NATURAL REGENERATION OF CANOPY TREES IN A TROPICAL DRY FOREST IN BOLIVIA

By

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NATURAL REGENERATION OF CANOPY TREES IN A TROPICAL DRY FOREST IN BOLIVIA

By

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Fruit production, seedling establishment, and sprouting of canopy trees were studied in a lowland tropical dry forest in the Department of Santa Cruz, Bolivia. Fruit production by reproductively mature trees was monitored over a 5 y period to assess variability among species, trees and years. The effects of tree size, crown area, crown position, and liana infestation on fruit production were also assessed. In a companion study, I assessed the effects of lianas on fruit production by *Caesalpinia pluviosa* with a liana cutting experiment. To determine how logging disturbances affect seedling recruitment, I monitored seedlings for 3 y in different microsites in permanent plots in two selectively logged plots and an unlogged control plot. I also experimentally assessed the effects of bromeliad cover, drought stress, and seed/seedling predators on seedling recruitment, survival, and growth. Finally, I monitored the emergence, survival, and growth rates of stump and root sprouts over a range of microsites.

Percentages of trees fruiting and numbers of fruits produced varied among species and years. In most species, trees that did and did not fruit did not differ in size or crown position, but in a few cases, the likelihood of fruiting increased with crown area. Contrary to my expectation, there no effect of liana cutting on *Caesalpinia pluviosa* fruit production was detected 3 yr after

cutting. Overall, the effect of logging on the proportion of trees fruiting and fruiting intensity varied among species.

Seedling densities 5 y after selective logging were higher in control than logged plots but this finding was greatly influenced by the most common species, *Acosmium cardenasii* (43% of seedlings enumerated). At the microsite level, *Acosmium* was found in highest densities in undisturbed areas while *Centrolobium microchaete,* another common species, was more common on log extraction paths. Seedling recruitment rates were higher in the unlogged plot and in the undisturbed portions of the logged forest plots, but seedling mortality rates were also higher in these areas. Mortality rates of naturally established seedlings varied greatly among species. Seven of 22 species suffered no mortality during the 2-y monitoring period, whereas relatively high mortality rates were observed for *Caesalpinia* (26%/y), *Sweetia fruiticosa* (25%/y), and *Machaerium scleroxylon* (22%/y).

Results of the experimental study on seedlings suggest that bromeliad competition and seed/seedling predators greatly affected tree seedling establishment. Soil moisture availability also affected seedling establishment, but only as an interaction with the bromeliad removal or predator exclosure treatments. The primary effect of the drought treatment was delayed germination. Despite these general trends, species varied substantially in their sensitivity to bromeliads, drought stress, and predators.

Root and stump sprouts constituted about 50% of the individuals <2 m tall of the canopy tree species studied, but the proportions of sprouts and true seedlings varied among species. Stump sprouting was common, but the probability of sprouting was not consistently related to stump diameter or height. Sprout growth rates were consistently high, at least initially, and sprouting is obviously important to post-logging regeneration in this dry tropical forest.

CHAPTER 1
FRUIT PRODUCTION OF TROPICAL DRY FOREST TREES IN BOLIVIA

Introduction

Tropical dry forests, which until very recently covered about 30% of Bolivia, are among the most threatened ecosystems in the world (Dinerstein et al. 1995). Bolivian dry forest are under siege; 32% has already been cleared (Camacho et al. 2001, Rojas et al. 2003) and most of the remainder is under intensive pressure for forest products, grazing, and further conversion. This pressure may be somewhat mitigated in the large portion of the dry forest managed for timber under the guidelines of Bolivia's 1996 Forestry Law (MDSP 1996, Nittler and Nash 1999). Even when these guidelines are followed, logging disturbances are larger in area than those that occur naturally. Given the documented effects of disturbance and habitat modification on reproductive success of tropical dry forest trees (Fuchs et al. 2003), the sustainability of managed forests even when the legally required "best management" practices are used, remains uncertain. To assess how forest management influences the reproduction of commercially valuable tree species, I explore the inter-tree and inter-annual variation in fruit production in a dry forest in lowland Bolivia.

A wide range of mechanistic explanations have been proposed for the marked variation in fruit production among years and among individuals in a wide variety of forested ecosystems (Abrahamson and Layne 2003, Snook et al. 2005). For seasonally dry tropical forests, inter-annual variation in rainfall, particularly as influenced by El Niño events, has often been invoked as the underlying cause of inter-annual variation in tree phenology and fruit production (Bullock 1995, Wright and Calderon 2006). Regarding individual tree characteristics that might influence reproductive output, several studies have reported a minimum size threshold for tree reproduction (Añez 2005, Wright et al. 2005). For trees that have attained reproductive maturity, several studies have shown a relationship between fruit production and stem diameter (Zuidema and Boot 2002, Wadt et al. 2005), crown area (Healy et al. 1999, Zuidema 2003), and crown position (Healy et al. 1999). Cover by lianas has also been shown to reduce fruit production by Brazil nuts “*Bertholletia excelsa* Bonpl.” (Zuidema and Boot 2002, Wadt et al. 2005, Kainer et al. 2006) and other species (Stevens 1987).

Anthropogenic and natural disturbances have been reported to influence canopy tree fruit production in a number of forests around the tropics but the results have been inconsistent. Logging increased fruit production by remnant trees in a subtropical humid forest in Meghalaya, India (Barik et al. 1996), as well as in a tropical montane forest in Costa Rica (Guariguata and Saenz 2002). In contrast, reproductive output of residual trees in a logged dipterocarp forest in Indonesia was lower than in an unlogged control area (Curran et al. 1999). Factors responsible for these contrasting results are not clear but, given the importance of natural regeneration to sustainable forest management, the issue deserves further exploration.

In this study in a seasonal lowland tropical forest in Bolivia I report on canopy tree fruit production over a 5-year period. I also examine the relationships between fruit production and crown features, tree size, and liana infestation. Using one common tree species that is often heavily liana-laden, I assess the effect of liana cutting on fruit production. Finally, I examine the effect of selective logging on fruit production by several common canopy tree species.

Methods

Study Area and Climate

Research was conducted at INPA Parket, a 30,000-ha tract of privately owned seasonally dry tropical forest located 30 km northeast of the town of Concepción (16° 6' 45" S and 61° 42' 47" W) and 250 km northeast of the city of Santa Cruz, Bolivia (Figure 1-1). The altitude is approximately 380 m, mean annual temperature is 24.3 °C, mean annual precipitation is 1150 mm (range 798-1859 mm/y), and there is a dry season that lasts about five months (May-October) during which most trees are leafless. Extreme annual variation in rainfall is in part related to the occurrence of El Niño events, which are typically wet in the study area. Many tree species in this forest flower at the end of rainy season with another peak in flowering at the beginning of dry season. Fruiting of the majority of species occurs in mid-dry season (see Table 1-1). The forest canopy is 20-25 m tall and dominated by *Tabebuia impetiginosa* (Mart. Ex DC.) Standl., *Anadenanthera macrocarpa* (Benth.) Brenan, *Astronium urundeuva* (Allemão) Engl., and *Centrolobium microchaete* (Mart. ex Benth.) Lima ex G. P. Lewis (Pariona 2006). The most abundant species are *Acosmium cardenasii* H. S. Irwin & Arroyo (≈ 38 trees/ha ≥ 20 cm diameter at breast height, DBH) and *Anadenanthera* (8 trees/ha ≥ 20 cm DBH). Currently, 21 tree species, including these dominants, are harvested for timber used mostly in the production of parquet flooring.

Species Studied

My studies focus on commercially valuable timber tree species, most of which produce seeds that are wind, gravity, or explosively dispersed (Table 1-1). Overall I consider 31 species (Table 1-1), of which 15 were used to determine the percentage of fruiting trees, 12 to compare the sizes of reproductively mature trees that did or did not fruit during a 2-y observation period, 6 to compare fruiting intensity in logged and unlogged areas, and 3 to determine the relationships between fruit production and DBH, crown area, crown position, and liana infestation. In addition, one species (*Caesalpinia pluviosa* DC.) was used to study the effect of liana cutting on fruit production. Most of the selected species have large or medium-sized fruits with small- to intermediate- sized seeds.

Of the 31 species considered in this study 25 have hermaphroditic flowers and 20 produce wind-dispersed seeds. Ten species have seeds as their dispersal units (e.g., *Amburana cearensis* (Allemao) A.C. Sm.) while in the other 21 species, entire fruits are the dispersal units (e.g., *Machaerium scleroxylon* Tul.). Twenty-four of the 31 species monitored for five years produced at least some fruits annually, but the intensity of fruiting varied substantially. *Cecropia concolor* Willd. produced fruits continuously whereas *Schinopsis brasiliensis* Engl. fruited supra-annually (sensu Newstrom et al. 1994). Peak fruiting for 23 of 31 species coincided with the dry season (May – September) with most seeds dispersed in the late dry season. *Spondias mombin* L. the only fleshy-fruited species in the study produced ripe fruit during the rainy season. Most of the species have only 1 seed per fruit, but *Ceiba samauma* (Mart.) K. Schum. and *Tabebuia* have more than 90 seeds/fruit. Wind-dispersed seeds or fruits typically have one (*Pterogyne nitens* Tul.) or both sides winged (e.g., *Platimiscium ulei* Harms), whereas *Zeyheria tuberculosa* (Vell.) Bureau seeds are entirely surrounded by a wing. Cottony fibers on the seeds of the Bombacaceae studied (*Ceiba* and *Chorisia speciosa* A. St.-Hil.) aid in their dispersal by wind.

Experimental Design and Data Collection

The study was conducted at two different sites at INPA Parket. The first site was within the Long-Term Silvicultural Research Plots (LTSRP) in Block # 1, 5-6 km south of the IBIF field station (16° 18’ 26.8”S, 61° 41’ 13.5”W). Four large-scales (20 ha) long-term research plots (LTRSP) were established by the Instituto Boliviano de Investigacion Forestal (IBIF). One of the plots I used is an unlogged control whereas the other was subjected to normal logging during which a mean of 4.3 trees/ha (4.7 m^3/ha of commercial timber) were harvested using standard reduced-impact-logging techniques that include road planning, directional felling, and retention of 20% of the harvestable trees as seed trees (Mostacedo et al. 2006). In each plot, I censused all individuals ≥ 20 cm DBH of the 15 most abundant tree species in two 20 x 400 m strips. The second site is a 1000 x 500 m plot that I established 2 km northeast of the IBIF field station (16° 14’ 58.5” S, 61° 41’ 47.4” W). In this plot, I censused individuals ≥ 20 cm DBH of *Anadenanthera* and *Caesalpinia* in twelve 20 x 500 m strips spaced at 100 m intervals. At both study sites the censused trees were marked, tagged, and mapped. To secure sufficient trees of *Caesalpinia* and *Zeyheria,* I marked additional trees around the LTRSP.

In total, I evaluated 440 trees of 15 species, 116 in the control plot and 147 in the logged plot of the LTRSPs. An additional 144 trees were monitored at the second site that, a year after plot establishment, was selectively logged. In 2003, I evaluated only six species from May-November including *Caesalpinia, Anadenanthera, Machaerium scleroxylon, Ceiba, and Zeyheria*. In 2004, every marked tree in the LTSRP plots was phenologically evaluated five times from May to November. I estimated the percentage of the crown bearing fruits, which I refer to as a measure of fruiting intensity; 100% fruiting intensity indicates that every terminal branch bears at least one fruit.

I estimated the number of fruits produced by each tree of three species, *Caesalpinia*, *Anadenanthera,* and *Zeyheria,* for 5 years (2002-2006). All of these species produce fruits with valves that are not removed by animals. By counting these undispersed fruit parts under fruiting trees, I avoided many of the difficulties associated with estimating seed production by species in which entire fruits are removed by animals. At the beginning of the study I installed five 2x2 m permanent plots on the ground below the crown of each tree in which I counted and removed all fruit valves. Subsequent censuses of fallen fruit valves in these plots over the next 5 y were used as quantitative estimates of fruit production. I also measured the DBH, crown area (based on two cardinal diameters), crown position (using the 5 categories of Dawkins (1958)), and liana infestation.

Liana-infested *Caesalpinia* trees (N=32) were used in a manipulative experiment on the effects of lianas on seed production. I measured the DBH and percentage of each tree's crown covered by lianas, paired the trees on the basis of liana infestation and DBH, and cut all the lianas on one tree of each pair, selected at random. Fruit production was measured for 3 y after treatment using the fruit-valve census method described above.

Data Analysis

To determine whether trees of the 12 monitored species that fruited in 2003 and 2004 differed in DBH from those that did not, I conducted Student's-t tests. I tested for simple linear relationships between the number of fruits (log-transformed) produced per tree and each tree's DBH, crown area, crown position, and liana cover separately and then ran multiple regressions for three monitored species (*Anadenanthera*, *Caesalpinia*, and *Zeyheria*) using the backward method to avoid co-linearity. Only independent variables that explained significant amounts of variance (P=<0.05) were included in the models. I ran X^2 tests to assess differences between logged and control plots in the percentage of trees fruiting. To compare maximum fruiting intensities in the logged and the control plot for the 6 monitored species, I ran Student's t-tests after first arcsine transforming the data to achieve normality (Zar 1981). Finally, I compared fruit production on liana-laden and liana-free trees using analyses of covariance with crown area or DBH as covariates. For all analyses, I used SPSS Version 12.0 (Field 2000).

Results

The percentage of trees fruiting in any particular year varied among species (Figure 1-2). Of 14 species monitored during 2004, 7 had >50% of trees in fruit and 4 had >80% of trees in fruit. For a few species that I also monitored in 2003, the percentage of fruiting trees was lower in 2003 than in 2004. For example, while only 25% of *Caesalpinia* trees fruited in 2003, 100% fruited in 2004. The opposite pattern was observed in *Zeyheria*; 40% fruited in 2003 and none in 2004.

For the 3 species I monitored for 5 years, there was a great deal of inter-annual variation in fruit production (Figure 1-3). For example, a high proportion of *Caesalpinia* trees fruited at 2-

year intervals whereas many *Zeyheria* trees fruited at 3-year intervals. In contrast, *Anadenanthera* fruited during each of the first 3 years of the study and not at all in the last 2.

Whether or not a tree fruited was generally not related to its DBH (Figure 1-4). The exceptions were *Caesalpinia* in 2004 when the trees that failed to fruit were larger than the trees that fruited (t=2.18, P=0.03) and *Zeyheria* in which the fruiting trees were larger in 2004, the only year in which it fruited (t=4.91, P<0.0001).

For the 3 species in which I monitored fruit production, the number of fruits produced did not vary with DBH or crown position but increased linearly with crown area (Figure 1-5). The backward multiple regression of fruit production on tree characteristics revealed that crown area explained the most variation (Table 1-2). In *Anadenanthera*, crown area explained 32% of the variance in fruit production while DBH, crown position, and liana cover together explained only an additional 10%. In the case of *Caesalpinia,* crown area explained 23% of the variance in fruit production and the other three variables only an additional 3%. In *Zeyheria*, crown area and crown position together explained only 24% of the variance, to which DBH and liana cover added an additional 1%.

There was no apparent effect of liana cutting on fruit production by *Caesalpinia* when the effects of either DBH or crown area are removed by ANCOVA (Table 1-3, Figure 1-6).

The percentage of trees fruiting in the logged and control plot was similar for 6 of 7 species. The only exception was *Centrolobium* in which only 27% of trees fruiting in the logged plot compared to 90% in the control plot (X^2=12.9, P<0.0001; Figure 1-7).

The effect of logging on fruit production varied among the 6 tree species studied (Figure 1-8). Logging apparently stimulated increased fruiting intensity of *Anadenanthera* (t=3.40, P=<0.0001). In contrast, fruiting intensity was higher in the unlogged plot for both *Centrolobium* (t=4.75, P=0.0008) and *Copaifera* (t=3.11, P=0.007). There was no difference in fruiting intensity between the logged and unlogged plot for *Aspidosperma* (t=0.68, P=0.5) and *Machaerium scleroxylon* (t=0.05, P=0.95).

Discussion

Fruiting of Trees in a Tropical Dry Forest

In any year, the proportion of reproductively mature trees that fruited generally varied a great deal among the canopy tree species I studied in lowland Bolivia. Only *Anadenanthera* trees produced fruit crops in both 2003 and 2004. In contrast, no trees of *Machaerium scleroxylon* and *M. acutifolium* fruited in 2003, but many did in 2004. Most of the trees of some species fruited in at least some years (e.g., *Caesalpinia*) while in others the percentage of fruiting trees was always <40%. Perhaps coincidentally, the five species with the greatest proportion of fruiting trees in 2004 were all legumes, which comprised 8 of the 14 species monitored. Few studies report annual variation in the proportions of fruiting trees but in a similar forest in Lomerio, Bolivia, only 29% and 36% of reproductively mature trees of 17 commercial tree species fruited during two years of monitoring (Justiniano and Fredericksen 2000). At the same site, there was a great deal of variation within species in the proportions of fruiting trees. For example, the proportion of *Copaifera* trees fruiting was similar to what I observed in INPA whereas none of the *M. scleroxylon* trees in Lomeria fruited during the two years of monitoring. In a tropical dry forest in Mexico studied by Bullock (1995), only 8-30% of *Jacaratia mexicana* A. DC. trees and 0-50% of *Cochlospermun vitifolium* (Willd.) Spreng. trees fruited in any one year. Similarly, in a study of *Swietenia macrophylla* King. on the Yucatan Peninsula, the proportion of fruiting trees varied a greatly among years (Snook et al. 2005). The proportion of *Hymenaea courbaril* L. trees fruiting in Costa Rica reportedly varied with water stress (Janzen 1978).

A larger proportion of trees of most species fruited in 2004 than in 2003 or 2005. Such community-wide synchrony in fruiting has been observed in many forests over the world but has been particularly well studied in the dipterocarp forests of Southeast Asia where "masting" has long been known (Appanah 1993, Wich and Van Schaik 2000). Less pronounced is the inter-annual variation in fruit production on Barro Colorado Island, where mast years are reportedly related to El Niño events (Wright and Calderon 2006). In the forest of this study, 2003 was at the end of an El Niño event, which was not followed by a strong La Niña. Nevertheless, synchronous fruiting in 2004 could have been due to the timing of water stress, as suggested by Bullock (1995).

The three species I followed for five years showed great inter-annual variation in the numbers of fruits produced per tree. The two legumes, *Anadenanthera* and *Caesalpinia*, followed the same interannual patterns; both had peak years in 2002 and 2004, but produced few fruits in 2003 and 2005. In contrast, the 35 *Zeyheria* trees I monitored produced no fruits in 2004 and 2005, but fruited in 2002, 2003, and 2006. Such interannual variation in fruit production is common in many species. For example, in a moist tropical forest in Panama, *Quararibea asterolepis* Pittier, *Tetragastris panamensis* (Engl.) Kuntze, and *Trichilia tuberculata* (Triana & Planch.) C. DC. showed great inter-annual variation in fruit production (De Steven and Wright 2002, Snook et al. 2005).

While I expected that the proportion of fruiting trees would increase with tree size, 12 of the 13 species I monitored in 2003 and 2004 did not display this pattern. In fact, in the case of *Caesalpinia*, the fruiting trees were significantly smaller than those that failed to fruit in 2004. Only *Zeyheria* displayed the expected pattern. The general failure to find a positive relationship between tree size and whether or not a tree reproduced runs counter to the results of two other studies on this topic, one conducted on Barro Colorado Island, Panama (Wright et al. 2005) and the other at my study site (Añez 2005). One explanation for the difference between my study and others in the literature is that whereas they typically used either flowering or fruiting as an indication of reproduction (Añez 2005, Wright et al. 2005), I used only fruiting. Nevertheless, while the probability of fruiting increased with tree size in *Copaifera*, *Sweetia* and *Machaerium*, it decreased in *Anadenanthera* and *Caesalpinia*.

Factors Affecting Fruit Production

Crown area was the best predictor of fruit production in many of the species I studied whereas DBH and crown position were not. Crown area was also a good predictor of fruit production in *Betholletia excelsa* trees in Amazonian Bolivia (Zuidema and Boot 2002), while DBH was more closely related to fruit production by *Swietenia* in Mexico (Snook et al. 2005) and *Pinus sylvestris* L. in Sweden (Karlsson 2000). Although several studies have shown strong positive correlations between tree size and fruit production (Karlsson 2000, Zuidema and Boot 2002, Wadt et al. 2005), the relationships revealed in my study were positive but weak. This difference might be related to the difficulty of making accurate DBH estimates of the trees in my study site, many of which have irregular-shaped trunks. It is also possible that crown position is not good predictor of fruit production in forests that are already open-canopied; certainly in my study site it was difficult to differentiate between dominant and co-dominant trees, and I doubt that they differ much in terms of light capture.

I expected liana cover to substantially impede fruit production (Stevens 1987), but my results did not support that expectation. For the 16 pairs of *Caesalpinia* trees from which I monitored fruit production for 3 y after cutting their lianas, fruit production was no higher than in the liana-laden control trees. I can offer a few explanations for this counter-intuitive result. For one thing, 3 y was perhaps not enough time for the trees to respond to the liberation from their liana loads. Then there is the problem that fruit production is extremely variable among individuals and among years in this species and others in my study site. Finally, I wonder whether the liana leaf phenology at my study site might have something to do with this result insofar as lianas are typically deciduous at the time of fruiting, which might reduce any deleterious effect they have on fruit production. Obviously, none of these explanations is very compelling and further monitoring is warranted.

Although I anticipated that by increasing canopy openness and reducing resource competition, logging would increase fruit production by remnant trees, my results were inconsistent at best. Firstly, the percentage of fruiting trees in most of species were similar between logged and control plots, except for *Centrolobium*. For some species (e.g., *Copaifera*, *Aspidosperma*, and *Sweetia*) in which there seemed to be a trend towards increased reproduction among remnant trees in selectively logged forest, statistical significance was not forthcoming perhaps due to small sample sizes (N < 20).

Secondly, 3 of the 6 species I monitored starting 1.5 y after selective logging showed no apparent effect of the treatment on fruit production, 2 of the species fruited less in the logged than in the control plot, and 1 species showed the opposite pattern. One reason for the observed decrease in fruit production might have been the effect of lowered tree density on pollinator effectiveness or offspring quality (Ghazoul and Shaanker 2004, Knight et al. 2005). Other factors that might have reduced fruit production include fruit abortion due to poor ovule fertilization in the extreme temperatures and low humid provoked by forest openness (Stephenson 1981, Aizen and Feinsinger 1994, Dafni and Firmage 2000) or due seed predation during the early stages of fruit formation (Stephenson 1981). For example, 1 tree/ha ≥ 40 cm DBH of *Copaifera* remained after logging of the pre-logging density of 1.7 trees/ha whereas in the unlogged plot, the population of adult trees was substantially higher (2.7 trees/ha). Similarly, in Southeast Asia, fruit production was reduced in a logged dipterocarp forest (Curran et al. 1999). In contrast, the most light-demanding tree species in my study forest, *Anadenanthera*, produced more fruit in logged than in unlogged areas. Similarly, *Ceiba aesculifolia* (Kunth) Britten & Baker f. in a dry forest in Mexico (Herrerias-Diego et al. 2006) and *Quercus costaricensis* in montane humid forest in Costa Rica (Guariguata and Saenz 2002) both increased fruit production in response to logging. Given the importance of this issue to sustainable timber stand management, more research is needed on the reproductive responses of trees to logging disturbances. These studies should integrate flower production, pollination, and fruit production and should be conducted on species representing a variety of densities and breeding systems.

