservation.

To finalize, we summarize some interesting findings. Eventhough supposedly belonging to the same guild, species have shown different strategies. The more light-demanding species were specialists with regard to topography, being associated with gentle slopes. Soil moisture seems to

be the most likely reason behind this finding. No pattern was found for rare or common species and topography classes. Also, there was no pattern regarding the abundance and level of light-demanding species, as one could expect. Seed dispersal patterns differed among species. The most light-demanding species -*S. parahyba*- dispersed its seeds at least up to 38 m, giving this species an advantage in colonizing large disturbances when they occur. More studies on species phenology are merited to improve forest management.

Despite the low abundance of some species, rarity in unlogged forests seems to be a successful reproductive strategy, at least for some species. There is the possibility that some could become common with disturbances and others may persist as being locally rare, but abundant in large areas, as found by Pitman *et al.* (1999) in the Amazon. Concerns arise for those rare species that do not increase their abundance with logging, which would become even less abundant if mature trees (i.e. seed trees) are removed. In these cases, a landscape approach would be particularly important, where the forest ecosystems, protected areas and protection zones within the forest management units may contribute towards the conservation of rare species on a larger scale. For forest management certification purposes, the certifiers should pay special attention to harvesting rare species, since these species are particularly vulnerable (Rabinowitz *et al.*, 1986; Jennings *et al.*, 2001).

Common species may or may not respond well to harvesting, and responses seem to be associated with the degree to which a species is light-demanding. Species that were found to be the most light-demanding were those that responded better to harvesting. However, species that did not increase abundance with harvesting, the less light-demanding, showed benefits from logging by increasing their levels of crown illumination, with the exception of one species. We do not know if increasing the level of disturbance will favor the regeneration of these species and the subsequent effect on their growth. The level of accepted disturbance has limits, and these limits have to be established by the resilience capacity of the forest, species recruitment, invasion of non-commercial species, species' conservation (fauna and flora), and environmental services of the forest ecosystem.

We have found that pioneer species are able to develop regeneration in the understory, but this abundance dramatically decreases in larger diameter size classes. The challenge for silviculturalists will be to ensure that seedlings and poles successfully reach larger sizes and

finally become harvestable trees. We conclude that planned harvesting may not be enough to ensure future crop trees. The probability that a given seed survives production, dissemination, germination, and develops from a germinant to a seedling, pole and, eventually, into a mature tree is extremely small. To understand these process it will be necessary to consider the ecological implications of many key aspects, such as pollination, fruit and seed production, dispersion, substrate, timing for seed dispersal and available substrate, moisture conditions for germination, growth conditions for early development, light conditions, predation and damages, soil moisture, fertility and soil's physical properties, fire and other natural phenomena, among others. There is much to learn and to improve, and the best way to face this challenge is by applying the adaptive management approach, a process of learning and improving.

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