Conclusions

In the seasonally dry tropical forest I studied in Bolivia, there was a lot of interannual variation in fruit production among species. Whether or not a reproductively mature tree fruits is generally not related to it size. The number of fruits produced per tree also did not consistently change with stem diameter or liana cover, but did increase with crown size. Base on these findings, I recommend protection of tree crowns during logging to increase fruit production. Even when I experimentally killed the lianas infesting the crowns of 16 *Caesalpinia* trees, I did not observe the expected increase in fruit production. To look at the effect of lianas cutting I recommend a long-term study to look at crown area recovery and fruit production. Similarly, after logging, remnant trees of some species increased their fruit production and some species decreased but most did not change. For most of the species, percentages of trees fruiting were similar between the control and the logged plot; only in *Centrolobium* was there a difference, with more trees fruiting in the control plot. The small and inconsistent effects of logging on fruit production in my study forest may be explained in part by the relatively low intensity of harvesting. Obviously, given the substantial inter-tree, inter-specific, and inter-annual variation in the fruiting of dry forest tree species, studies of more than a few years are needed.

Table 1-1. Overview of reproductive characteristics of the tree species studied in a tropical dry forest in Bolivia.

Species	Family	Abbreviation	Breeding System	Dispersal Type	Dispersal Unit	Fruiting* Frequency	Fruiting	Seed Dispersal	# Seeds / Fruit
Acosmium cardenasii	Fabaceae	ACCA	Hermaphrodite	Wind	Fruit	Continuous	Mar-Aug, Oct-Feb	May-Sep, Feb	1.2
Amburana cearensis	Fabaceae	AMCE	Hermaphrodite	Wind	Seed	Annual	Jun-Aug	Sep	1
Anadenanthera macrocarpa	Mimosaceae	ANMA	Hermaphrodite	Gravity	Seed	Annual	Mar-Sep	Jul-Oct	10.9
Aspidosperma rigidum	Apocynaceae	ASRI	Hermaphrodite	Wind	Seed	Annual	Mar-Sep	Sep-Nov	-
Astronium urundeuva	Anacardiaceae	ASUR	Dioecious	Wind	Fruit	Annual	Aug-Oct	Oct	1
Attalea phalerata	Arecaceae	ATPH	Monoecious	Animal	Fruit	Continuous	Oct-Apr	Feb-May	
Caesalpinia pluviosa	Mimosaceae	CAPL	Hermaphrodite	Explosive	Fruit	Annual	Mar-Sep	Ago-Nov	4.4
Capparis prisca	Capparaceae	CAPR	Hermaphrodite	Animal	Fruit	Annual			
Cariniana ianeirensis	Lecythidaceae	CAIA	Hermaphrodite	Wind	Seed	Annual	May-Sep	Oct	-
Cecropia concolor	Cecropiaceae	CECO	Monoecious	Animal	Fruit	Continuous	Oct-Mar	Feb-Mar	-
Cedrela fissilis	Meliaceae	CEFI	Hermaphrodite	Wind	Seed	Annual	Jul-Aug†	Aug-Sep	-
Ceiba samauma	Bombacaceae	CESA	Hermaphrodite	Wind	Seed	Annual	Jun-Aug	Ago	90.4
Centrolobium microchaete	Fabaceae	CEMI	Hermaphrodite	Wind	Fruit	Annual	Apr-Sep	Jul-Sep	1-2
Chorisia speciosa	Bombacaceae	CHSP	Hermaphrodite	Wind	Seed	Annual	Jul-Aug	Sep	-
Copaifera chodatiana	Caesalpinaceae	COCH	Hermaphrodite	Gravity	Seed	Annual	Mar-Sep	Jul-Oct	1
Cordia alliodora	Boraginaceae	COAL	Hermaphrodite	Wind	Fruit	Annual	Jul-Ago	Ago	1
Gallesia integrifolia	Phytolacaceae	GAIN	Hermaphrodite	Wind	Fruit	Annual	May-Sep	Oct-Nov	1
Genipa americana	Rubiaceae	GEAM	Hermaphrodite	Animal	Fruit	Annual	Dec-Feb	Feb-Mar	-
Hymenaea courbaril	Caesalpinaceae	HYCO	Hermaphrodite	Gravity	Fruit	Annual	Jul-Oct	Oct-Nov	3.3
Machaerium cf. *acutifolium*	Fabaceae	MAAC	Hermaphrodite	Wind	Fruit	Supra-annual	Apr-May	May	1
Machaerium scleroxylon	Fabaceae	MASC	Hermaphrodite	Wind	Fruit	Annual	Apr-Sep	Aug-Sep	1
Myrcianthes spp.	Myrtaceae	MYSP	Hermaphrodite	Animal	Fruit	Annual	Jan-Feb	Feb	-
Phyllostylon rhamnoides	Rhamnaceae	PHRH	Hermaphrodite	Wind	Fruit	Supra-annual	Oct	Oct	1
Platimiscium ulei	Fabaceae	PLUL	Hermaphrodite	Wind	Fruit	Annual	Jul-Aug	Aug-Sep	1
Pterogyne nitens	Caesalpinaceae	PTNI	Hermaphrodite	Wind	Fruit	Annual	Apr-May	May-Aug	1
Schinopsis brasiliensis	Anacardiaceae	SCBR	Dioecious	Wind	Fruit	Supra-annual	Ago-Sep	Sep	1
Spondias mombin	Anacardiaceae	SPMO	Hermaphrodite	Animal	Fruit	Annual	Jan-Feb	Feb	1-2
Sweetia fruticosa	Fabaceae	SWFR	Hermaphrodite	Wind	Fruit	Annual	Oct	Oct-Nov	1
Syagrus sancona	Arecaceae	SYSA	Monoecious	Zoo	Fruit	Annual	Nov-Dec†	Dec-Jan	1
Tabebuia impetiginosa	Bignoniaceae	TAIM	Hermaphrodite	Wind	Seed	Annual	Jul	Ago	90.7
Tabebuia serratifolia	Bignoniaceae	TASE	Hermaphrodite	Wind	Seed	Annual	Ago	Sep	-
Zeyheria tuberculosa	Bignoniaceae	ZETU	Hermaphrodite	Wind	Seed	Supra-annual	Jun-Jul	Jul	≈30

(*) Clasification made by Newstron et al. (1994). (†) Data extracted from Justiniano and Fredericksen (2000).

Table 1-2. Results of the best model after backward regression steps to remove non-significant variables ($P > 0.1$) sequentially from the full multiple regression model including tree size (DBH), percent liana infestation, crown area, and crown position as independent variables to explain fruit production. Number of trees (N), standardized regression coefficients (β), Student-t test values (t), significance levels (P), and coefficients of multiple determination (R^2) are noted.

Variables	N	β	t	P	R^2
Anadenanthera macrocarpa					
Crown Area	30	0.560	3.59	0.001	0.32***
Caesalpinia pluviosa					
Crown Area	50	0.480	3.81	<0.0001	0.23**
Zeyheria tuberculosa					
Crown Area	35	0.450	2.89	0.007	0.24*
Crown Position	35	0.282	1.81	0.080	

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

Table 1-3. Analysis of covariance to determine the liana cutting effect in fruit production of *Caesalpinia pluviosa*. The co-variables considered were crown area and DBH.

Source	Crown Area			DBH		
	Mean Square	F	P	Mean Square	F	P
Co-variable	42438.5	2.35	0.14	22090.0	1.18	0.29
Liana cutting	9135.0	0.57	0.48	9673.0	0.52	0.48
Error	18020.7			18747.0		

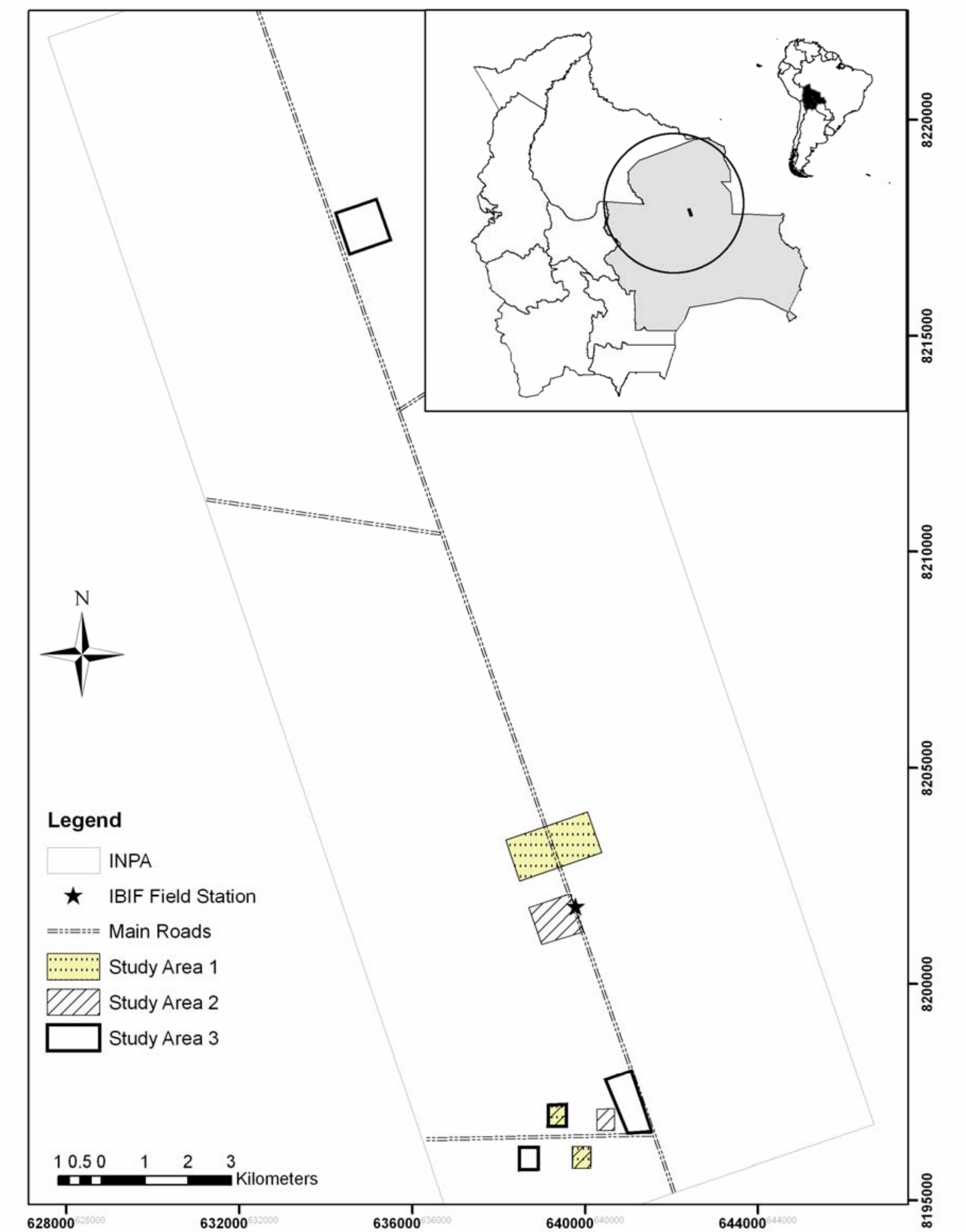

Figure 1-1. Locations of the study areas in Bolivia. Study Area 1 was where I conducted fruit production research (Chapter 1); Study Area 2 was used for seedling recruitment study (Chapter 2); and, Study Area 3 was the site for the sprouting studies (Chapter 3). The map is georeferenced using a Universal Transverse Mecator (UTM) System, Zone 20.

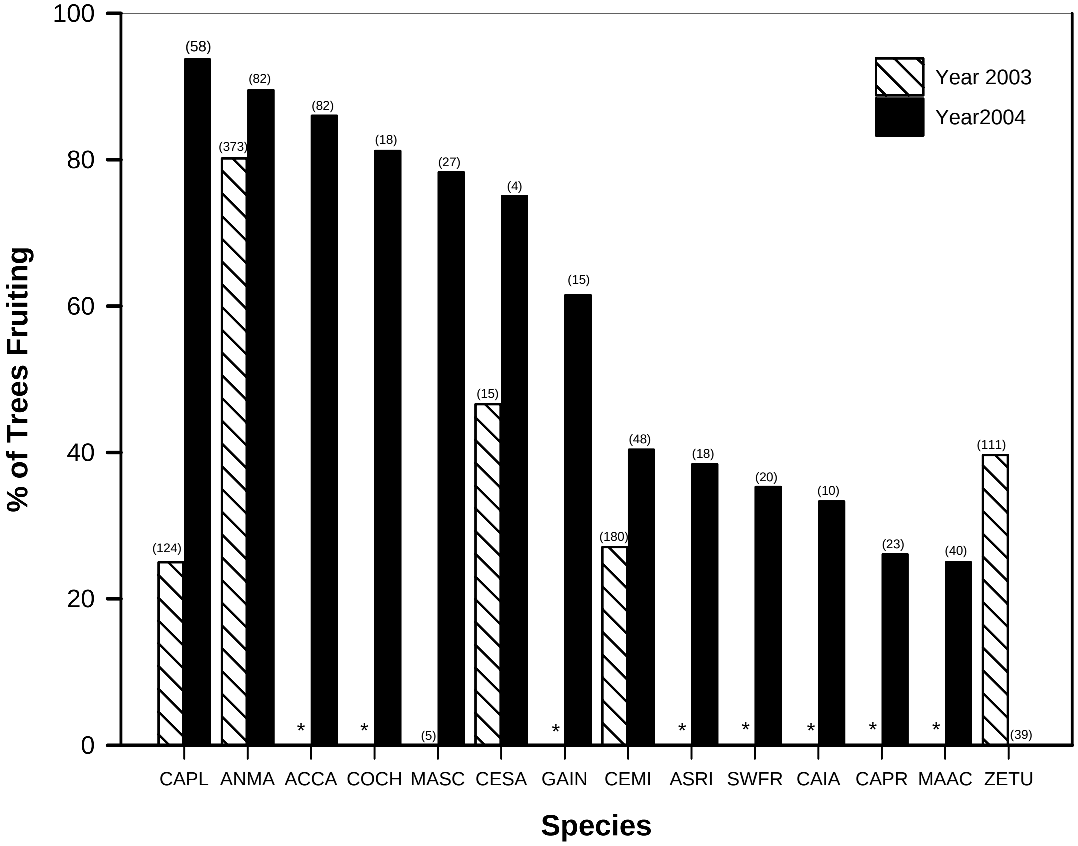

Figure 1-2. Percentage of trees fruiting in 2003 and 2004 (note that none of these species are dioecious). Asterisks indicate years in which a species that was not evaluated. Abbreviations of species are given in Table 1-1. Numbers in parenthesis indicate the number of trees evaluated for each species and year.

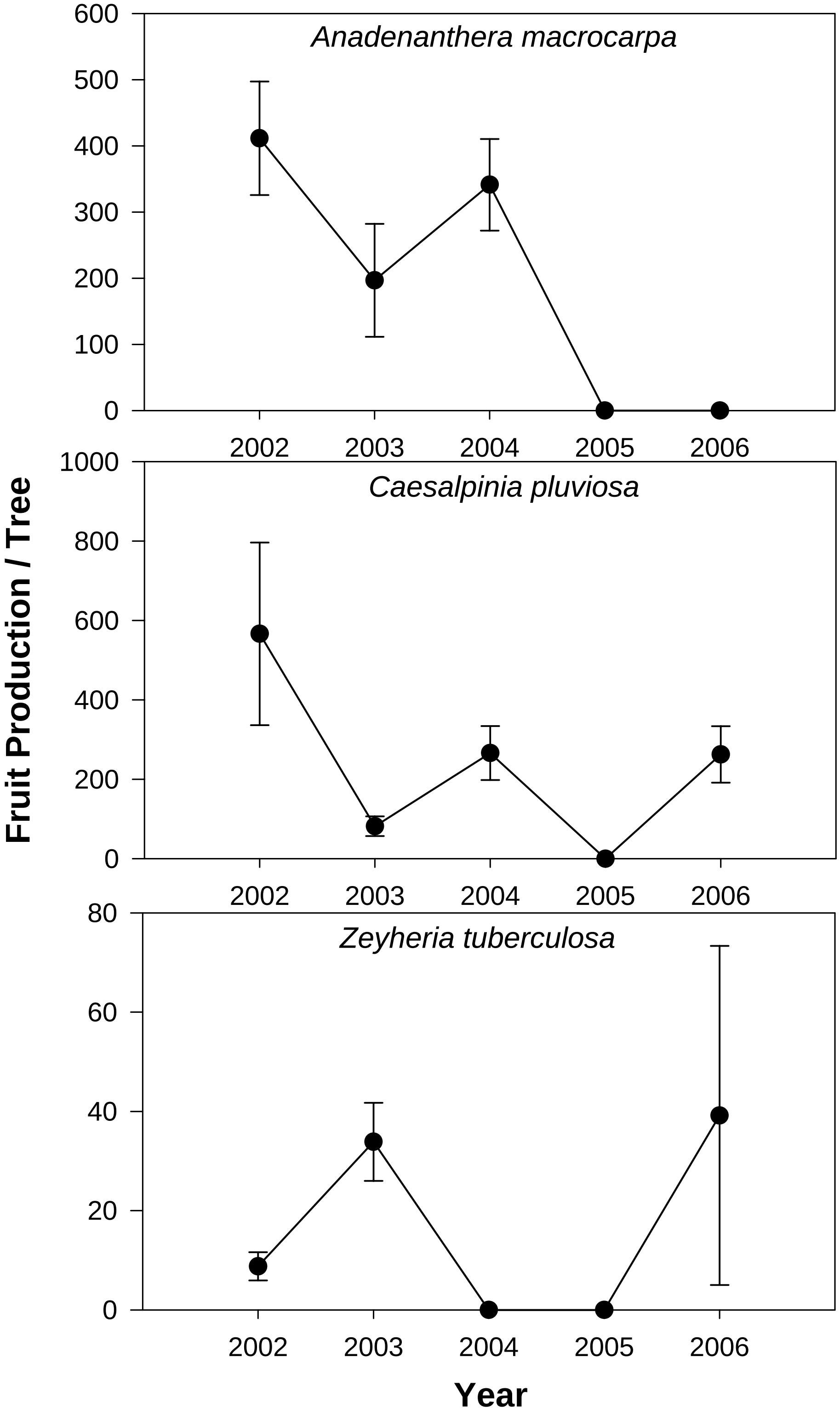

Figure 1-3. Annual variation in fruit production in three timber species. Vertical lines show one standard error. Note the differences in the y-axis scales.

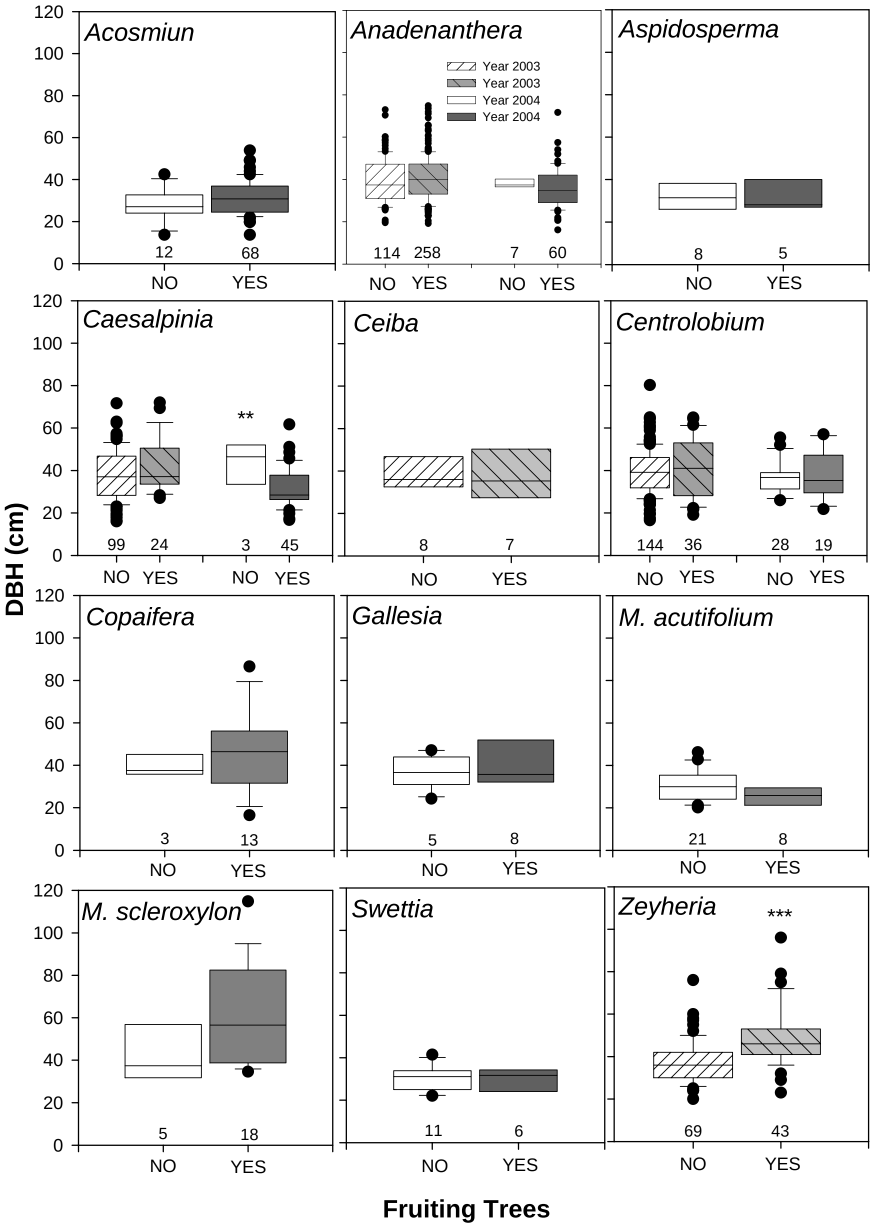

Figure 1-4. Comparison of the sizes (DBH) of fruiting and non-fruiting trees in 2003 and 2004 (note that none of these species are dioecious and all the trees were reproductively mature). Numbers indicate the sample size for each year and each species. Asterisks indicate significant size differences between fruiting and non-fruiting trees as determined with Student-t test. P-value: * ≤ 0.05, ** ≤ 0.001, *** ≤ 0.001.

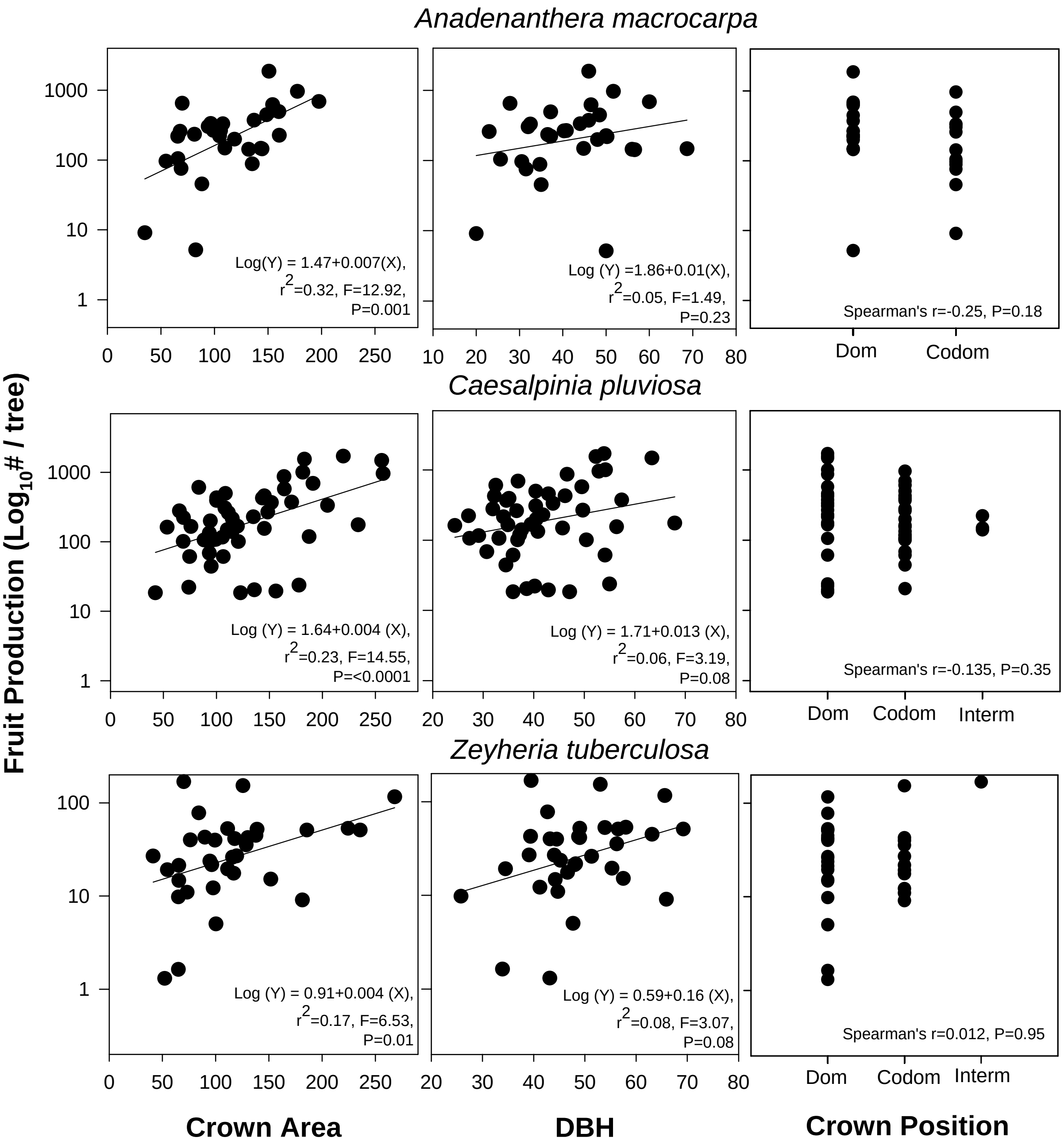

Figure 1-5. Simple linear regressions between crown area, tree size (DBH) in relation to log transformed fruit production data for three timber species. Spearman correlations were run to determine the relationships between crown position (ordinal variable) and fruit production. Crown position numbers refer to dominant (Dom), co-dominant (Codom), and intermediate exposure (Interm) trees.

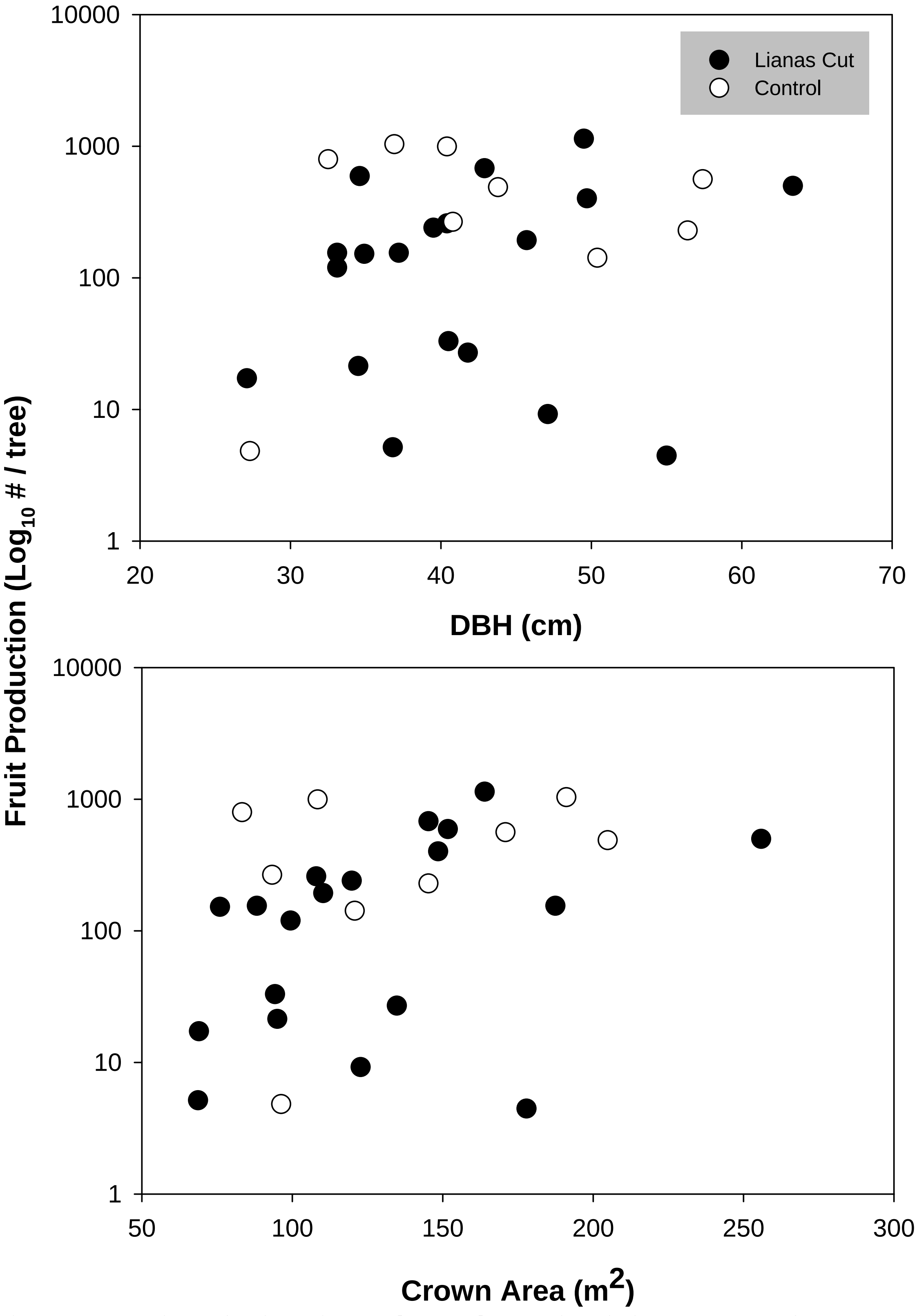

Figure 1-6. Fruit production of *Caesalpinia pluviosa* in relation to DBH and crown area for trees with cut or uncut lianas.

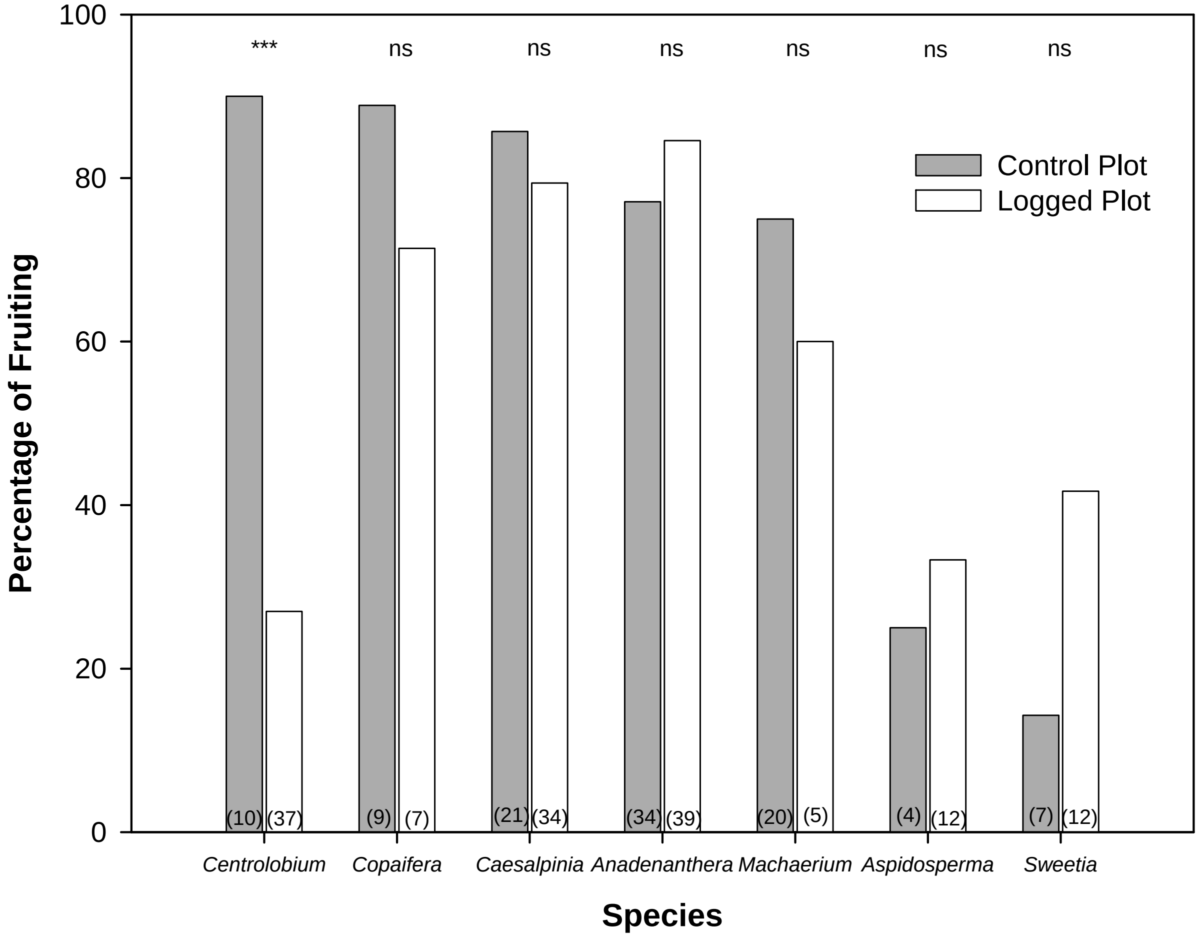

Figure 1-7. Percentages of trees fruiting in a logged and an unlogged plot. Number of trees evaluated is noted in parenthesis. Differences between logging intensities were tested using X^2 test at 95% of confidence. *** = <0.0001; ns = non significant.

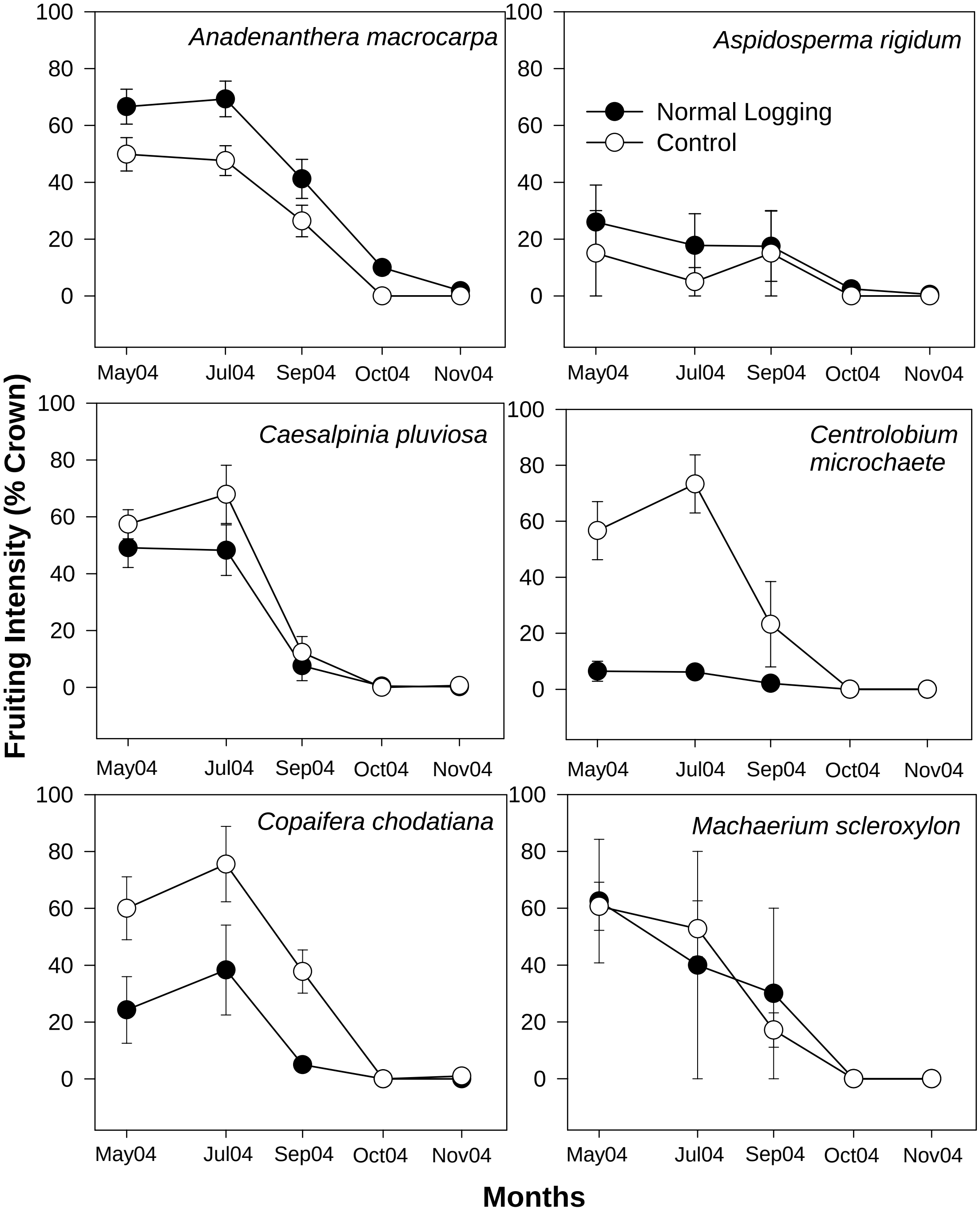

Figure 1-8. Average fruiting intensities (% of crown cover) of timber tree species evaluated in areas subjected to normal selective logging and nearby unlogged control areas in a tropical dry forest. Vertical lines indicate standard errors.

CHAPTER 2
BIOTIC AND ABIOTIC FACTORS AFFECTING TREE SEEDLING DYNAMICS IN A DRY TROPICAL FOREST

Introduction

Among the many factors that affect tree seedling establishment in tropical forests, seed predation, pathogen effects on seedlings , and light availability figure prominently (Janzen 1971, Augspurger 1984, Hammond 1995, Huante et al. 1998, Kobe 1999). Given that this view is mostly supported by studies conducted in moist and wet forests, the relative importances of these factors might differ in seasonally dry forests (Gerhardt 1994, Holbrook et al. 1995). Given the widespread mismanagement and destruction of these forests (Steininger et al. 2001, Pacheco 2006), it is increasingly important to increase our knowledge of ecological processes, such as regeneration, that might lead to their improved management. To further this knowledge, I monitored seedling populations and conducted experimental studies across a gradient of forest management intensities in a seasonally dry lowland tropical forest in Bolivia. In the experiments, I planted seeds of canopy tree species and manipulated moisture availability, seed and seedling predation, and competition with an abundant understory bromeliad, *Pseudananas sagenarius* (Arruda) Camargo).

Seasonally dry tropical forests are characterized by low total rainfall (typically < 1500 mm) and annual periods of drought (i.e., months during which evapotranspiration exceeds precipitation usually assumed to be months with <100 mm of precipitation)(Holdridge 1967). The rainfall regime of Bolivian, and apparently many other tropical dry forests (Gerhardt 1996a), is also characterized by huge interannual variation in precipitation, dry season duration, temporal continuity of rainfall during the rainy and dry seasons, and the starting and ending dates of the seasons. In addition, paleoecological and archaeological data predict that the dry seasons in tropical dry forests in South America will be extended in duration and drier in the future (Mayle et al. 2007). These sources of environmental variation are critical because, although the tree species characteristic of tropical dry forests are presumably adapted to seasonal drought, mortality is reportedly concentrated during dry seasons and dry years (Khurana and Singh 2001, McLaren and McDonald 2003).

Within species and age cohorts, the probability of mortality reportedly decreases with increasing seedling size, presumably because larger individuals have greater access to soil water (Khurana and Singh 2001). Seedling growth rates typically increase with increasing illumination but, due to high temperatures and soil surface drying, seedlings growing in large canopy gaps may suffer high risks of mortality, even if they grow larger than their shaded counterparts in the understory. In other words, in a forest with a 6-month rainy season, a newly germinated seedling has 6 mo to grow large enough to survive the subsequent dry season. Based on this idea, I conducted an experiment in which I manipulated the duration and intensity of the dry season and monitored the survival and growth of seedlings of canopy tree species that germinated from sown seeds. In recognition of the importance of inter-specific competition and seed/seedling predators to seedling dynamics, I also manipulated these factors in a factorial experiment.

In addition to tolerating drought, tropical tree seedlings must compete for light, water, and nutrients with plants of various growth forms including lianas (Gerwing 2001, Schnitzer and Bongers 2002), ferns (George and Bazzaz 1999), and ground bromeliads (Fredericksen et al. 1999, George and Bazzaz 1999). In the seasonally dry forests of the Chiquitania of lowland Bolivia, competition with a clonal ground bromeliad, *Pseudananas sagenarius*, seems particularly intense. This bromeliad covers 25-30% of the ground surface in my study area where it presumably competes for light and soil resources. Furthermore, its leaves intercept both rain and falling seeds (Fredericksen et al. 1999), which should affect tree seedling recruitment, growth, and survival. Finally, by providing cover to small mammals and other animals avoiding predators, bromeliads may also affect rates of seed and seedling predation. To investigate these effects, I included a bromeliad removal treatment in my experimental study on the survival and growth of canopy tree seedlings.

Predators often reduce seed and seedling survival in tropical forests (Janzen 1971, Hulme 1996, Asquith et al. 1997). Given that seed predation rates, at least by mammals, typically increase with seed size (Moles and Westoby 2003), and given that most tree species in dry tropical forests have small, wind-dispersed seeds, rates of seed predation may be lower in dry than in humid forests. On the other hand, given the seasonal scarcities of food in dry forests, seed and seedling predation might be particularly intense, especially for seedlings that remain leafed out and succulent during the early dry season. To investigate the importance of seed and seedling predation, as influenced by seasonality, I experimentally manipulated both soil moisture and accessibility to predators using the planted seeds of canopy tree species.

In this chapter I present the results of a study in which I monitored the survival and growth of tree seeds planted in plots in which I experimentally manipulated soil moisture, seed and seedling predator access, and competition with ground bromeliads. The chapter also includes the results of 3 y of monitoring of seedling establishment, growth, and survival in a large control plot and two otherwise similar plots subjected to different intensities of timber harvesting 7 mo prior to commencement of my study. I hypothesized that seedling survival and growth are reduced by bromeliad cover, drought stress, and predators. I also hypothesized that the establishment, survival, and growth of naturally regenerated seedlings differs among plots subjected to different intensities of disturbance resulting from forest management activities.

Methods

Study Area and Climate

This study was conducted during 2003-2006 in the 30,000 ha seasonally dry lowland forest (Holdridge 1967) owned by INPA PARKET, about 30 km from Concepción, Bolivia (16° 6' 45"S, 61° 42' 47"; Figure 1-1). The study area is located in the transition zone between the forests of the Amazon Basin and those of the Gran Chaco and is locally referred to as Chiquitano dry forest (Killeen et al. 1998, Ibisch and Mérida 2003). Based on 30 years of data collected in Concepción, the annual average temperature in the area is 24.3 °C with a minimum average temperature of 12.9° C, generally in July, and maximum average temperature of 31°C, generally in November. Over the 30-year monitoring period, the annual average of rainfall was 1100 mm but ranged from 700-2000 mm/year, with wet years corresponding with El Niño events (Coelho et al. 2002) (Figure 2-1). Both 2005 and 2006 were dry years, with only 980 and 1050 mm of precipitation, respectively. The rainy season typically runs from October to April, but in 2005, the rains started in September and rain fell at regular intervals until March of 2006. The 2006 rainy season, in contrast, started in October but then no rain fell in November, with more regular rains commencing again in December.

The set of Long-Term Silvicultural Research Plot (LTSRPs) established at this site by the Instituto Boliviano de Investigaciones Forestales (IBIF) was used for a portion of this study. The LTSRP at INPA includes four 20-ha plots that vary in management intensity: unlogged control; normal logging; improved management; and, intensive management (Mostacedo et al. 2006). For this study, the improved management plot was not used. In the "normal logging" plot, the logging company harvested a mean of 4.3 trees/ha (4.7 m^3/ha) using their standard reduced-impact-logging techniques that include road planning, directional felling, and the retention of 20% of the harvestable trees as seed trees. The mean density of trees ≥ 10 cm DBH before logging was 427 individuals/ha, of which 40% were *Acosmium cardenasii* (after first mention of a species I will refer to it by its generic name; for a complete list of scientific names see Table 2-1). The company used these same logging techniques in the "intensive management" plot to harvest a mean of 8.1 trees/ha (8.2 m^3/ha). While harvesting the "intensive management plot," the skidder drivers mechanically scarified the soil surface in an average of 0.6 felling gaps/ha (mean area = 50 m^2/ha) where there was no existing regeneration of commercial timber species. After logging of the intensive management plot, future crop trees (i.e., well-formed trees of commercial species 10-40 cm DBH) were liberated from liana cover (by slashing the lianas with a machete; 21 trees/ha) and liberated from competition from nearby non-commercial trees (by poison girdling; 1.7 trees/ha). These last two treatments for enhancing the growth of future crop trees were not applied in the normal logging plot. In the unlogged forest plot, the mean density of trees > 10 cm DBH was 432 individuals/ha, of which 38% were *Acosmium* (Table 2-1). The total basal area of trees >10 cm DBH in the unlogged plot averaged only 19.6 m^2/ha and 38% of the trees were liana infested (18% severely so).

Canopy openness in the early dry season (May 2003), as measured with a spherical densiometer (Lemmon 1957) held 1 m above the ground at 140 equally spaced points in the 10 ha permanent plots, averaged 8% in the 20 ha control (unlogged) plot, 13% in the plot subjected to normal selective logging in November 2002, and 14% in the plot that was intensively harvested and silviculturally treated also in November 2002 (Figure 2-2). I remeasured canopy openness at the same points in March 2006 and found increases in canopy cover in both of the treated plots, but not in the control plot (Figure 2-2).

Experimental Design and Data Analysis

Response of regeneration to silvicultural treatment intensity

Plants 5-100 cm tall of 22 species of subcanopy, canopy, and emergent tree species (Table 2-2) that originated from seeds or sprouts were monitored in subplots in three of the 20-ha (400 x 500 m) LTSRP plots. In the central 10 ha (400 x 250 m) of each plot, I located 144 pairs of 2 x 1 m subplots separated by 2 m at 25 m intervals (data from the paired plots were subsequently combined). Each seedling was marked, mapped, and measured for height at regular intervals of one year for 3 y. The site of each plot pair was categorized in one of the following microsites: undisturbed forest (includes natural canopy gaps and high stature forest); logging road; and, logging gap. Undisturbed forests were categorized as those sites in which the structure of the forest did not change during logging. I initially separated skid trails from primary and secondary logging roads, but because of small sample sizes, these sites are combined into a category referred to as log extraction paths. Logging gaps were sites where the canopy was opened during tree felling and log extraction. Based on the literature (Whitmore 1998, Mostacedo and Fredericksen 1999, Pinard et al. 1999) and field observations, each tree species was placed in one of the following ecological groups: light-demanding pioneer; long-lived pioneer; partially shade tolerant; or, shade tolerant.

I compared seedling abundances among the harvesting treatment plots and microsites using repeated measures ANOVA (Scheiner and Gurevitch 2001). Measurement dates were considered to be a within-subject factor, while harvesting treatment and microsites were considered as between-subject factors.

Seedling recruitment rates (*R*) were calculated using the compound interest equation (McCune and Cottam 1985):

$$R = (1 + Bx)^{1/x} - 1 \tag{2-1}$$

where *Bx* is the birth rate in the period *x* calculated for each year and for each m^2 of ground area. As recruitment rate I calculated the number of new seedlings of each species in each harvesting treatment m^2/year.

Mortality rate (*M*) expressed as percentage per year was calculated as (Primack et al. 1985, Sheil et al. 1995)

$$M = 1 - [1 - (N_0 - N_1) / N_0]^{1/t} \tag{2-2}$$

where N_0 is the number of living seedlings at time 0, N_1 is the number of living seedlings at time N_1, and *t* is the time period between N_0 and N_1. Mortality rates were calculated by species and harvesting treatment.

I calculated the relative growth rate (RGR) as

$$RGR = \frac{(Ln(H_1) - Ln(H_0))}{t_1 - t_0} \tag{2-3}$$

where, H_0 is the seedling at the initial measurement, H_1 is the height at the second measurement, t_0 is the initial time, and t_1 is the time of the second measurement (Hoffmann and Poorter 2002). I compared RGR of harvesting treatments, microsites and species using repeated measures ANOVA. For all analyses I used SPSS Version 12.0. For each factor, I also conducted Bonferoni or LSD *post hoc* comparisons at the 95% confidence level.

Factors affecting seedling establishment and growth

Tree species used in the following experimental studies were selected on the basis of seed availability in May-September 2005 when I collected seeds from 3-10 trees per species. Of the six species used in the experiment, 4 are wind-dispersed, 2 are dispersed by animals, 2 are characterized as light-demanding, and 4 are considered shade tolerant (Table 2-1). Brief descriptions of the species follow:

Amburana cearensis (Allemão) A. C. Sm. usually produces one 0.49 g dry weight winged seed per dehiscent legume. *Aspidosperma rigidum* Rusby produces elliptical seeds that weigh 0.24 g and are surrounded by a wing. *Ceiba samauma* (Mart.) K. Schum. produces 0.17 g seeds that are covered by fine, cotton-like fibers that aid in wind dispersal. *Pterogyne nitens* Tul. produces single-seeded wind-dispersed samaras with 0.16 g seeds. *Copaifera chodatiana* Hassl. seeds are red, weigh 0.33 g, are covered with a white aril, and are animal-dispersed. *Hymenaea courbaril* L. produces round, large (3.9 g), and animal-dispersed seeds in indehiscent legumes.

The experiment used a split-plot design (Montgomery 2001) in which ground bromeliad cover, water availability, and seed and seedling predation were experimentally manipulated (Figure 2-3). The 2 m^2 experimental plots were comprised of the two 1 m^2 subplots which were replicated 40 times in 10 blocks separated by at least 40 m. The experiment commenced in July 2005 and was monitored until December 2006.

The terrestrial bromeliad manipulated in this study is *Pseudananas sagenarius*, locally known as “garabata.” Rosettes of this clonal species are about 1 m high and cover $1m^2$ each. Their colonies typically cover 15-40% of the ground in Chiquitano dry forest in clumps up to 2000 m^2. This species is more common in mature than in young stands (Kennard et al. 2002) and its abundance is reduced by fire (Fredericksen et al. 1999).

The water availability treatment involved either irrigating or withholding water from plots by adding water or shielding plants from rainfall during what is typically the transition between the dry and rainy seasons (late September). Rainfall inputs directly into the drought treatment plots were prevented by covering them with 2.0 x 1.5 m roofs of transparent plastic.

The rain shelters were left for the first 3 mo of what is normally the dry season. The irrigated plots received natural rainfall plus 10 liters of water every 15 days (=20 mm/mo) starting on 21 September 2005 and finishing in at the end of November when rainfall were more frequent. Soil water tensions at 0-10 cm depth in one droughted and one irrigated plot in each of four blocks were monitored hourly with Watermark® soil moisture sensors attached to data loggers; rainfall inputs were monitored adjacent to the four irrigated plots (Figure 2-1). Droughted plots simulated years with prolonged dry seasons whereas the irrigated plots simulated wet years with short dry seasons.

To exclude seed and seedling predators, half of the plots were surrounded by 60 cm high, 1-mm mesh wire netting fastened to the ground. The exclosures were erected before the seeds were sown and were maintained for the duration (15 mo) of the experiment. In each treatment plot, I randomly sowed seeds of all tree species described above (Table 2-1). Each seedling establishing from a planted seed was marked, mapped, and its height measured five times between September 2005 and December 2006.

Treatment effects on seedling abundance were tested using repeated measures ANOVA for a split plot design (Scheiner and Gurevitch 2001) with bromeliads (present or absent) as the main factor, and irrigation, predator exclosure, and time as subplot factors. Seedling heights (RGR) for each time period were compared between treatments for each factor using t-test with sequential Bonferroni corrections (Sankoh et al. 1997). Due to seedling mortality over the study, the sample sizes varied so I could not run repeated measures ANOVA on the RGR data. I ran the analysis for all 6 species combined and for each species separately.

Results

Response of Regeneration to Management Intensities

Three years after logging and silvicultural treatment, seedling densities varied with management intensities and among microsites. Although 22 species are included in Table 2-1, only data from the most abundant 11 species are presented. Densities were higher in the control than in the harvested areas, but did not differ between the normal harvesting and the intensive management plots (Figure 2-4). However, seedling densities without *Acosmium*, was higher in normal harvesting and lower in the control plot (Figure 2-4). This pattern was maintained five years after logging for all species combined, but for nine of the 11 species evaluated, there were treatment differences and temporal trends (Table 2-2). For example, *Copaifera* seedling density increased with increasing management intensity. In contrast, *Machaerium acutifolium* Vogel seedling densities did not differ between the two logged plots but were significantly higher in the normal logging plot than in the control plot. In contrast, seedling densities were lower in the intensive management plot than in the normal logging or control plot for four *Acosmium*, *Phyllostylon rhamnoides* (J. Poiss.) Taub., and *Machaerium scleroxylon* Tul.

Seedling densities varied markedly among microsites. Overall, undisturbed sites had the highest seedling density (Table 2-3). This pattern was observed at the species level for *Acosmium*, *Caesalpinia pluviosa*, *M. scleroxylon* and *Phyllostylon.* In contrast, *Centrolobium microchaete* seedling densities were higher on logging roads than in other microsites. The other nine species had statistically similar seedling densities among microsites (Table 2-3**).**

Overall, seedling mortality rates were higher in undisturbed areas than in harvested areas and the mortality rate was higher in 2004 than in 2005 (Figure 2-5). In 2004, 47% and 66% of the seedlings died in the normal and intensive management plot, respectively. In 2005, mortality was still higher in undisturbed control plots, but the ratio was reduced (Table 2-4). At species level, mortality rates were generally higher in undisturbed control plots than in either of the logged plots. On average, the highest (22-26%/y) mortality rates were for *Sweetia fruticosa* Spreng., *Caesalpinia,* and *M. scleroxylon*. At the other end of the spectrum, *Gallesia integrifolia* (Spreng.) Harms and *Piptadenia viridifolia* (Kunth) Benth. suffered no mortality (Table 2-4).

Over all species, the recruitment of new seedlings was 0.8 seedlings /m^2 /y. Recruitment was three times higher in undisturbed areas than harvested areas (Figure 2-5) and marginally higher (0.91 seedlings /m^2 /y) in 2004 than in 2005 (0.63 seedlings /m^2 /y). *Acosmium* had the highest recruitment rate (0.26 seedlings/m^2/y), followed by *Phyllostylon* (0.13 seedlings/m^2/y) and *M. acutifolium* (0.08 seedlings/m^2/y). *Acosmium* and *M. acutifolium* recruited mostly in undisturbed forest, *Phyllostylon* recruits were common in the normally logged plot, and *Pterogyne* and *Aspidosperma* recruited most new seedlings in the intensive management plot (Table 2-4).

Factors Affecting Seedling Growth and Establishment

Seedling growth

Relative growth rates of seedlings differed among the three logging microsites either in 2004 (F=4.19, P=0.01) or in 2005 (F=10.76, P=<0.0001). In both years, RGRs were higher on loging roads and logging gaps than in undisturbed microsites. RGRs were higher in 2004 than in 2005 (F=5.64, P=0.018) and were higher for long-lived pioneer species RGRs than partial shade tolerant and shade tolerant species (F=15.63, P=<0.0001).

RGRs differed among years, species, and microsites following patterns that were not consistent. For example, the RGRs of *Acosmium*, *Aspidosperma*, *Copaifera,* and *Sweetia* were higher in 2004 than in 2005 (F=7.74, P=0.005). For *Aspidosperma* and *Caesalpinia,* RGRs did not differ among undisturbed sites, logging roads, and logging gaps. Among microsites, RGRs for *M. acutifolium* were higher in logging roads and logging gaps than in undisturbed microsites in 2004 but not in 2005. RGRs of *Acosmium* and *Sweetia* were similar among microsites in 2004 whereas in 2005, seedlings grew faster in logging roads and logging gaps than in undisturbed microsites.

Monthly RGRs of seedlings in the experimental plots were similar in bromeliad-free and bromeliad-infested plots at different times (t_1=0.14, P_1=0.89; t_2=2.01, P_2=0.05; t_3=0.48, P_3=0.63; t_4=0.04, P_4=0.39). Similarly, RGRs were did not differ in the droughted and irrigated plots (t_1=0.89, P_1=0.37; t_2=0.87, P_2=0.39; t_3=0.93, P_3=0.35; t_4=0.88, P_4=0.38) or between the exclosure and non-exclosure plots (t_1=0.01, P_1=0.99; t_2=0.12, P_2=0.90; t_3=0.40, P_3=0.69; t_4=0.36, P_4=0.72; Figure 2-10). At the species level, RGRs were also similar in bromeliad-free and bromeliad-infested plots, droughted and irrigated plots, and exclosure and non-exclosure plots (Table 2-6, 2-7, 2-8).

Seedling establisment

In general, tree seedling establishment was suppressed by bromeliads, but responses to bromeliad cover varied among species (Figure 2-6). Based on the six species for which there are sufficient data, four had similar numbers of seedlings in bromeliad patches and bromeliad-free areas. For the other two species (*Hymenaea* and *Pterogyne*), seedling abundances were lower in bromeliad covered plots (Table 2-5, Figure 2-7).

The effects of the drought and irrigation treatments varied over time (Figure 2-6). Seedlings were initially about 150% more abundant in the irrigated than in the droughted plots (Figure 2-8), but this difference diminished over time. This pattern was consistent among species except for *Aspidosperma*, which had more seedlings in the droughted than in the irrigated plots (Table 2-5).

Excluding seed and seedling predators generally resulted in higher seedling densities (Figure 2-6), with some variation among species (Figure 2-9). *Amburana*, *Copaifera,* and

Hymenaea seedlings were more common within the excloures than in the open-access plots (Table 2-5). In contrast, the exclosure treatment had no effect on seedling densities of *Aspidosperma*, *Ceiba,* and *Pterogyne.*

There were some significant interactions among factors both overall and at the species level. In particular, irrigated plots with bromeliads from which predators were excluded had higher seedling densities than plots that were irrigated and open to seed and seedling predators (Table 2-5).

At the species level there were significant interactions among treatments only for *Ceiba* and *Copaifera*. For *Ceiba* in the bromeliad covered plots, irrigation and predator exclosure increased seedling densities relative to the droughted and open-access plots. For *Copaifera* in the bromeliad-infested plots, irrigation and predator exclosure resulted in higher seedling densities. In the bromeliad-free plots, drought coupled with predator exclosure resulted in higher seedling densities than drought alone.

Discussion

Logging Effects on Seedlings Dynamics

Logging usually affects seedling densities due to direct effects and creation of microsites that differ in environmental conditions, especially light intensities (Beaudet and Messier 2002, van Rheenen et al. 2004). In most tropical forests, seedling densities of light-demanding species increase on open microsites. In this study, however, overall seedling densities were higher in undisturbed forest than in selectively logged areas (Figure 2-2). Similarly, total seedling densities were higher on undisturbed microsites compared to microsites created by logging. In contrast, at a site only 40 km from INPA, with a similar forest type and rainfall regime Fredericksen and Mostacedo (2000) reported that seedlings of commercial timber species increased in abundance on log landings, roads, and logging gaps.

At the species level, the majority of species (64%) had similar seedling densities among microsites; only three shade-tolerant species had higher seedling densities in undisturbed microsites. One light-demanding species, *Centrolobium*, had higher seedling densities on skid trails and log landings compared to other microsites.

There are several potential explanations for observed differences between the results of this study and those of Fredericksen and Mostacedo (2000). The forest canopy of Las Trancas where the latter conducted their work is dominated by *Anadenanthera*, a light-demanding species, whereas INPA Parket is dominated by *Acosmium*, which is more shade tolerant. Results without *Acosmium* show that harvested plots have higher seedling densities than control plot (Figure 2-4). The simple difference in dominants might account for some of the overall differences observed between the sites. Another difference between the two studies is that *Anadenanthera* seedlings emerging from seeds dispersed immediately before logging were extremely abundant at Las Trancas (100-200 individuals/m^2; personal observation). In contrast, seedlings of *Acosmium* were never as abundant at INPA and those that were present were apparently the result of several years of recruitment.

Open microsites created by logging may be disadvantageous for seedling recruitment in INPA Parket because such sites are extremely hot and dry, especially during the dry season. On the other hand, it is possible that even though there were disturbances associated with fallen trees, roads, and skid trails, the canopy could still be too closed at INPA to promote abundant seedling recruitment (Jackson et al. 2002). In addition, the densities of understory plants and other competitors might remain high in gaps, thus suppressing seedling recruitment in disturbed areas, especially of shade-intolerant species (Beckage et al. 2000, Schnitzer et al. 2000). On the log extraction paths, soil compaction might negatively affect seedling establishment and growth.

Finally, several species in this study are shade-tolerant, including the dominant (*Acosmium*), and do not require disturbed areas for regeneration.

Seedling recruitment rates were 70% lower in the logged plots than in the unlogged control plot and recruitment decreased with management intensity. Because of increases in light availability associated with logging, I expected more recruitment in logged plots than in unlogged plots. One explanation for this result could be that logging decreased seed-tree densities, which limited seed inputs (Forget et al. 2001, Makana and Thomas 2004, Grogan and Galvao 2006). Similarly, in French Guiana, Forget et al. (2001) reported that for all but one species, recruitment was not favored by logging. The importance of retention of seed trees was shown by Grogan and Galvao (2006), who reported that mahogany (*Swietenia macrophylla*) seed production near gaps was important for recruitment. In addition, even if seed production is not limiting, logging may create microsites that are not appropriate for seed germination and seedling growth due to soil compaction (Pinard et al. 1996) or other factors. Site preparation (e.g., soil scarification) in logging gaps and skid trails can enhance regeneration, as shown by Pinard et al. (1996) in a dipterocarp forest in Malaysia, but such treatments do not always have beneficial effects (Heuberger et al. 2002).

Seedling mortality rates were nearly 50% lower in the logged plots than in the unlogged plot, which was the opposite of what I expected. Several studies report that seedling mortality usually increases as harvesting intensity increases (Chapman and Chapman 1997, Saenz and Guariguata 2001), but the logging intensities in my plots were all low. Nevertheless, mortality of some plant species decreases as light intensity increases. For example, in a tropical rain forest in Costa Rica, Kobe (1999) found that mortality rates of three of four canopy species monitored decreased as light levels increased in the understory.

There was considerable interspecific variation in both recruitment and mortality rates. For example, for three tree species (*Acosmium*, *Aspidosperma*, and *Copaifera*) that are in the same shade tolerant guild the percentage of recruitment ranged from 7.5-15.5 %/y. The mortality rates for the same species ranged from 0.019-0.255 individuals/m^2/y. *Acosmium,* because of its dominance, drives the overall patterns of recruitment and mortality.

Apparently, while recruitment rates are reduced by disturbance, the seedlings that do establish grow sufficiently during the rainy season to survive the subsequent dry season. In contrast, in the relatively closed conditions of the control plot, few of the abundant new recruits survive the drought stress of their first dry season. Similarly, seedlings of a light-demanding species (*Anadenanthera*) established abundantly, but died rapidly in the control plot.

Temporal changes in recruitment and mortality are related to variation in seed production and rainfall regime (Kitajima and Fenner 2000, Khurana and Singh 2001). In this study, seed production, seedling recruitment, and seedling mortality rates were all higher during 2003-2004, a dry year, than during 2004-2005, a relatively wet year with a short dry season.

Within the logged plots, seedling RGRs were typically higher in disturbed microsites, but there was some variation among species. Over the 2 y monitoring period, seedlings grew faster on log extraction paths than undisturbed microsites. In a similar study in the same area but using large transects, seedlings in skid trails and logging gaps grew faster than seedlings in undisturbed forest (van Andel 2005). Contrary to my expectations, *Acosmium*, a shade-tolerant species, had the highest RGR on log extraction paths while RGRs of *Anadenanthera,* a light-demanding species, not vary among microsites. Overall it appears that disturbed microsites are favorable for seedlings, but this pattern seems to be driven by *Acosmium,* the most abundant species. For most of the species it seems that, in contrast to wetter tropical forests, RGRs of tropical dry forest seedlings are not governed primarily by light availability and have a different relationship to disturbance than wet and moist forest tree species (Khurana and Singh 2001).

Factors Affecting Seedling Establishment and Growth

Soil moisture availability is a key factor influencing seedling growth in dry forests (Khurana and Singh 2001). In my study, seedlings that lost their leaves during the dry season (e.g., *Amburana* and *Aspidosperma*) grew slowly, while the evergreen species (e.g., *Copaifera* and *Pterogyne*) grew faster. I also found that bromeliad cover significantly reduced seedling growth rates.

Ground bromeliads interfered with the establishment and growth of tree seedlings in this study, as has been described for another forest in Bolivia (Fredericksen et al. 1999), as well as on Barro Colorado Island in Panama (Brokaw 1983). As in those other two studies, I also observed substantial interspecific variation in seedling responses to bromeliads. The observation that the irrigation treatment eliminated the generally negative effect of bromeliads on seedling survival and growth suggests that the rain-trapping effect of bromeliad rosettes, coupled with any water they draw from the soil, is the cause of their deleterious effect. Perhaps the species that were not sensitive to the presence of bromeliads (*Amburana*, *Ceiba*, *Copaifera*, and *Pterogyne*) are more drought-tolerant than the other species.

I expected that experimentally shortening the dry season by irrigation would increase the establishment and growth of tree seedlings, while exacerbating dry season drought would have the opposite response. Instead, what I found that the principal impact of the drought treatments was the timing of seed germination, but not all species were affected. Seeds in the droughted plots did not germinate until after I removed the roofs and allowed rain to fall on the soil; seedlings then reached the same densities as in the irrigated plots. A similar study in mahogany in a dry forest in Guanacaste, Costa Rica reported the same effect of water availability on seedling density (Gerhardt 1996b). Similarly, RGR were not affected by drought stress.

The tendency for species overall (except *Aspidosperma*) was higher densities in the irrigated than in the droughted plots at the time of germination. This tendency suggests that longer rainy seasons, such as those occurring during El Niño years, can have dramatic effects on seedling establishment (Gilbert et al. 2001, Engelbrecht and Kursar 2003). The same pattern of increased mortality during dry years was revealed by the mortality of naturally established seedlings during this study (Figure 2-5).

Due to a variety of morphological, physiological, and phenological traits, tree species differ in the susceptibility of their seedlings to drought stress (Table 2-4; (Reader et al. 1993, Khurana and Singh 2001, McLaren and McDonald 2003). For example, *Amburana* seedlings reduce their moisture requirements by being dry season deciduous, leaf areas of *Aspidosperma* seedlings decline substantially during the dry season, and *Acosmium* is noteworthy for its deep root system (Wright 1991, Engelbrecht and Kursar 2003).

Seed or seedling predation seems to be a very important factor for seedling establishment in tropical dry forests (Janzen 1971, Hulme 1996). I found that plots with exclosures had higher seedlings densities than open plots. Exclosures prevented seedling herbivory, but not all types of seed predation because insects and other small seed predators were not excluded (Grol 2005). In tropical dry forests, herbivory has the most impact on tree regeneration when seedlings are emerging, not after roots and stems are lignified (Kitajima and Augspurger 1989, Lucas et al. 2000). Once browsed, established seedlings usually resprout, but only lignified seedlings survive. In some cases, herbivory damage could be superficial and not dramatically impact the growth and survival of seedlings (personal observation).

There were some species in which exclosure treatments had an effect on established seedlings, while for others there were similar. For example, *Hymenaea*, a species with a large seed and seedlings larger than *Ceiba*, had a higher established seedling caused by the exclosure plots. Several studies support the hypothesis that large seeds are usually most predated (Blate et al. 1998, Dalling and Hubbell 2002), but see Moles et al. (2003). Likewise, *Aspidosperma* and *Pterogyne* have seeds that probably were predated mostly by small insects (i.e., bruchid beetles) which were not deterred by the exclosures.

Conclusions

Five years after selective logging and silvicultural treatments, overall tree seedling densities were higher in the control plot than in the two logged plots. It is important to point out that this result was heavily influenced by the reduced seedling densities in the logged plots of the dominant species, the shade-tolerant *Acosmium*. Other species, which were less common everywhere (e.g., C*entrolobium*, *Copaifera,* and *Machaerium cf. acutifolium*), actually increased in response to forest management activities, and many other species were not affected. Within the logged plots, undisturbed microsites had higher seedling densities except for *Centrolobium*, a light-demanding species that sprouts readily from damaged lateral roots, which was more abundant on log extraction paths.

Seedling recruitment rates were higher in the unlogged control plot and on undisturbed microsites in the logged plots, but seedling in these areas also suffered higher mortality rates than seedlings in disturbed areas. The higher turnover rates of seedlings under closed canopy conditions coupled with their observed lower growth rates suggests that rapid growth under open conditions during the rainy season is critical for seedling survival during the subsequent dry season. This result is somewhat surprising given that, even undisturbed forest in my study area, the canopy is 30-40% open after leaf fall.

Mortality rates of naturally established seedlings varied greatly among species. Seven of 22 species suffered no mortality during the 2-y monitoring period, whereas relatively high mortality rates were observed for *Caesalpinia* (26%/y), *Sweetia* (25%/y), and *Machaerium scleroxylon* (22%/y). Mortality rates of these species in the control and logged plots followed similar patterns.

Bromeliad competition and seed/seedling predators greatly reduced seedling recruitment in this tropical dry forest. Experimentally augmented soil moisture also increased seedling establishment, but only in interaction with bromeliad removal or predator exclosure. Experimental droughting delayed germination but did not influence seedling densities once the treatment terminated and rainfall was allowed into the plots. Despite these general trends, species varied in their sensitivities to bromeliads, drought stress, and predators.

Finally, seedling growth was not promoted by experimentally lengthening the rainy season. Nevertheless, the larger seedlings that developed during the extended rainy season were more likely to survive the subsequent dry season. Given that global change models consistently predict that the study region will receive less rainfall and suffer longer dry seasons in the future (e.g., Mayle et al. 2007), regeneration failures are likely to become more common.

Table 2-1. Spatial distributions, crown position, ecological group, geographical range, tree densities and basal area of timber species in a Bolivian tropical dry forest.

Scientific Name	Family	Spatial Distribution	Crown Position	Ecological Group	Deciduous	Range	Stem Density (#/ha >10 cm DBH)	Basal Area (m^2/ha)
Acosmium cardenasii	Fabaceae	Homogeneous	SC	TS	None	R	159.25	6.89
*Amburana cearensis**	Fabaceae	Random	CA	PS	May-Aug	W	0.005	0.006
Anadenanthera macrocarpa	Mimosaceae	Homogeneous	EM	L	Jun-Oct	W	13.67	2.00
*Aspidosperma rigidum.**	Apocynaceae	Clumped	SC	PS	Jul-Sep	I	12.92	0.40
Astronium urundeuva	Anacardiaceae	Clumped	CA	L	Jul-Sep	W	0.08	0.07
Caesalpinia pluviosa	Caesalpinaceae	Homogeneous	CA	PS	Aug-Sep	I	15.17	1.18
*Ceiba samauma**	Bombacaeae	Random	CA	L	Jul-Aug	W	0.67	0.07
Centrolobium microchaete	Fabaceae	Clumped	CA	L	Jun-Oct	I	11.42	0.55
Chorisia speciosa	Bombacaceae	Random	SC	L	Jul-Aug	W	16.67	0.82
*Copaifera chodatiana**	Caesalpinaceae	Random	EM	TS	None	R	5.33	0.51
Cordia alliodora	Boraginaceae	Random	SC	L	Jun-Aug	W	2.83	0.05
*Hymenaea courbaril**	Caesalpinaceae	Random	CA	PS	None	W	0.17	0.06
Machaerium acutifolium	Fabaceae	Homogeneous	SC	LL	None	I	27.17	0.34
Machaerium scleroxylon	Fabaceae	Random	EM	PS	Jul-Sep	I	4.25	0.68
Phyllostyllon rhamnoides	Rhamnaceae	Clumpled	SC	TS	None	I	4.42	0.63
*Pterogyne nitens**	Caesalpinaceae	Homogeneous	CA	LL	None	W	0.17	0.01
Schinopsis brasiliensis	Anacardiaceae	Random	EM	LL	Aug-Sep	I	0.25	0.144
Sweetia fruticosa	Fabaceae	Random	CA	PS	Jul-Sep	I	12.8	0.22
Tabebuia impetiginosa	Bignoniaceae	Homogeneous	CA	LL	Jul-Sep	W	1.83	0.27
Zeyheria tuberculosa	Bignoniaceae	Random	CA	PS	Oct-Nov	I	2.75	0.04
Others							142.90	4.67
Total							434.00	19.60

Crown position: (EM) = emergent, (CA) = canopy, (SC) = sub-canopy.

Ecological group: (L) = light-demanding pioneer, (LL) = Long-lived pioneer, (PS) = partially shade tolerant, (TS) = shade tolerant.

Geographical range: (R) = restricted, (I) = intermediate, (W) = widespread. Restricted species are those that are found only in one type of forest and are limited to the Chiquitano dry forest in Bolivia. Intermediate species are those that are found in two or three forest types but are either restricted to Bolivia or are only rarely found in neighboring countries. Widespread species are found in several forest types and in other countries.

Species marked with asterisks were used in the seedling survival experiment.

Table 2-2. Means of seedling densities in an unharvested control plot, a plot subjected to normal timber harvesting, and a plot subjected to more intensive harvesting followed by silvicultural treatments. Subplots within the main treatment plots are treated as replicates. Different letters indicate statistical differences ($P<0.05$) among harvesting treatments as indicated by repeated measures ANOVAs and LSD *post hoc* tests.

Scientific Name	Unharvested		Normal Logging		Intensive Management		Mean Square	F	P
Acosmium cardenasii	1.42	(0.09)^{c}	1.03	(0.09)^{b}	0.63	(0.09)^{a}	64.89	18.90	0.0001
Anadenanthera macrocarpa	0.09	(0.01)^{b}	0.06	(0.01)^{b}	0.01	(0.01)^{a}	0.67	8.15	0.0001
Aspidosperma rigidum	0.01	(0.02)^{b}	0.06	(0.02)^{a}	0.11	(0.02)^{a}	1.11	5.33	0.005
Caesapinia pluviosa	0.12	(0.02)^{b}	0.09	(0.02)^{b}	0.02	(0.02)^{a}	1.17	11.50	0.001
Centrolobium microchaete			0.02	(0.01)^{a}	0.01	(0.01)^{a}	0.03	1.89	0.170
Chorisia speciosa	0.005	(0.003)^{a}	0.01	(0.003)^{a}	0.002	(0.003)^{a}	0.01	2.31	0.100
Copaifera chodatiana	0.10	(0.04)^{b}	0.05	(0.04)^{b}	0.32	(0.04)^{a}	8.40	12.33	0.0001
Machaerium acutifolium	0.04	(0.13)^{c}	1.31	(0.14)^{b}	0.72	(0.13)^{a}	166.75	22.17	0.0001
Machaerium scleroxylon	0.12	(0.01)^{b}	0.004	(0.01)^{a}	0.001	(0.01)^{a}	1.85	48.46	0.0001
Phyllostylon rhamnoides	0.31	(0.02)^{b}	0.00	(0.02)^{a}	0.01	(0.02)^{a}	12.68	64.74	0.0001
Sweetia fruticosa	0.03	(0.01)^{a}	0.02	(0.01)^{b}	0.05	(0.01)^{a}	0.07	2.53	0.080

Table 2-3. Mean seedling densities (#/m^2) for 3 years (2003-2005) of commercial tree species in microsites created by logging in a Chiquitano dry forest. Sample size for each microsite type is noted within brackets; standard errors of the means are noted in parenthesis. Seedling densities in the different microsites were compared with repeated measures ANOVA with microsites as the between-subject factor and time as the within-subject factor. Different letters indicate different significance between treatments using pairwise Least Significant Difference (LSD) tests.

Scientific Name	Logging Gap [100]	Log Extraction Path [54]	Undisturbed [337]	Mean Square	F	P
Acosmium cardenasii	0.701 (0.103)^{b}	0.389 (0.140)^{b}	0.945 (0.056)^{a}	24.92	7.88	<0.0001
Anadenanthera macrocarpa	0.018 (0.015)	0.049 (0.021)	0.050 (0.008)	0.119	1.71	0.18
Aspidosperma rigidum	0.044 (0.024)	0.026 (0.033)	0.056 (0.013)	0.07	0.39	0.68
Caesalpinia pluviosa	0.024 (0.015)^{b}	0.037 (0.020)^{b}	0.073 (0.008)^{a}	0.32	4.71	0.009
Ceiba samauma	0.000 (0.001)	0.000 (0.001)	0.001 (0.000)	0.0001	0.68	0.50
Centrolobium microchaete	0.008 (0.005)^{b}	0.022 (0.007)^{a}	0.005 (0.003)^{b}	0.02	2.86	0.05
Chorisia speciosa	0.004 (0.003)	0.002 (0.004)	0.004 (0.002)	0.001	0.23	0.79
Copaifera chodatiana	0.092 (0.045)	0.086 (0.061)	0.146 (0.024)	0.51	0.85	0.43
Gallesia integrifolia	0.000 (0.003)^{b}	0.000 (0.004)^{b}	0.007 (0.002)^{a}	0.009	3.69	0.03
Machaerium acutifolium	0.609 (0.133)	0.668 (0.181)	0.519 (0.072)	2.13	0.40	0.67
Machaerium scleroxylon	0.008 (0.011)^{b}	0.000 (0.015)^{b}	0.048 (0.006)^{a}	0.29	7.89	<0.0001
Phyllostylon rhamnoides	0.007 (0.025)	0.000 (0.035)	0.122 (0.014)	2.203	11.34	<0.0001
Pterogyne nitens	0.000 (0.004)	0.006 (0.005)	0.005 (0.002)	0.003	0.91	0.41
Sweetia fruticosa	0.015 (0.009)	0.011 (0.012)	0.031 (0.005)	0.05	2.24	0.11
Overall Species	1.543 (0.180)^{b}	1.302 (0.245)^{b}	2.019 (0.098)^{a}	52.87	5.44	0.005

Table 2-4. Establishment and mortality rates of seedlings of commercial tree species monitored over a 3 y period in a control plot and plots subjected to two harvesting intensities (N=144 subplots/treatment plot).

Scientific Name	Mortality Rate (% of Seedlings / y)				Number of New Seedlings (#/m^2 / y)			
	Undisturbed	Normal Logging	Intensive Management	Overall	Undisturbed	Normal Logging	Intensive Management	Overall
Acosmium cardenasii	17.0	11.7	9.8	12.8	0.489	0.176	0.101	0.255
Anadenanthera macrocarpa	21.6	5.4	18.8	15.2	0.106	0.079	0.003	0.062
Aspidosperma rigidum	14.5	2.5	5.5	7.5	0.007	0.013	0.037	0.019
Caesalpinia pluviosa	35.8	23.2	18.8	25.9	0.117	0.064	0.011	0.064
Ceiba samauma	0.0	0.0	0.0	0.0	0.001	0.001	0.001	0.001
Centrolobium microchaete	0.0	10.7	43.8	18.2	0.000	0.006	0.000	0.002
Chorisia speciosa	0.0	0.0	0.0	0.0	0.004	0.004	0.000	0.003
Copaifera chodatiana	24.1	8.2	14.3	15.5	0.125	0.015	0.050	0.063
Gallesia integrifolia	0.0	0.0	0.0	0.0	0.034	0.000	0.000	0.011
Machaerium cf. acutifolium	16.1	12.4	12.6	13.7	0.003	0.138	0.106	0.082
Machaerium scleroxylon	34.7	30.8	0.0	21.8	0.157	0.012	0.001	0.056
Phyllostylon rhamnoides	19.5	10.0	0.0	9.8	0.381	0.004	0.011	0.132
Pterogyne nitens	43.8	0.0	0.0	14.6	0.000	0.001	0.022	0.008
Sweetia fruticosa	41.4	24.8	8.3	24.8	0.020	0.010	0.004	0.011
Overall	22.0	12.4	11.2	15.2	1.446	0.523	0.354	0.775

Table 2-5. Results of repeated measure analysis of variance for a split plot design run for seedling density for all species combined or six timber tree species analyzed separately. Double asterisks indicate between subject factors while the unmarked variables are within subject factors.

Source	Type III Sum of Squares	Degrees of Freedom	Mean Square	F	P-value
All species					
Time (Ti)	44.01	4	11.00	25.88	<0.0001
Bromeliad (Br)(**)	163.20	1	163.20	9.99	0.005
Time*Bromeliad (Br)	4.95	4	1.24	2.90	0.03
Irrigation (Ir)	27.83	1	27.83	2.74	0.11
Irrigation*Bromeliad	7.16	1	7.16	0.70	0.41
Exclosure (Ex)	79.66	1	79.66	13.01	0.002
Ex*Br	18.71	1	18.71	3.06	0.09
Ti*Ir	13.99	4	3.49	10.81	<0.0001
Ti*Ir*Br	1.92	4	0.48	1.48	0.22
Ti*Ex	7.75	4	1.94	5.76	<0.0001
Ti*Ex*Br	1.43	4	0.36	1.06	0.38
Ir*Ex	11.73	1	11.73	1.31	0.27
Ir*Ex*Br	16.60	1	16.60	1.86	0.19
Ti*Ir*Ex	0.58	4	0.14	0.39	0.81
Ti*Ir*Ex*Br	0.35	4	0.09	0.24	0.92
Amburana cearensis					
Time (Ti)	1.74	4	0.44	7.72	<0.0001
Bromeliad (Br)(**)	0.83	1	0.83	0.43	0.53
Time*Bromeliad (Br)	0.13	4	0.03	0.58	0.68
Irrigation (Ir)	3.01	1	3.01	1.87	0.20
Irrigation*Bromeliad	1.09	1	1.09	0.68	0.43
Exclosure (Ex)	4.50	1	4.50	2.59	0.14
Ex*Br	2.52	1	2.52	1.45	0.26
Ti*Ir	1.35	4	0.34	6.03	0.001
Ti*Ir*Br	0.08	4	0.02	0.36	0.84
Ti*Ex	0.55	4	0.14	2.39	0.07
Ti*Ex*Br	0.22	4	0.05	0.95	0.44
Ir*Ex	8.87	1	8.87	3.10	0.10
Ir*Ex*Br	0.09	1	0.09	0.03	0.86
Ti*Ir*Ex	1.03	4	0.26	3.65	0.01
Ti*Ir*Ex*Br	0.08	4	0.02	0.29	0.88
Aspidosperma rigidum					
Time (Ti)	1.16	4	0.29	8.59	<0.0001
Bromeliad (Br)(**)	0.59	1	0.59	0.25	0.63
Time*Bromeliad (Br)	0.04	4	0.009	0.28	0.89
Irrigation (Ir)	5.37	1	5.37	1.78	0.23
Irrigation*Bromeliad	1.31	1	1.31	0.43	0.53
Exclosure (Ex)	0.19	1	0.19	0.10	0.76
Ex*Br	2.6	1	2.6	1.38	0.28

Table 2-5. Continued.

Source	Type III Sum of Squares	Degrees of Freedom	Mean Square	F	P-value
Ti*Ir	0.32	4	0.08	1.95	0.13
Ti*Ir*Br	0.08	4	0.02	0.47	0.76
Ti*Ex	0.12	4	0.03	1.18	0.34
Ti*Ex*Br	0.13	4	0.03	1.24	0.32
Ir*Ex	1.50	1	1.50	0.87	0.39
Ir*Ex*Br	1.15	1	1.15	0.67	0.44
Ti*Ir*Ex	0.08	4	0.02	0.76	0.56
Ti*Ir*Ex*Br	0.08	4	0.02	0.76	0.56
<u>*Ceiba samauma*</u>					
Time (Ti)	0.53	4	0.13	2.02	0.12
Bromeliad(Br)(**)	7.75	1	7.75	4.65	0.07
Time*Bromeliad (Br)	0.05	4	0.01	0.21	0.93
Irrigation (Ir)	1.00	1	1.00	0.72	0.43
Irrigation*Bromeliad	0.53	1	0.53	0.38	0.56
Exclosure (Ex)	0.001	1	0.001	0.004	0.95
Ex*Br	0.06	1	0.06	0.54	0.49
Ti*Ir	0.30	4	0.08	1.06	0.39
Ti*Ir*Br	0.03	4	0.007	0.10	0.98
Ti*Ex	0.12	4	0.03	0.91	0.47
Ti*Ex*Br	0.05	4	0.01	0.42	0.79
Ir*Ex	1.69	1	1.69	9.28	0.023
Ir*Ex*Br	0.79	1	0.79	4.35	0.082
Ti*Ir*Ex	0.13	4	0.03	0.94	0.46
Ti*Ir*Ex*Br	0.09	4	0.02	0.67	0.62
<u>*Copaifera chodatiana*</u>					
Time (Ti)	4.1	4	1.03	15.09	<0.0001
Bromeliad (Br)(**)	2.96	1	2.96	1.49	0.24
Time*Bromeliad (Br)	0.16	4	0.04	0.60	0.66
Irrigation (Ir)	1.88	1	1.88	3.64	0.07
Irrigation*Bromeliad	0.06	1	0.06	0.12	0.73
Exclosure (Ex)	3.53	1	3.53	3.18	0.09
Ex*Br	0.03	1	0.03	0.03	0.87
Ti*Ir	0.73	4	0.18	3.59	0.01
Ti*Ir*Br	0.41	4	0.10	2.03	0.10
Ti*Ex	0.53	4	0.13	2.25	0.07
Ti*Ex*Br	0.13	4	0.03	0.56	0.69
Ir*Ex	0.56	1	0.56	0.76	0.39
Ir*Ex*Br	5.13	1	5.13	6.96	0.02
Ti*Ir*Ex	0.12	4	0.03	0.59	0.67
Ti*Ir*Ex*Br	0.31	4	0.08	1.46	0.22
<u>*Hymenaea courbaril*</u>					
Time (Ti)	1.85	4	0.46	16.09	<0.0001
Bromeliad (Br)(**)	1.63	1	1.63	3.16	0.09
Time*Bromeliad (Br)	0.09	4	0.02	0.83	0.51

Table 2-5. Continued.

Source	Type III Sum of Squares	Degrees of Freedom	Mean Square	F	P-value
Irrigation (Ir)	0.37	1	0.37	1.33	0.27
Irrigation*Bromeliad	1.13	1	1.13	0.47	0.51
Exclosure (Ex)	5.28	1	5.28	13.23	0.003
Ex*Br	0.26	1	0.26	0.65	0.44
Ti*Ir	0.30	4	0.07	1.96	0.11
Ti*Ir*Br	0.14	4	0.03	0.90	0.47
Ti*Ex	1.4	4	0.35	8.53	<0.0001
Ti*Ex*Br	0.08	4	0.02	0.49	0.74
Ir*Ex	0.08	1	0.08	0.45	0.52
Ir*Ex*Br	0.28	1	0.28	1.58	0.23
Ti*Ir*Ex	0.42	4	0.10	2.95	0.03
Ti*Ir*Ex*Br	0.18	4	0.05	1.29	0.28
Pterogyne nitens					
Time (Ti)	1.09	4	0.27	6.68	<0.0001
Bromeliad (Br)(**)	2.12	1	2.12	7.74	0.02
Time*Bromeliad (Br)	0.39	4	0.09	2.36	0.07
Irrigation (Ir)	0.26	1	0.26	1.40	0.25
Irrigation*Bromeliad	0.71	1	0.71	4.03	0.07
Exclosure (Ex)	0.05	1	0.05	0.21	0.65
Ex*Br	0.18	1	0.18	0.75	0.41
Ti*Ir	0.62	4	0.16	4.65	0.003
Ti*Ir*Br	0.08	4	0.02	0.63	0.64
Ti*Ex	0.09	4	0.02	0.62	0.65
Ti*Ex*Br	0.14	4	0.03	0.98	0.43
Ir*Ex	0.13	1	0.13	0.71	0.42
Ir*Ex*Br	0.01	1	0.01	0.06	0.81
Ti*Ir*Ex	0.11	4	0.02	0.45	0.77
Ti*Ir*Ex*Br	0.06	4	0.02	0.45	0.51

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Table 2-6. Mean relative height growth rates (± 1SE) of seedlings of commercial tree species in response to bromeliad cover removal evaluated in 4 times. Significant differences between treatments were evaluated using t-tests at 95% of confidence level with sequential Bonferroni corrections ($P_B = 0.0125$).

Species	Date	Bromeliad		No Bromeliad			
		N	Mean (SE)	N	Mean (SE)	t-test	P
Amburana cearensis	Jan06	11	0.032 (0.019)	18	-0.025 (0.026)	1.57	0.13
	March 06	10	0.046 (0.029)	22	0.063 (0.021)	0.43	0.67
	May 06	8	-0.022 (0.012)	21	-0.015 (0.010)	0.37	0.72
	Dec 06	6	0.026 (0.009)	17	0.024 (0.008)	0.14	0.89
Aspidosperma rigidum	Jan06	8	-0.009 (0.021)	19	0.020 (0.019)	0.89	0.38
	March 06	9	-0.0004 (0.018)	21	0.096 (0.027)	2.22	0.03
	May 06	9	0.0145 (0.02)	21	-0.003 (0.004)	1.57	0.13
	Dec 06	8	0.027 (0.006)	19	0.014 (0.003)	1.84	0.08
Ceiba samauma	Jan06	2	0.170 (0.026)	12	0.080 (0.035)	1.02	0.33
	March 06	3	0.090 (0.046)	15	0.103 (0.028)	0.20	0.84
	May 06	4	-0.038 (0.015)	16	-0.022 (0.008)	0.93	0.37
	Dec 06	3	0.022 (0.008)	7	-0.010 (0.011)	1.65	0.14
Copaifera chodatiana	Jan06	20	0.038 (0.015)	34	0.029 (0.015)	0.36	0.72
	March 06	25	0.033 (0.010)	39	0.056 (0.017)	0.99	0.33
	May 06	18	-0.014 (0.009)	38	0.005 (0.007)	1.44	0.15
	Dec 06	8	0.009 (0.007)	26	0.018 (0.006)	0.76	0.45
Hymenaea courbaril	Jan06	1	0.346574	8	0.141 (0.101)	0.68	0.52
	March 06	9	0.026 (0.046)	17	0.028 (0.023)	0.05	0.96
	May 06	6	0.009 (0.016)	18	-0.012 (0.019)	0.62	0.54
	Dec 06	0	-	2	0.016 (0.010)	-	-
Pterogyne nitens	Jan06	2	0.084 (0.007)	9	0.109 (0.058)	0.20	0.85
	March 06	2	0.230 (0.078)	16	0.107 (0.027)	1.49	0.15
	May 06	3	0.024 (0.024)	13	0.032 (0.014)	0.53	0.81
	Dec 06	3	-0.009 (0.013)	6	-0.036 (0.014)	0.53	0.25

Table 2-7. Mean relative height growth rates (± 1SE) of seedlings of commercial tree species in irrigated and droughted plots evaluated 4 times. Significant differences between treatments were determined using t-test at 95% of confidence level with sequential Bonferroni corrections ($P_B = 0.0125$).

Species	Date	Irrigated		Droughted			
		N	Mean (SE)	N	Mean (SE)	t-test	P
Amburana cearensis	Jan06	25	-0.006 (0.021)	4	0.015 (0.035)	0.40	0.69
	March 06	21	0.044 (0.018)	11	0.084 (0.035)	1.11	0.28
	May 06	19	-0.024 (0.012)	10	-0.002 (0.005)	1.34	0.19
	Dec 06	15	0.025 (0.008)	8	0.024 (0.013)	0.10	0.92
Aspidosperma rigidum	Jan06	7	-0.006 (0.066)	20	0.017 (0.081)	0.66	0.51
	March 06	7	0.152 (0.072)	23	0.041 (0.014)	2.39	0.02
	May 06	7	0.004 (0.017)	23	0.002 (0.004)	0.19	0.85
	Dec 06	6	0.024 (0.008)	21	0.016 (0.003)	0.93	0.36
Ceiba samauma	Jan06	13	0.074 (0.026)	1	0.346	2.82	0.01
	March 06	11	0.086 (0.033)	7	0.125 (0.037)	0.76	0.46
	May 06	14	-0.029 (0.009)	6	-0.017 (0.011)	0.75	0.46
	Dec 06	6	-0.013 (0.009)	4	0.019 (0.015)	1.89	0.09
Copaifera chodatiana	Jan06	35	0.039 (0.011)	19	0.022 (0.024)	0.72	0.47
	March 06	37	0.040 (0.013)	27	0.056 (0.021)	0.66	0.51
	May 06	31	0.001 (0.008)	25	-0.003 (0.009)	0.30	0.76
	Dec 06	18	0.008 (0.006)	16	0.024 (0.007)	1.76	0.09
Hymenaea courbaril	Jan06	9	0.164 (0.092)	-	-	-	-
	March 06	15	0.020 (0.023)	11	0.037 (0.042)	0.38	0.71
	May 06	12	-0.001 (0.011)	12	-0.012 (0.029)	0.11	0.74
	Dec 06	1	0.026	1	0.005	-	-
Pterogyne nitens	Jan06	10	0.107 (0.052)	1	0.077	0.18	0.86
	March 06	10	0.085 (0.036)	8	0.165 (0.037)	1.53	0.15
	May 06	8	0.025 (0.021)	8	0.035 (0.014)	0.40	0.70
	Dec 06	3	-0.036 (0.029)	6	-0.023 (0.009)	0.53	0.61

Table 2-8. Mean relative height growth rates (± 1SE) of seedlings of commercial tree species in response to mammal exclosure evaluated 4 times during 2006. Significant differences between treatments were evaluated using t-test at 95% of confidence level with sequential Bonferroni corrections ($P_B = 0.0125$).

Species	Date	Exclosure		No Exclosure			
		N	Mean (SE)	N	Mean (SE)	t-test	P
Amburana cearensis	Jan06	22	-0.011 (0.023)	7	0.021 (0.019)	0.76	0.45
	March 06	23	0.059 (0.018)	9	0.052 (0.041)	0.20	0.84
	May 06	21	-0.013 (0.007)	8	-0.026 (0.022)	0.72	0.48
	Dec 06	18	0.018 (0.007)	5	0.047 (0.012)	1.79	0.09
Aspidosperma rigidum	Jan06	17	0.015 (0.018)	10	0.004 (0.027)	0.35	0.73
	March 06	17	0.075 (0.034)	13	0.056 (0.021)	0.43	0.67
	May 06	17	-0.002 (0.006)	13	0.008 (0.008)	1.05	0.30
	Dec 06	17	0.020 (0.004)	10	0.014 (0.006)	0.99	0.33
Ceiba samauma	Jan06	7	0.094 (0.039)	7	0.092 (0.051)	0.04	0.97
	March 06	8	0.141 (0.032)	10	0.069 (0.034)	1.52	0.15
	May 06	9	-0.018 (0.007)	11	-0.031 (0.011)	0.88	0.39
	Dec 06	3	0.002 (0.013)	7	-0.001 (0.013)	0.17	0.87
Copaifera chodatiana	Jan06	31	0.022 (0.017)	23	0.047 (0.011)	1.13	0.26
	March 06	39	0.058 (0.012)	25	0.029 (0.022)	1.28	0.21
	May 06	35	0.002 (0.007)	21	-0.006 (0.011)	0.69	0.49
	Dec 06	21	0.014 (0.006)	13	0.018 (0.007)	0.39	0.70
Hymenaea courbaril	Jan06	8	0.178 (0.103)	1	0.053	0.40	0.70
	March 06	24	0.028 (0.023)	2	0.026 (0.026)	0.02	0.98
	May 06	21	-0.005 (0.017)	3	-0.013 (0.025)	0.16	0.88
	Dec 06	1	0.005	1	0.026	-	-
Pterogyne nitens	Jan06	7	0.142 (0.060)	4	0.039 (0.073)	1.05	0.32
	March 06	9	0.082 (0.032)	9	0.159 (0.041)	1.51	0.15
	May 06	8	0.028 (0.017)	8	0.032 (0.018)	0.14	0.89
	Dec 06	4	-0.025 (0.017)	5	-0.029 (0.015)	0.15	0.89

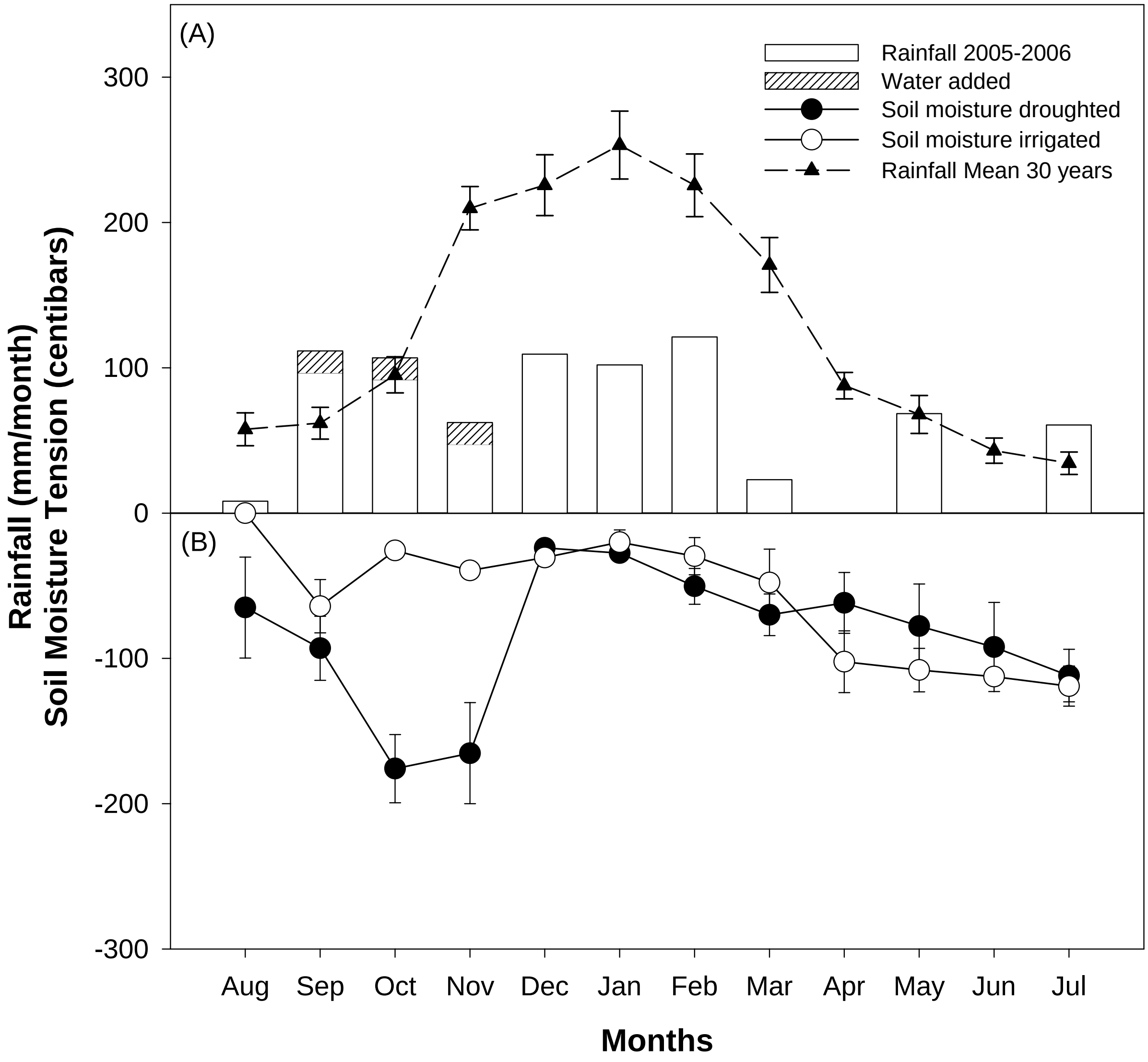

Figure 2-1. Monthly rainfall (A) and soil moisture tension measured by Watermark® soil sensors (B). Also shown in A is the water added to the irrigated soil plots. Vertical lines indicate ±1 standard (N=4).

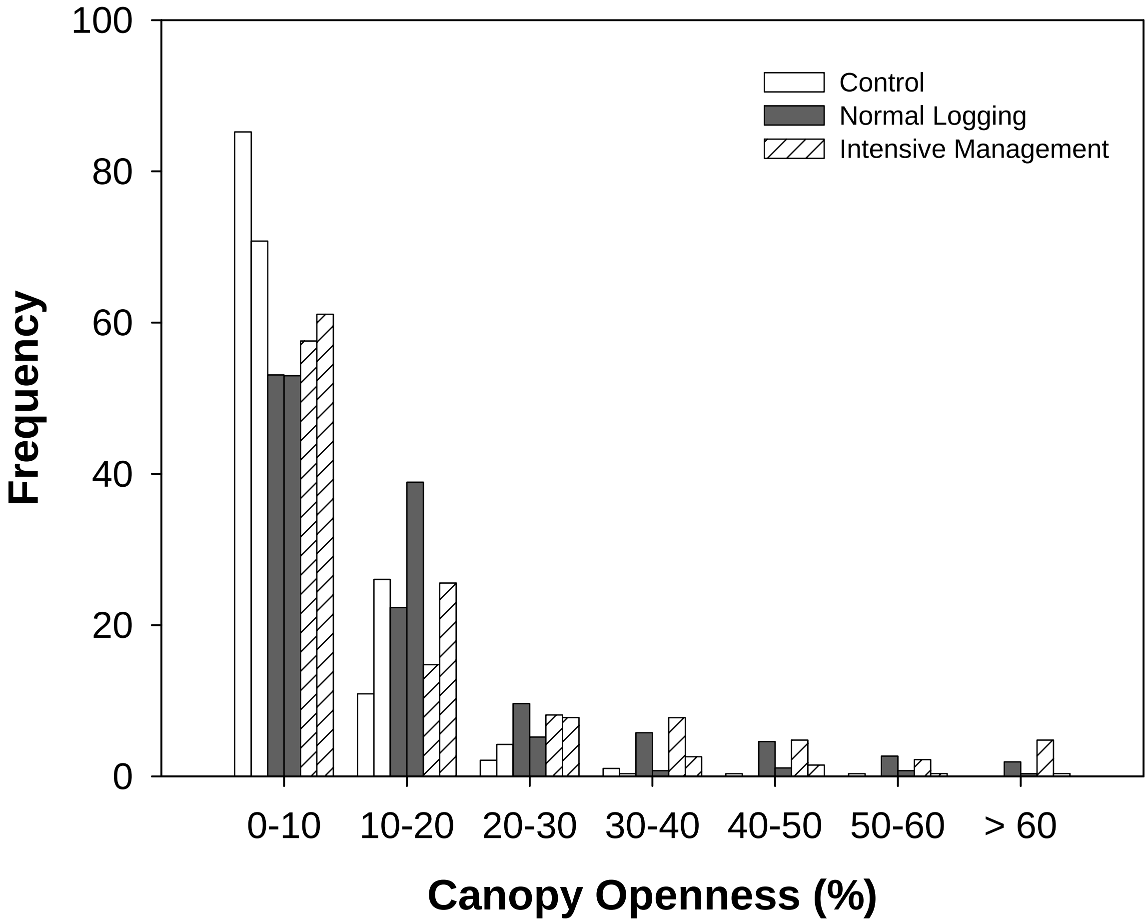

Figure 2-2. Canopy openness in an unlogged control plot, an area subjected to normal timber harvesting (4.7 m^3/ha harvested), and an area subjected to intensive harvesting (8.2 m^3/ha) 8 months (left-hand bar) and 42 months (right hand bars) after logging. Canopy openness measures were made with a spherical densitometer at the end of the rainy season at 1 m above ground at 144 equally spaced points in each 10 ha plots.

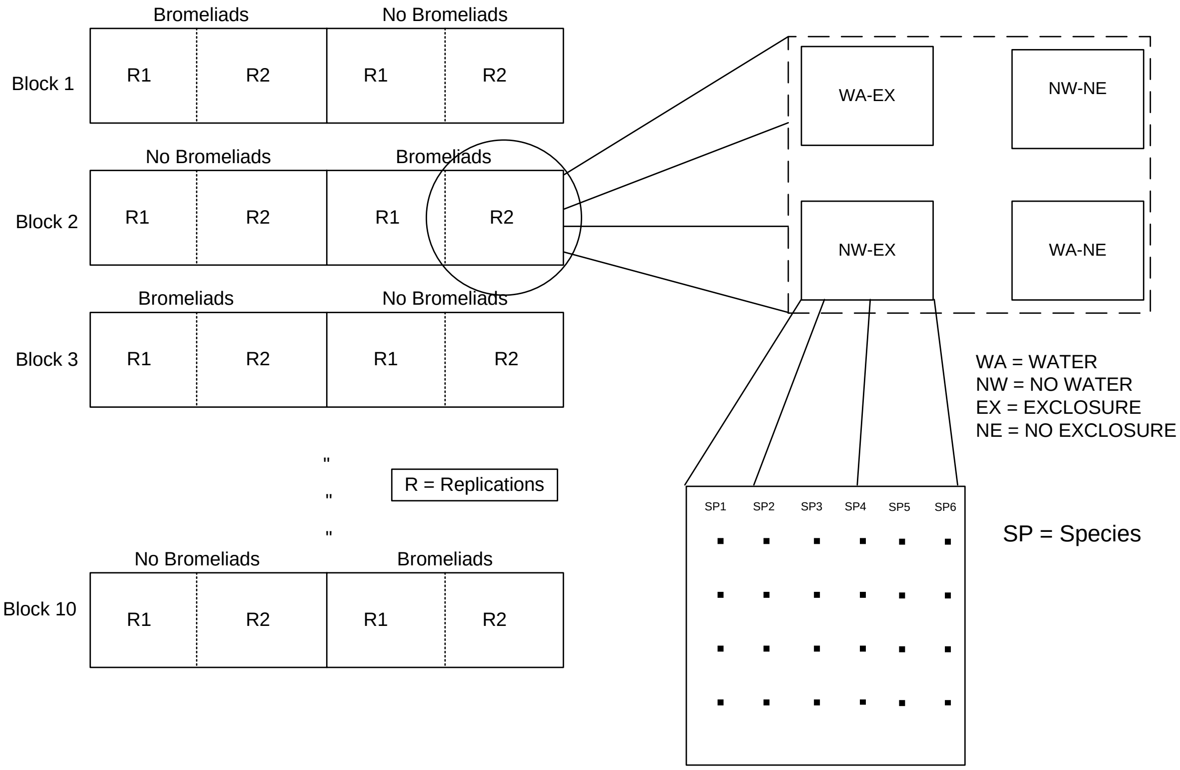

Figure 2-3. Design of the experiment on the effects of ground bromeliads, irrigation, extended drought, and seed and seedling predator exclosures on seedling establishment.

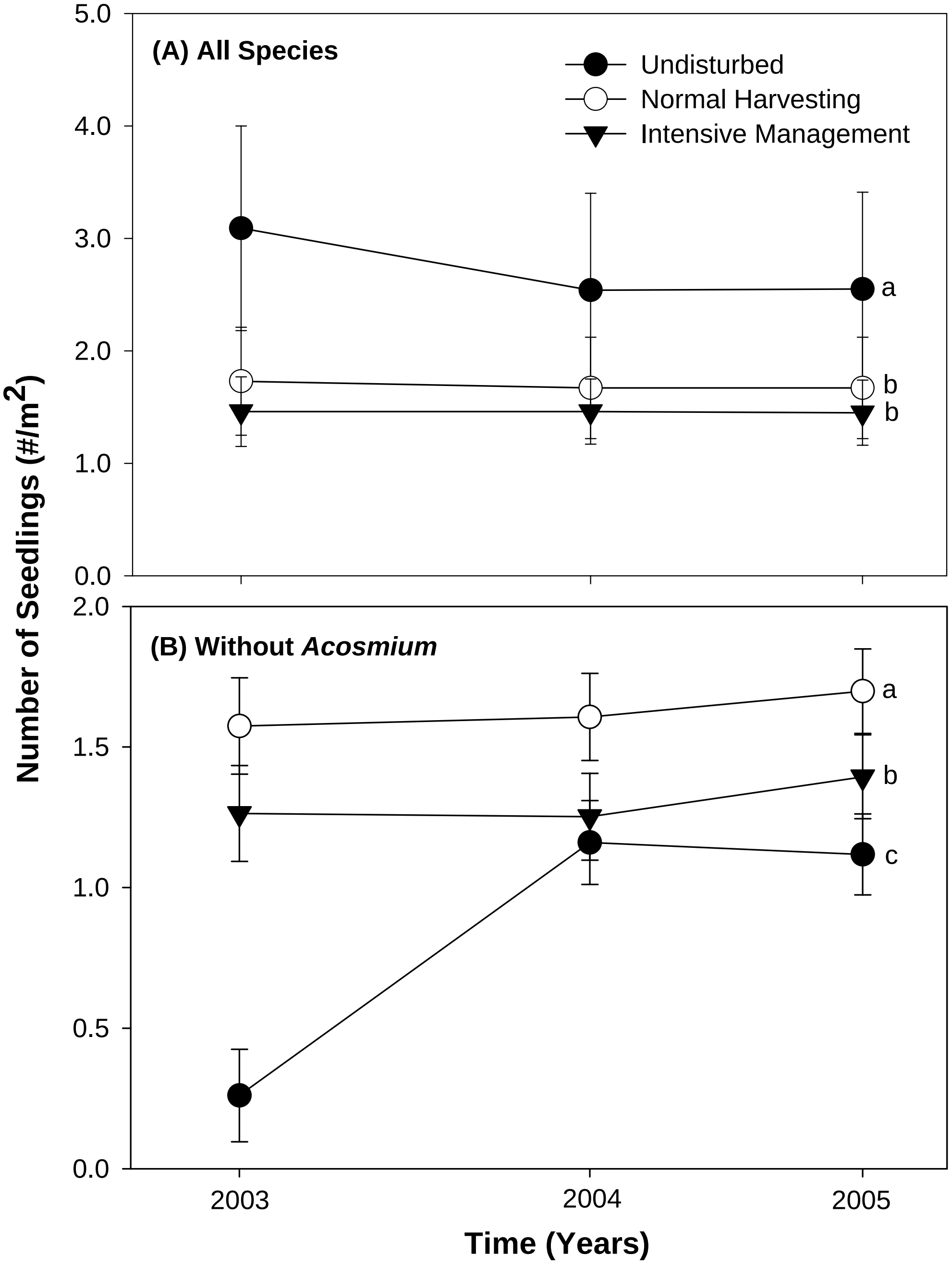

Figure 2-4. Seedling densities of 11 timber species (A) and 10 species without *Acosmium cardenasii* (B), the most dominant species, in a control plot, a plot subjected to normal timber harvesting, and a plot subjected to intensive timber stand management. The forestry treatments were carried out in 2001, 19 mo prior to the first census. Data are from 4 m^2 subplots distributed regularly in a grid with 25 m spacing through each 10 ha treatment plot. Vertical lines indicate standard errors. Different letters indicate different significance between treatments using pairwise LSD tests at 95% confidence.

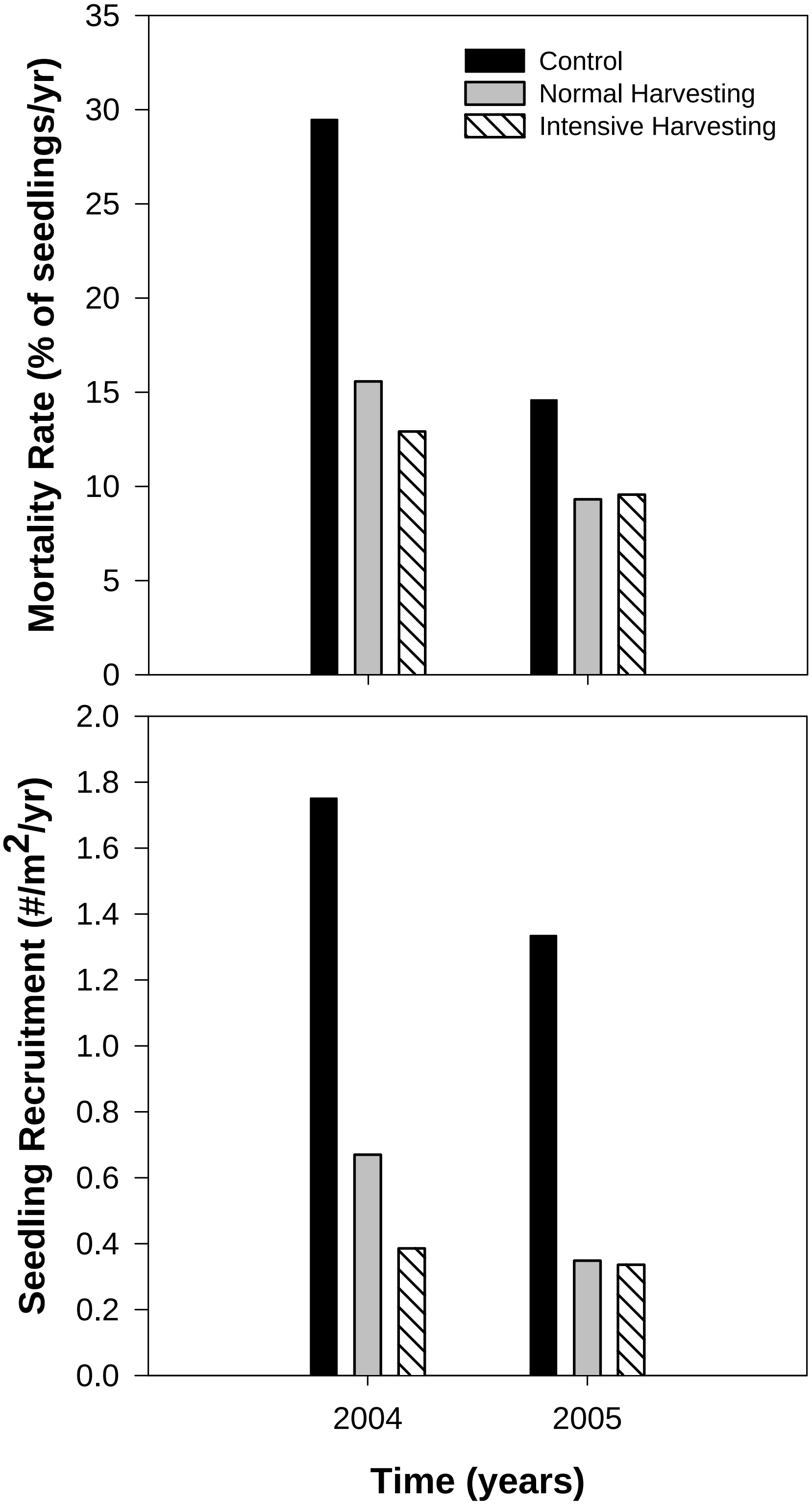

Figure 2-5. Temporal changes in seedling recruitment (#/m^2/y) and mortality for commercial tree species in a Chiquitano dry forest in Bolivia.

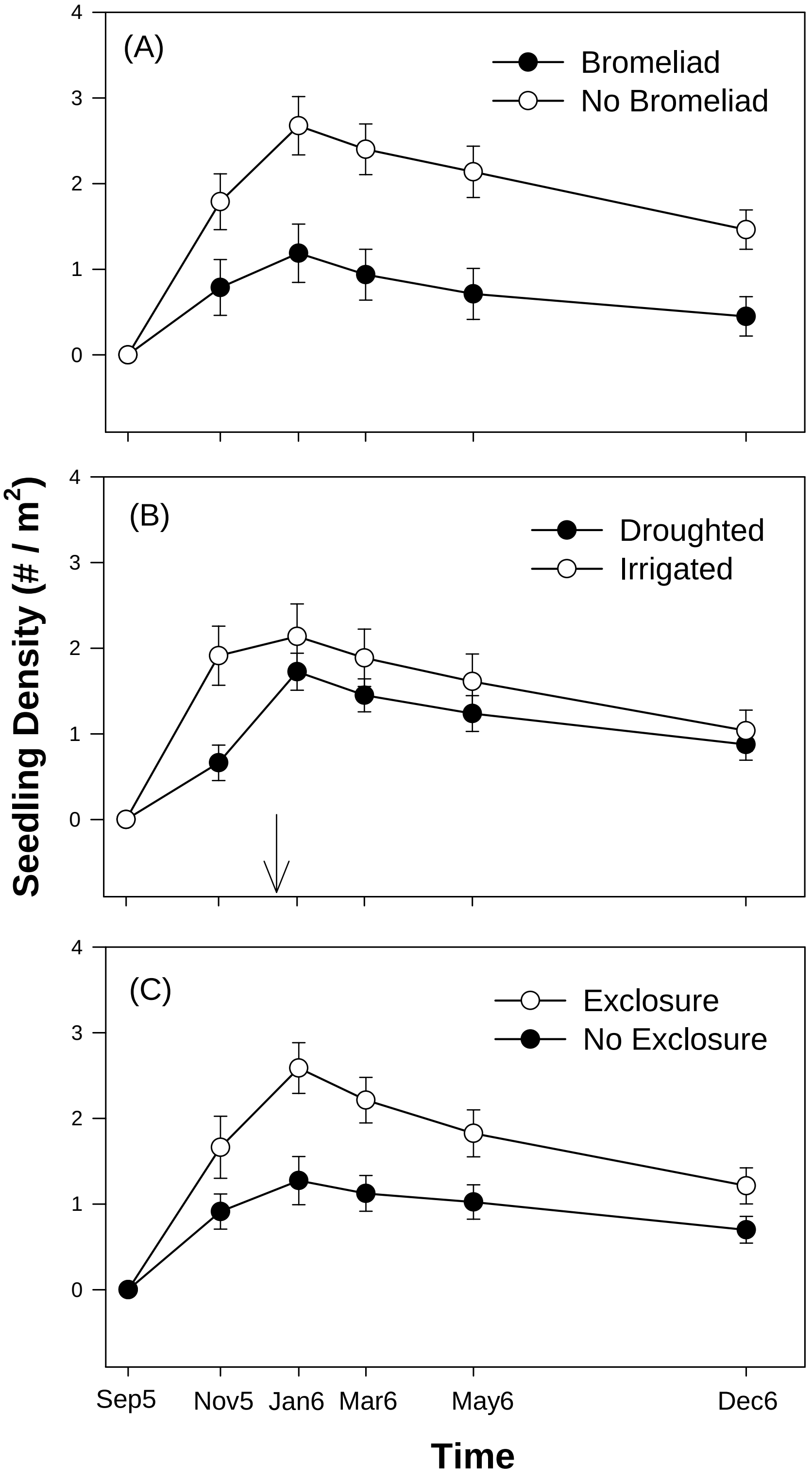

Figure 2-6. Seedling density over time in response to (A) bromeliad cover, (B) irrigation or drought, and (C) mammalian seed predators. Arrow indicates the time when I stopped the irrigation and shielding plants from rainfall. Vertical lines show standard errors of the means (N=40).

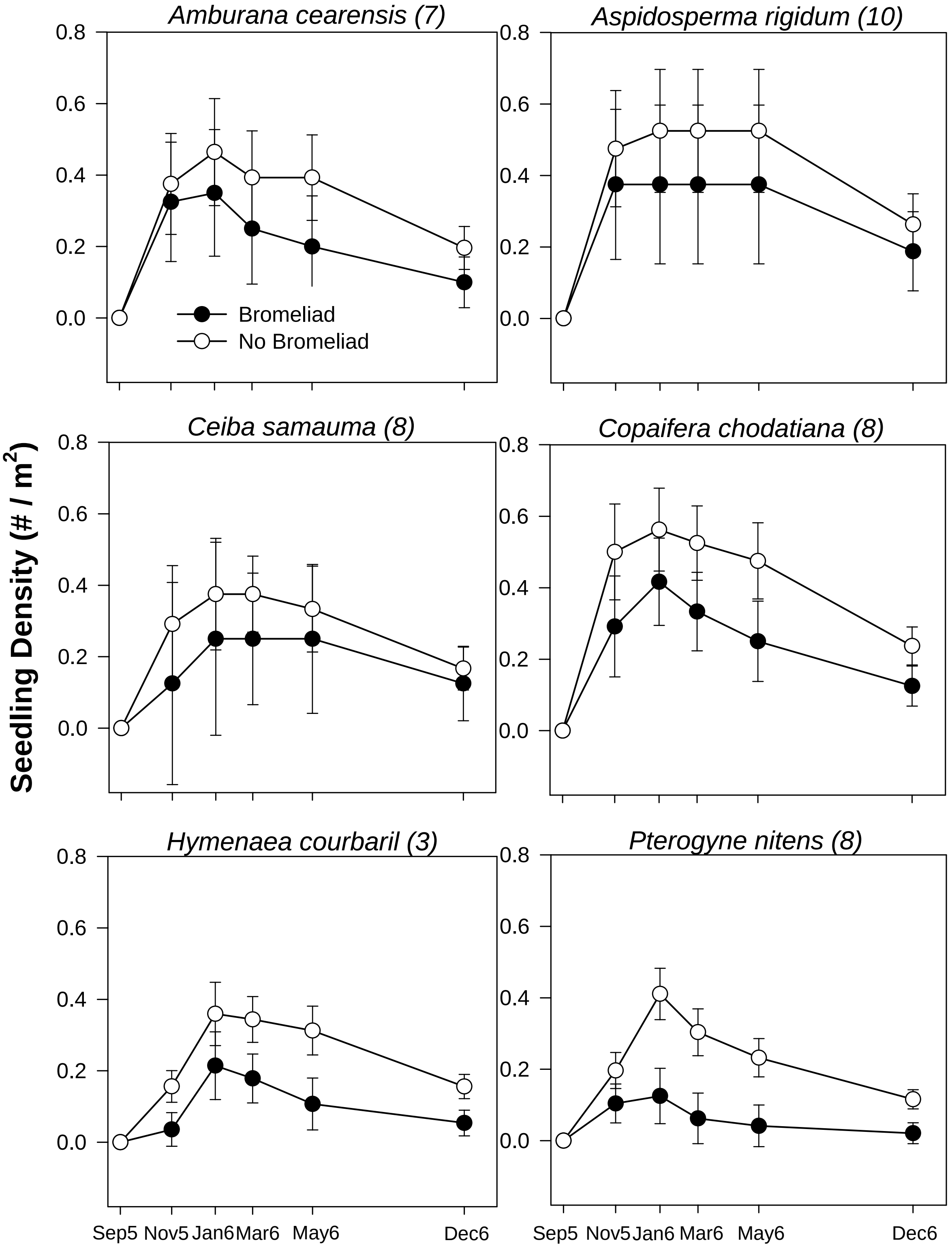

Figure 2-7. Mean densities (± 1SE) of seedlings of commercial timber tree species in 2 m^2 plots (N=40) with bromeliads (filled dots) and without bromeliads (open dots). The number of seeds sown in each 1 m^2 plot is indicated after each species name.

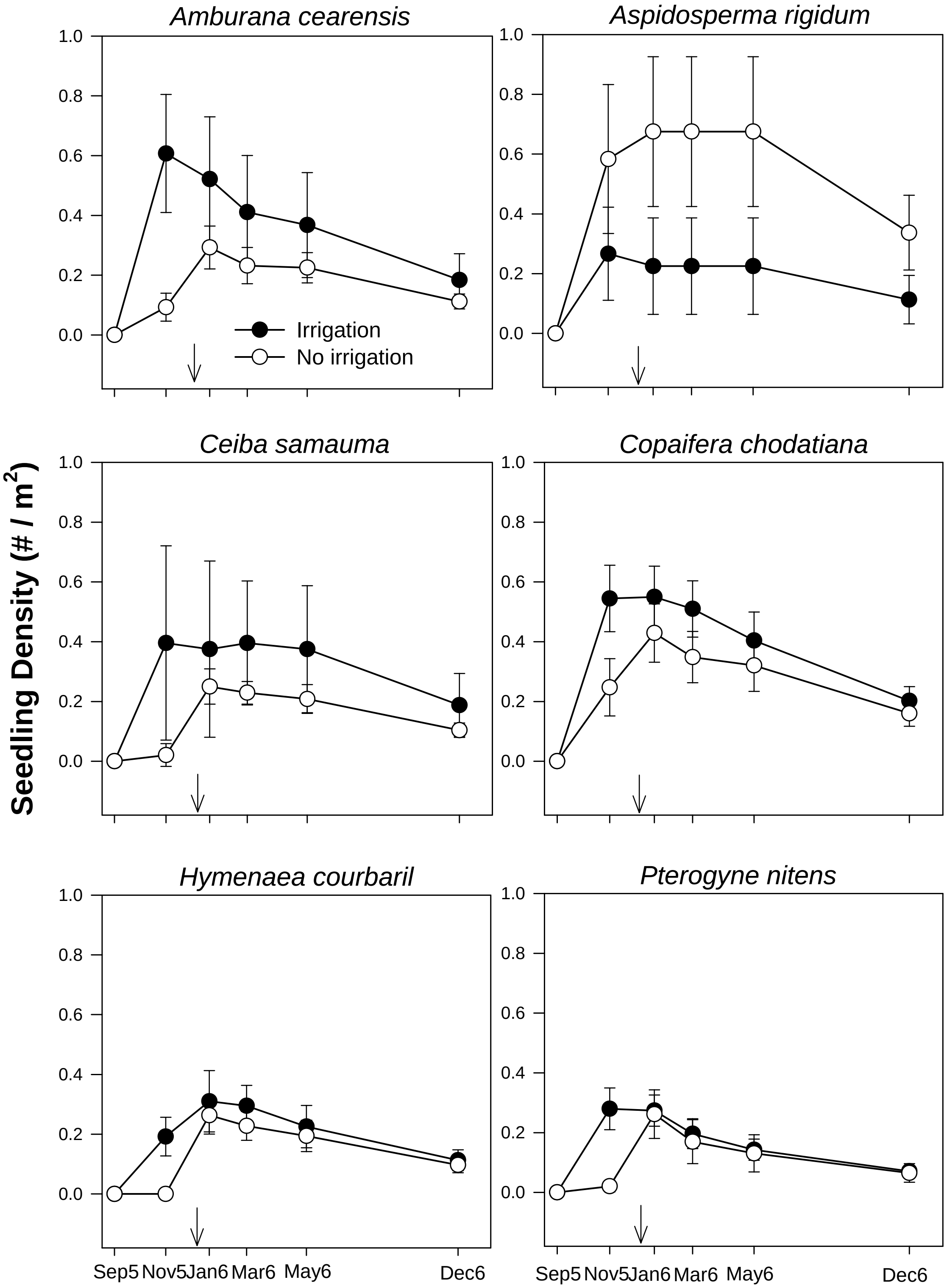

Figure 2-8. Mean of seedling densities (± 1SE) in irrigated and droughted experimental plots. Note differences in y-axis scales. Arrows indicate the time when I stopped the irrigation and shielding plants from rainfall.

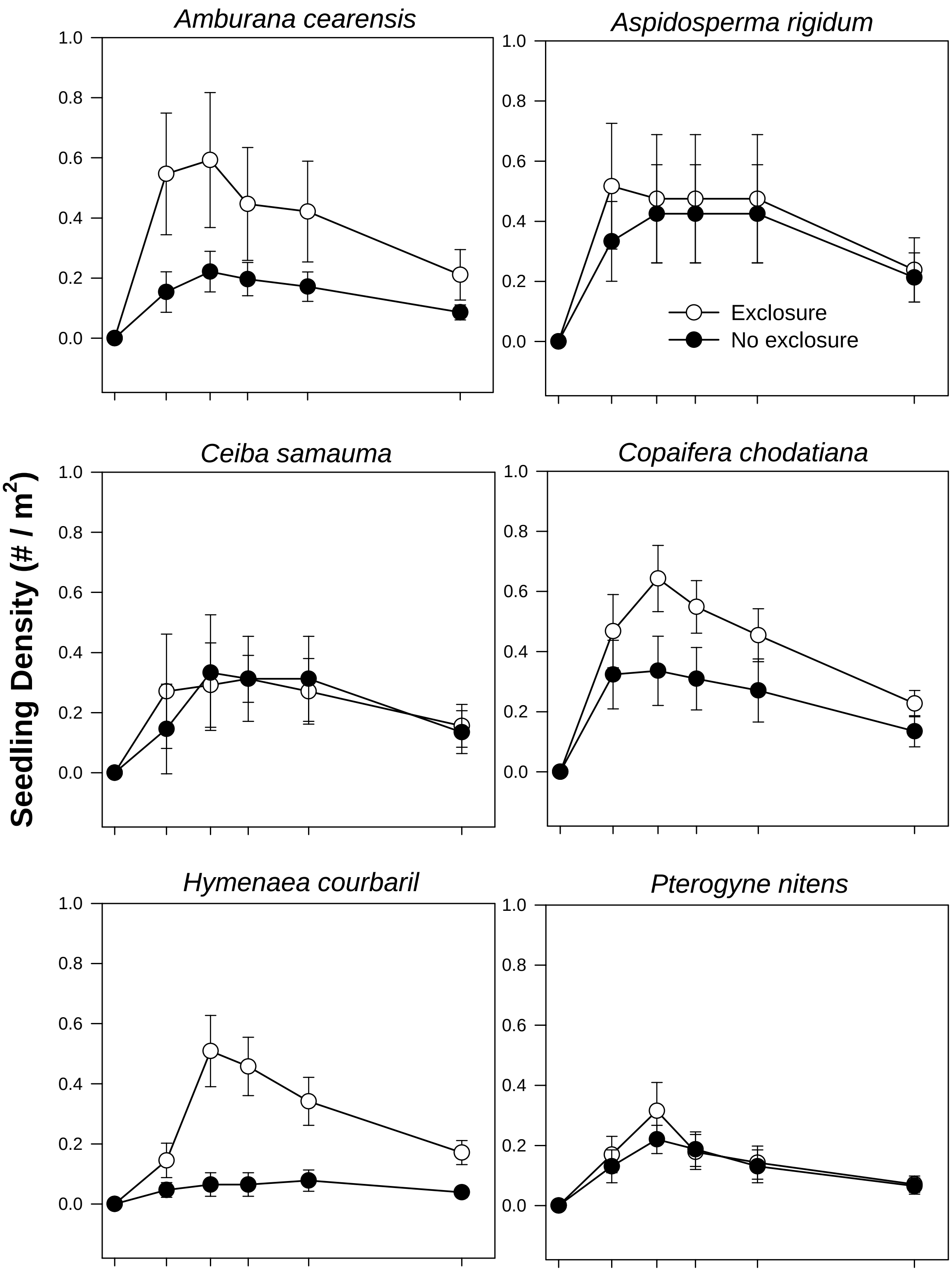

Figure 2-9. Mean seedling densities (±1 SE) in control plots (closed dots) and in plots from which mammals were excluded (open dots).

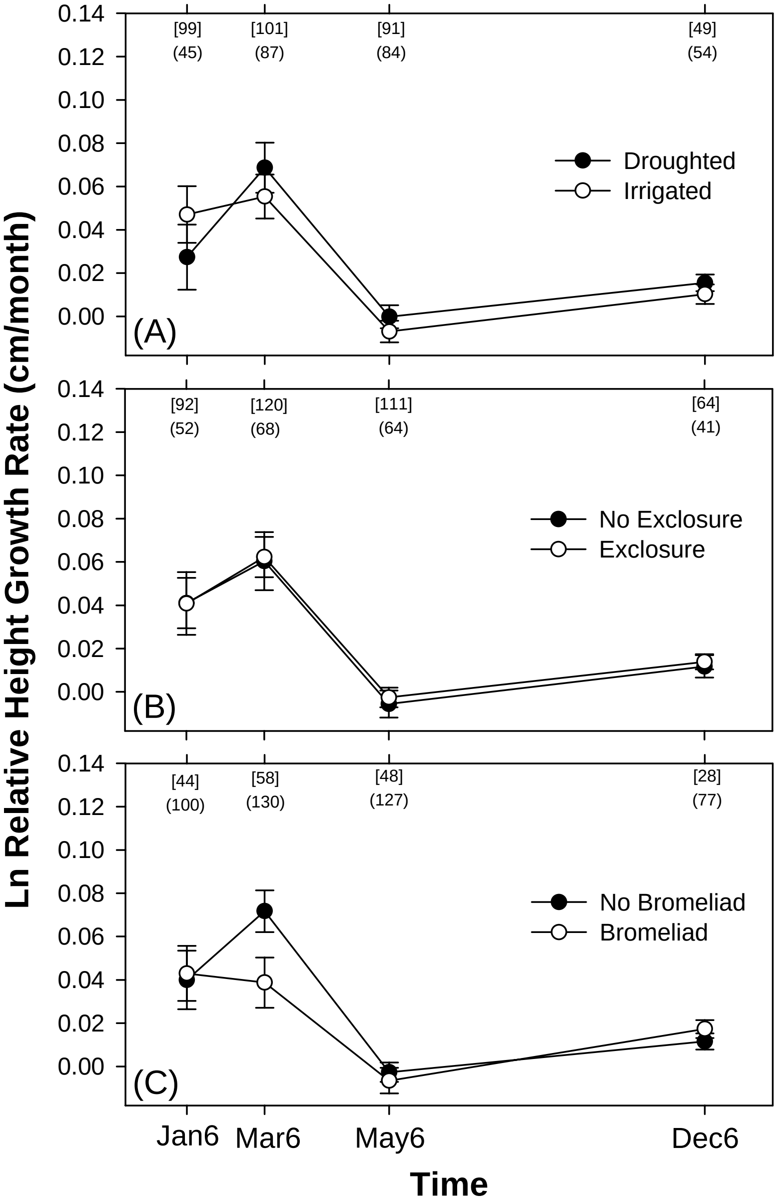

Figure 2-10. Mean relative growth height growth rates (± 1SE) of seedlings of commercial tree species in response to three experimental treatments: (A) irrigation or drought; (B) mammalian seed predator exclusion; and, (C) bromeliad cover. Numbers indicate the number of seedlings used for each evaluation; numbers in brackets are the seedlings in irrigated, exclosure, or bromeliad-cover plots while numbers in parenthesis are for droughted, non-exclosure, and no-bromeliad plots. There were no significant differences between treatments for each time calculated with t-test at the 95% confidence level with sequential Bonferroni corrections (repeated-measures ANOVA was not suitable because sample sizes declined over the study period due to seedling mortality).

CHAPTER 3
CONTRIBUTION OF ROOT AND STUMP SPROUTS TO NATURAL REGENERATION IN A LOGGED TROPICAL DRY FOREST IN BOLIVIA

Introduction

Securing sufficient natural regeneration of commercial tree species after logging is critical for sustainable forest management. Most studies of tropical forest regeneration focus on tree recruitment from seeds and, consequently, regeneration is often viewed as depending on seed production, seed dispersal, seed viability, and the environmental requirements for seed germination and seedling establishment (Holl 1999, Dalling and Hubbell 2002, De Steven and Wright 2002). In tropical dry forests, many tree species produce abundant and well-dispersed seeds with high viability, but due to seed predation (Janzen 1971), water stress (Gerhardt 1994), and a multitude of other factors, successful recruitment from seed is rare for many species in these forests (Mostacedo and Fredericksen 1999). Furthermore, in forests in general and in dry forests in particular, tree seedlings that do become established often grow more slowly than sprouts (Miller and Kauffman 1998, Khurana and Singh 2001).

Given the limitations on seed dispersal and germination, as well as on seedling establishment and survival, successful dry forest regeneration after logging, severe windstorms, or fires may depend greatly on contributions from stump and root sprouts (Kruger et al. 1997, Kammesheidt 1998, Miller and Kauffman 1998, Gould et al. 2002, Homma et al. 2003). The general capacity of dry forest tree species to sprout may be an adaptive response to a history of fire (e.g., Bond and Midgley 1995) or other disturbances. Whatever the ultimate cause, in a variety of seasonal tropical forests, logging reportedly stimulates abundant stump sprouting of felled and broken trees, and root sprouting from superficial roots damaged by heavy equipment (Kauffman 1991, Kammesheidt 1998, Miller and Kauffman 1998, Kammesheidt 1999, Bell

2001). In the Chiquitano dry forest in Bolivia, although sprouting has been reported few times following logging (Fredericksen et al. 2000) and fires (Gould et al. 2002, Kennard and Putz 2005), little is known about the overall contributions of sprout-origin plants to forest recovery. Whereas interspecific comparisons of sprouting ability are numerous for Mediterranean ecosystems (Bellingham 2000, Pausas 2001), how this ability varies with light requirements and other ecological attributes is less clear for tropical dry forest species (but see Paciorek et al. 2000 for resprouting across the spectrum of shade tolerance of trees on Barro Colorado Island). Sprouting is of interest to forest managers and ecologists because sprouts often have more rapid grow rates than true seedlings (Daniel et al. 1979, Clark and Hallgren 2003).

The purpose of this study was to examine the contribution of sprouts to the natural regeneration of a tropical dry forest following logging. More specifically, I (1) characterized stump and root sprouting features of the commercial canopy tree species. I (2) quantified the effect of logging on relative abundances and growth rates of stump sprouts, root sprouts, and true seedlings. I (3) related the species-specific probabilities of stump sprouting as a function of stump diameter and stump height; and I (4) explored how sprouting varies with the ecological requirements of canopy tree species.

Methods

Study Area

This study was conducted on the property of INPA Parket (hereafter INPA), a 30,000-ha tract of privately-owned seasonally dry tropical forest 30 km NE of the town of Concepción (16° 6' 45"S, 61° 42' 47"), 250 km northeast of the city of Santa Cruz de la Sierra, Bolivia (Figure 1-1). The study area is flat to gently sloping, with an altitude of approximately 380 m, mean annual temperature of 24.3 °C, and mean annual precipitation of 1100 mm. During the 5-mo dry season (May-October), most trees are deciduous and many tree species flower and fruit following rain events in the mid- to late-dry season. The forest canopy is 20-25 m tall with common species including *Acosmium cardenasii*, *Tabebuia impetiginosa*, *Anadenanthera macrocarpa*, *Astronium urundeuva*, and *Centrolobium microchaete* (Pinard et al. 1999); after first mention, species will be referred to by their generic names (for full names see Table 3-1). Currently, 21 tree species, including those mentioned above, are harvested for timber processed mostly into parquet flooring.

During the rainy season, canopy openness, as measured 1 m above the ground with a spherical densiometer, was 8% and 14% in control and logged areas, respectively. During the dry season, canopy openness triples because many tree species are deciduous. The understory is dense, partially due to the abundance of lianas, and typically 30-40% of the ground is covered by the bromeliad, *Pseudananas sagenarius*.

Experimental Design and Data Collection

Stump sprouts

I sampled sprouts from the stumps of harvested trees in three areas that varied in time since logging. The first area (50 ha) was selectively logged by INPA Parket (≈ 4 trees/ha and 4 m^3/ha, and 10-12 species harvested) 1 y before I began my study. Here I mapped, marked, and measured the diameters and heights of the stumps and all stump sprouts of the five most commonly harvested tress (*Anadenanthera*, *Centrolobium*, *Copaifera chodatiana*, *Tabebuia*, and *Zeyheria tuberculosa*; tree densities reported in Table 2-1) and monitored sprout survival and height growth for one year. The second study area (40 ha) is located in the 20-ha permanent plots maintained by the Instituto Boliviano de Investigación Forestal (IBIF) for monitoring forest dynamics after logging. Two years prior to my study, 4-8 trees/ha (5.3-6.4 m^3/ha, 14 species) were logged from these plots. I monitored sprouting as described above. The third area (30 ha) was logged (2-3 trees/ha, ≈3 m^3/ha, and 5-7 species harvested) 5 y before my study. I measured the frequency and height of stump sprouts of six tree species (*Anadenanthera*, *Caesalpinia*, *Centrolobium*, *Copaifera*, *M. scleroxylon*, and *Tabebuia*) in this area, using a 7 m telescoping measuring rod.

In 2003 I checked for sprouts on the stumps of trees harvested in 1998 (6 species), 2001(10 species), and 2002 (6 species). The 498 stumps evaluated in the three areas were from trees $\geq$ 40 cm DBH that were felled with chainsaws 10-90 cm height above ground. Each species was placed in one of the following four ecological guilds based on field observations and the literature (Whitmore 1998, Mostacedo and Fredericksen 1999, Poorter et al. 2006): light-demanding pioneers have light requirements and are short-lived; long-lived pioneers also are light-demanding but are longer lived; somewhat shade tolerant species establish in the shade but only mature under moderate to high light intensities; and, shade-tolerant species can establish and survive in the shade. I counted all sprouts and measured the heights of the two tallest on each stump (from the point of origin) as well as the height and diameter of each stump dating from the 2001 and 2002 harvests.

Comparison of different juvenile types in relation to microsites created by logging

In two of IBIF's 20-ha experiment plots, I compared the densities and sizes of seedlings and sprouts < 2 m tall in the following microsites created by an episode of selective logging that occurred 1.5 years prior to my study: logging gaps (280-330 m^2, N = 16); logging roads (N = 16); log landings (N = 8); primary skid trails (N = 16); and, secondary skid trails (N = 16). Secondary skid trails were those used to extract a single log, while primary skid trails were those where skidder had extracted $\geq$ 2 logs. In each microsite, all plants < 2 m tall of 16 canopy tree species in 10 x 4 m plots were classified as having developed directly from a germinated seed or sprouted from a root or stem; determination of plant origin often involved excavation, but was generally unambiguous.

Data Analysis

I used logistic regression to determine the probability of a stump sprouting in relation to its diameter and height for each the five species that sprouted frequently (*Anadenanthera, Centrolobium, Copaifera, Tabebuia,* and *Zeyheria*). Nagelkerke R-square values were used to determine the percentage of variance explained by each regression and a Hosmer and Lemeshow X^2 goodness-of-fit tests was used to determine the significance of each relationship (Field 2000).

To determine whether there are relationships between stump diameter and height (independent variables) with the number and maximum heights of sprouts (response variables), I used linear regressions or nonlinear regression analyses based on linear, quadratic, cubic, and inverse models. For each species, the simplest (i.e., fewest parameters) model with a high R^2 value was selected in which each parameter had a reasonable biological explanation.

Analyses of variance (ANOVAs) followed by Tukey's post-hoc comparisons were used to compare densities of seedlings and root or stem sprouts among logged microsites. Absolute relative annual height growth rates of stump sprouts were calculated for 10 species based on their height 2 y after logging, and heights after 1, 2, and 5 y after logging for 6 species. Stump sprout heights were compared among ecological guilds using ANOVAs and Tukey's post-hoc tests. For each species and ecological guild, an ANOVA and then Tukey's post-hoc comparison were used to compare mean growth among origin types (i.e., stump sprout, root sprout, or true seedling). All analyses were carried out with SPSS 12.0 for Windows.

Results

Sprout Characterization.

Stump sprouting was common after logging in the dry forest studied; 27 of the 31 species monitored at least occasionally reprouted from stumps; 62% did so frequently (Table 3-1). *Centrolobium*, *Zeyheria*, and *Tabebuia* were the most frequent stump sprouters (Figure 3-1).

Among the six commercial tree species monitored, the proportion of stumps with living sprouts decreased with time since logging (Figure 3-2). Overall, for stumps censused 1, 2, and 5 years after logging the proportion of stumps with live sprouts was 55%, 43%, and 38%, respectively, but the rate of stump sprout mortality varied by species. In particular, 80% of the *Caesalpinia* stumps and 73% of the *Centrolobium* stumps had live sprouts 5 y after the trees were felled. Whereas high proportions of *Anadenanthera* and *Copaifera* stumps initially sprouted (23 and 13%, respectively), neither species had living stump sprouts in the plot logged 5 y prior to my study.

Root sprouting was also common after logging in the tropical dry forest of INPA. Of the 31 tree species monitored (Table 3-1), 16 sprouted from lateral roots, 7 species at high frequencies. *Acosmium cardenasii*, *Centrolobium*, and *Casearia gossypiosperma* were the most frequent root sprouters.

Most of the 27 species that frequently sprouted from roots or stumps were shade tolerant (9) or at least partially shade-tolerant (8). Light-demanding pioneer species sprouted infrequently, if at all (e.g., *Astronium*, *Piptadenia viridifolia*, *Acacia bonariensis,* and *Schinopsis brasiliensis*). The most frequent sprouters were the long-lived pioneer species, *Centrolobium* and *Tabebuia*, and the partial shade-tolerant species, *Zeyheria* (Table 3-1).

Caesalpinia pluviosa had the higher (20.0±4.4) number of sprouts per stump, followed by *Centrolobium* (15.4±1.47) and *Zeyheria* (14.2±1.5). The other four of the seven species monitored had < 5 sprouts/stump (SE=0.5), with the absolute lowest numbers observed in *Copaifera* and *Anadenanthera* (Figure 3-3)

Considering all sprouted stumps, there was a significant negative linear relationship between the number of sprouts per stump and stump diameter (Table 3-2). In contrast, when species were considered separately, the only species that showed a significant (quadratic) relationship between number of sprouts and stump diameter was *Copaifera,* and that relationship was positive (i.e., opposite from the overall trend). For all species considered together, there was a negative linear relationship between the number of sprouts and stump height, but the relationship varied among species. The number of *Caesalpinia* sprouts increased with stump height whereas in *Centrolobium* and *Tabebuia*, the relationship was negative (Table 3-2).

Sprout height growth, based on measures of the tallest stump sprouts 1-5 y after the trees were cut, generally decreased with stump diameter, but species varied in this relationship. Only 3 of the 7 species for which I have sufficient data showed significant trends: *Caesalpinia* showed a positive cubic relationship; in *Machaerium* the relationship was inverse positive; and, *Copaifera* had a quadratic and positive relationship (Table 3-2). Sprout height growth rates decreased with stump height when all of the species were considered together. In contrast, at the species level, only *Caesalpinia* and *Machaerium* showed significant relationships between sprout growth rates and stump height, but in the former the relationship was negative and quadratic and the latter, positive and inverse (Table 3-2).

The probability of stump sprouting as related to stump diameter varied among species (Figure 3-3). In *Copaifera*, *Anadenanthera*, *Tabebuia*, and *Centrolobium,* the proportions of sprouted stumps were approximately 0.17, 0.24, 0.57, and 0.97, respectively, and did not vary with stump diameter. In *Zeyheria*, sprouting reached 98% of the stumps 38-40 cm diameter but decreased to only 40% among stumps 90 cm in diameter (Figure 3-4).

The probability of sprouting in relation to stump height also varied among species Figure 3-5). The proportions of sprouted stumps of *Copaifera*, *Anandenanthera,* and *Centrolobium* did not vary with stump diameter. In contrast, a *Tabebuia* stump 10 cm tall was almost certain to sprout (0.98) whereas this probability declined to 0.13 for a 72 cm tall stump. In *Zeyheria*, the probability of sprouting was high (0.91) and did not vary with stump height (Figure 3-5).

Juvenile Types and the Effects of Logging

In the plots censused 1.5 years after logging, 45% of juveniles < 2 m tall of canopy tree species were root and stem sprouts, not true seedlings (Figure 3-6). At the species level there was great variation in the proportions of true seedlings (Figure 3-7). All 15 species evaluated were represented by some sprouts and sprouted at least occasionally from roots whereas only 9 species were represented by stem sprouts. Three species sprouted predominantly from roots whereas stem sprouting was the predominant mode of regeneration in only one species. Light-demanding species tended to regenerate more from seeds and root sprouts than from stem sprouts (F=12.10, P=<0.0001), while partially shade tolerant and shade tolerant regenerated more from seeds (F=4.46, P=0.01; F=8.01, P=0.0004; respectively).

Densities of plants < 2 m tall of canopy tree species did not vary among the logging microsites (F = 1.37, P = 0.24), but microsites differed in the relative contributions of true seedlings and sprouts (Table 3-3). True seedlings were twice as abundant as root and stem sprouts combined in logging gaps (F = 9.91, P = 0.0001). In contrast, there was no difference in plant density by origin in logging roads (F = 0.38, P = 0.68). Densities of plants from root sprouts and true seedlings were similar in log landings (F = 1.95, P = 0.18). On primary skid trails most plants <2 m tall were true seedlings, with fewer root sprouts, and almost no stem sprouts (F = 13.57, P < 0.0001). On secondary skid trails, true seedlings were much more common than plants of either sprout type (F = 4.6, P = 0.01).

Growth of Stump Sprouts

Based on measures of the tallest sprout per stump, the growth rates of stump sprouts varied among species by more than an order of magnitude (Figure 3-8). *Anadenanthera* (197 cm/y), *Centrolobium* (195 cm/y) and *Zeyheria* (185 cm/y) had the highest growth rates, while *Aspidosperma* (3.5 cm/y) and *Copaifera* (25 cm/y) had the lowest. Stump sprouts of light-demanding pioneer species grew faster than those of shade-tolerant species, but there was a great deal of within species variation, especially in the growth rates of the latter (Table 3-4). Stump sprouts of long-lived pioneer species grew at about the same rates as shade tolerant species.

Among individuals of canopy tree species < 2 m tall, root and stem sprouts both grew faster than seedlings and in 5 of 12 species monitored, root sprouts grew faster than stem sprouts (Table 3-5). *Centrolobium* and *Chorisia speciosa* had the highest root sprout growth rates. I found no *Anadenanthera*, *Aspidosperma*, *Casearia arborea*, *M. scleroxylon*, *Phyllostylon rhamnoides,* or *Piptadenia* stem sprouts (Table 3-5). Among the root sprouters, light-demanding and long-lived pioneer species grew faster than partially shade tolerant and shade tolerant species. Among the stem sprouters and true seedlings, shade-tolerant species grew slower than belonging to other light-syndrome classes (Table 3-6).

Stump sprout heights varied over time and among the six species censused 1, 2, and 5 y after logging (Figure 3-9). Apparent absolute growth rates (cm/y) increased through the second year and then height increments stopped except in *Centrolobium*, which continued to grow at a rapid rate through the fifth year. *Anadenanthera* sprouts were apparently growing rapidly through the second year, but I could find no live stumps in the plot logged 5 y prior to my census.

Discussion

Of the 31 canopy tree species studied in a dry tropical forest in Bolivia, 27 (87%) have some capacity to sprout from either roots or stumps. Sprouting is apparently characteristic of many tropical dry forest tree species and helps them persist in an environment where stress is severe and disturbances are frequent (Bellingham 2000, Bond and Midgley 2001). As observed in the USA (Jones and Raynal 1988) and Mexico (Dickinson 1998), root sprouting was promoted by logging damage to roots in my study species. The high proportion of species that sprouted from broken and cut stems in INPA may be related to the high frequency with which stems lose their terminal buds due to herbivore browsing during the dry season when other browse is scarce as well as to the direct effects of drought stress (Bossard and Rejmanek 1994, Del Tredici 2001, Groll 2005).

Natural Regeneration and Shade Tolerance: True Seedlings vs. Sprouts

Scarcity of natural regeneration from seeds is common for most tree species in tropical dry forest in Bolivia (Mostacedo and Fredericksen 1999). The main reasons for this scarcity appear to be high seed predation, low seed viability, and high seedling mortality during the dry season. Sprouting from broken and cut stems, along with root sprouting, appears to be a very important regeneration mechanisms in tropical dry forests in Brazil (Castellani and Stubblebine 1993), Jamaica (Bellingham et al. 1994), and Venezuela and Paraguay (Kammesheidt 1999), including the forest I studied in Bolivia where 45% of the regeneration of canopy trees originated from root or stem sprouts.

Sprouting is a common mode of tree regeneration in forests around the world. For example in oak forests in the USA (Clark and Hallgren 2003, Nyland et al. 2006) and in boreal forest in Russia (Homma et al. 2003), trees reportedly regenerate mainly from sprouts. Sprouting seems to represent the predominant mode of regeneration in forests frequently subjected to logging, wind damage, and fire (Bond and Midgley 2001).

Natural regeneration by sprouting from lateral roots was common in some commercial species in my study site. In particular, *Centrolobium*, *Tabebuia*, *Aspidosperma*, and *M. scleroxylon* regenerated mostly from root sprouts. *Centrolobium* was previously reported as a root sprouting species (Fredericksen et al. 2000), but the importance of this mode of regeneration in the other species has apparently been overlooked. It remains to be seen whether root sprouts mature into sound trees, and there are reasons to suspect that they will not. First of all, given that most new stems emerge from damaged stems or roots, sprouts of all sorts seem particularly prone to butt and root rots. Second, I observed that several *Centrolobium* root sprouts that were 5-8 cm DBH 5 y after sprouting still had not developed their own root systems. Those that I excavated emerged from large diameter roots running about 5 cm below the soil surface but had developed almost no roots of their own and were thus mechanically unstable when pushed perpendicular to the orientation of the source root. Given the general importance of root sprouting after fires, logging, and other severe disturbances, such as found in tropical dry forest in Paraguay and moist semi-deciduous forest in Venezuela (Kammesheidt 1999), root sprout longevity is an issue that deserves more attention from researchers.

Partially shade-tolerant and shade-tolerant species were more likely to sprout than light-demanding species. Most of the partially shade-tolerant species in INPA sprouted from either roots or stems; similar findings were reported for a moist but seasonal tropical forest in Panama (Paciorek et al. 2000). In contrast, in a moist tropical forest but after slash-and-burn agriculture of eastern Paraguay, light-demanding species contributed more sprouts than shade-tolerant species (Kammesheidt 1998). Although some light-demanding species in INPA did not sprout (13%), others stump sprouted frequently, such as species in the Bombacaceae and Flacourtiaceae. Furthermore, the light-demanding pioneer species that did sprout grew faster than sprouts from other ecological groups.

Allometric Relationships with Stump Sprouting

The weak and inconsistent trends in the relationship between either stump diameter or stump height and the growth rates or number of sprouts per stump means that I have little basis on which to make firm recommendations for sprout management. Consistent patterns in sprout responses are also not apparent in the literature. Whereas several studies mention that in the first years after tree cutting there is a positive relationship between stump diameter and sprout growth rates (Jobidon 1997), other studies report the opposite (Trani et al. 2005), and generally the relationship does not remain significant after a few years. These results suggest that factors other than stump size controls sprouting (McConnaughay et al. 1996, Masri et al. 1998).

The probability of sprouting varied substantially among species but I observed no effect of stump diameter on the probability of sprouting in four of the five species studied. For example, *Centrolobium* had the highest probability of stump sprouting (97%), while *Copaifera* had the lowest (17%). In contrast, *Zeyheria* showed a decreasing probability of stump sprouting with increasing stump diameter, a pattern also observed in a wetter but still seasonal tropical lowland forest in Panama (Putz and Brokaw 1989) and in an oak forest in southern Indiana (Weigel and Peng 2002). The probability of stump sprouting did not vary either with stump height except in *Tabebuia*, in which the probability decreased with stump height. These results suggest that harvesting trees of any tree size will promote same probability of sprouting, except for *Zeyheria* in which it is better to cut smaller trees and in *Tabebuia* in which low stumps are preferred if sprouting is to be encouraged.

Growth of Stem and Root Sprouts Compared with True Seedlings

One advantage of natural regeneration via sprouting is that sprouts typically grow more rapidly than true seedlings, at least initially (Gould et al. 2002, Kennard et al. 2002), which was confirmed by this study. I also observed that small plants of sprout origin typically appeared less affected by drought than true seedlings (Personal Observation). Nevertheless, in my study forest as well as in Australia (Enright and Goldblum 1999) and South Africa (Kruger et al. 1997), true seedlings of some species grew just as fast as sprouts. In several species, especially light-demanding pioneers (e.g., *Cordia*, *Casearia*), height growth rates were similar between true seedlings and root or stem sprouts.

Conclusions

Due to the high costs and frequent failures of seed and seedling planting, natural regeneration is critical for the sustainable management of tropical dry forest tree species in Bolivia. Given that so many tree species sprout prolifically from stumps of all sizes or from lateral roots, especially after mechanical damage, sprouts need to be considered as a source of regeneration. The abundance of sprouts and their typically rapid growth rates, when compared with those of true seedlings, adds to the potential value of sprouts for forest management. In forests not designated for timber stand management, sprouts deserve at least as much attention from researchers as seeds and true seedlings. That said, future studies should consider the long-term fates of sprouts. The observation in this study that the stump sprouts of most species essentially stopped growing after 2 y needs to be verified and otherwise explored, as do the factors that cause high rates of mortality of the sprouted stumps of some species. In the case of root sprouts, which were also abundant in my study area, long-term monitoring is needed to determine whether they ever grow up to be sound, canopy trees.

Table 3-1. Frequency of root and stem sprouting and shade tolerance of commercial and non-commercial canopy tree species in a tropical dry forest in Bolivia. Shade tolerance is base on Pinard et al. (1999), and Mostacedo and Fredericksen (1999): L=Light-demanding pioneer, LL=Long-lived pioneer, PS=Partially shade tolerant, ST=Shade tolerant.

Species	Abbreviation	Family	Resprout Type/ Frequency		Shade Tolerance
			ROOT	STEM	
Commercial Timber Species					
Amburana cearensis (Allemão) A.C. Sm.	AMCE	Caesalpinaceae	No	Yes/Low	PS
Anadenanthera macrocarpa (Benth.) Brenan	ANMA	Mimosaceae	No	Yes/Low	L
Aspidosperma rigidum Rusby	ASRI	Apocynaceae	Yes/Low	Yes/High	ST
Astronium urundeuva (Allemão) Engl.	ASUR	Anacardiaceae	No	No	L
Caesalpinia pluviosa DC.	CAPL	Caesalpiniaceae	Yes/Low	Yes/High	PS
Cariniana ianeirensis R. Knuth	CAIA	Lecythidaceae	Yes/Low	Yes/High	LL
Cedrela fissilis Vell.	CEFI	Meliaceae	Yes/Low	Yes/Low	L
Centrolobium microchaete (Mart. ex Benth.) Lima ex G. P. Lewis	CEMI	Fabaceae	Yes/High	Yes/High	L
Copaifera chodatiana Hassl.	COCH	Caesalpiniaceae	Yes/Low	Yes/High	ST
Cordia alliodora (Ruiz & Pav.) Oken	COAL	Boraginaceae	Yes/Low	Yes/Low	L
Hymenaea courbaril L.	HYCO	Caesalpiniaceae	Yes/Low	Yes/Low	PS
Machaerium scleroxylon Tul.	MASC	Fabaceae	Yes/Low	Yes/High	PS
Phyllostylon rhamnoides (J. Poiss.) Taub.	PHRH	Rhamnaceae	No	Yes/High	ST
Platymiscium ulei Harms	PLUL	Fabaceae	No	Yes/High	L
Schinopsis brasiliensis Engl.	SCBR	Anacardiaceae	No	No	L
Sweetia fruticosa Spreng.	SWFR	Fabaceae	No	Yes/Low	PS
Tabebuia impetiginosa (Mart. ex DC.) Standl.	TAIM	Bignoniaceae	Yes/Low	Yes/High	LL
Tabebuia serratifolia (Vahl) G. Nicholson	TASE	Bignoniaceae	Yes/High	Yes/Low	LL
Zeyheria tuberculosa (Vell.) Bureau	ZETU	Bignoniaceae	No	Yes/High	PS
Non-commercial Species					
Acacia bonariensis Gillies ex Hook. & Arn.	ACBO	Mimosaceae	No	No	L
Acosmium cardenasii H.S. Irwin & Arroyo	ACCA	Fabaceae	Yes/High	Yes/High	ST
Aspidosperma cylindrocarpon Müll. Arg.	ASCY	Apocynaceae	Yes/High	Yes/High	LL
Capparis prisca J.F. Macbr.	CAPR	Capparaceae	No	Yes/High	ST
Casearia gossypiosperma Briq.	CAGO	Flacourtiaceae	Yes/High	Yes/High	L
Ceiba samauma (Mart.) K. Schum.	CESA	Bombacaceae	No	Yes/Low	L
Chorisia speciosa A. St.-Hil.	CHSP	Bombacaceae	Yes/High	Yes/High	L
Eriotheca roseorum (Cuatrec.) A. Robyns	ERRO	Bombacaceae	No	Yes/Low	L
Gallesia integrifolia (Spreng.) Harms	GAIN	Phytolacaceae	No	Yes/High	LL
Machaerium acutifolium Vogel	MAAC	Fabaceae	Yes/High	Yes/Low	PS
Piptadenia viridiflora (Kunth) Benth.	PIVI	Mimosaceae	No	No	L
Spondias mombin L.	SPMO	Anacardiaceae	No	Yes/Low	PS

Table 3-2. Summary of the best models and their significances from the regression analyses between stump diameter or stump volume (independent variables) and the heights of stump and numbers of sprouts per stump (dependent variables). Tests were made for species that were sampled with > 8 individuals at alpha = 0.05. Models: L=Linear, Q=Quadratic, C=Cubic, I=Inverse. Signs mean positive (+) or negative (-) relationship between two variables.

Scientific Name	# of sprouts					Height of sprouts			
	Model	R^2	DF	F	P	Model	R^2	F	P
<u>Stump Diameter</u>									
Anadenanthera macrocarpa	L	0.015	36	0.56	0.461	L	0.034	1.27	0.2680
Caesalpinia pluviosa	Q(+)	0.267	18	3.27	0.061	C(+)	0.406	6.16	0.0090
Centrolobium microchaete	L	0.005	90	0.41	0.522	L	0.012	1.09	0.3000
Copaifera chodatiana	Q(-)	0.390	21	6.71	0.006	Q(-)	0.536	12.11	<0.0001
Machaerium scleroxylon	Q	0.365	5	1.44	0.321	I(+)	0.630	10.24	0.0190
Tabebuia impetiginosa	L	0.026	54	1.45	0.234	L	0.010	0.54	0.4660
Zeyheria tuberculosa	L	0.001	62	0.05	0.819	I	0.036	2.33	0.1320
All species	L(-)	0.020	301	5.61	0.020	L(-)	0.040	3.95	0.0400
<u>Stump Height</u>									
Anadenanthera macrocarpa	L	0.01	36	0.49	0.49	L	0.001	0.03	0.87
Caesalpinia pluviosa	L(+)	0.4	19	12.90	0.002	Q(-)	0.32	4.24	0.03
Centrolobium microchaete	I(-)	0.36	90	49.96	<0.0001	I	0.02	2.06	0.16
Copaifera chodatiana	L	0.03	22	0.66	0.42	L	0.02	0.42	0.52
Machaerium scleroxylon	L	0.006	6	0.04	0.85	I(+)	0.62	10.03	0.02
Tabebuia impetiginosa	I(-)	0.34	59	29.82	<0.0001	L	0.02	0.90	0.35
Zeyheria tuberculosa	I	0.03	63	2.06	0.16	L	0.008	0.53	0.47
All Species	L(-)	0.03	311	8.91	0.003	I(-)	0.16	56.6	<0.0001

Table 3-3. Mean (± 1SE) densities of true seedlings, stem sprouts, and root sprouts in 10 x 4 m plots in microsites created during selective logging. Different letters indicate differences between microsites in the densities of plants of different origins using Tukey *post hoc* comparisons with 95% of confidence.

Microsites	Seedling	Stem Sprout	Root Sprout	Mean of Square	F	P
Logging Gaps	78.75 (10.47)^{a}	21.87 (5.18)^{b}	23.44 (8.82)^{b}	11341	9.91	0.0001
Logging Roads	28.43 (11.45)^{a}	8.33 (3.33)^{a}	26.09 (6.80)^{a}	513	0.38	0.68
Landings	34.58 (15.84)^{a}	0.62 (0.62)^{a}	24.64 (7.83)^{a}	1411	1.95	0.18
Primary Skid Trail	50.15 (9.47)^{a}	4.21 (1.87)^{c}	24.06 (4.89)^{b}	8493	13.57	0.0001
Secondary Skid Trail	59.84 (11.49)^{a}	31.41 (10.62)^{b}	19.53 (5.17)^{b}	6866	4.64	0.01

Table 3-4. Mean (± 1SE) of stump sprout height growth rates (cm/year) by ecological groups. Different letters indicate significant differences between ecological groups using Tukey *post hoc* comparisons with 95% confidence.

Ecological Group	N	Mean	Mean Square	F	P
Light-demanding Pioneer	47	194.7 (17.4)[a]	57005.7	5.85	0.001
Long-lived Pioneer	6	84.8 (17.8)[c]			
Partially Shade Tolerant	24	159.5 (12.3)[b]			
Shade Tolerant	4	14.5 (8.8)[c]			

Table 3-5. Means (± 1SE) of stem heights by species that sprouted from stems or roots compared to the heights of seedlings. Different letters indicate significant differences in plant origins within species using Tukey *post hoc* comparisons at the 95% confidence level.

Species	Seedling	Stem Resprout	Root Sprout	Mean Square	F	P
Acosmium cardenasii	18.3(2.3)^{b}	42.4(4.0)^{a}	46.2(3.6)^{a}	28623	27.35	0.0001
Anadenanthera macrocarpa	25.1(1.5)^{b}	-	72.6(10.6)^{a}	11042	19.6	0.0001
Aspidosperma rigidum	30.0	-	55.0(5.68)	568	1.76	0.22
Caesalpinia pluviosa	54.7(16.5)	100.5(29.8)	112.5(29.8)	6770	1.90	0.18
Casearia arborea	125.0(52.0)	-	105.0(90.1)	300	0.037	0.86
Casearia gossypiosperma	102.7(10.9)	100.0(19.5)	78.8(13.8)	1844	0.97	0.39
Centrolobium microchaete	67.8(26.6)^{b}	138.7(39.9)^{a}	154.2(4.8)^{a}	32850	5.15	0.006
Chorisia speciosa	141.2(15.7)	-	125.0(22.2)	352	0.20	0.67
Copaifera chodatiana	31.7(16.6)	61.4(12.9)	33.0(28.8)	961	1.15	0.37
Cordia alliodora	135.0(39.1)	155.0(67.6)	55.0(67.6)	3040	0.66	0.60
Machaerium acutifolium	33.6(2.5)^{b}	59.2(5.3)^{a}	60.7(4.1)^{a}	23291	21.09	0.0001
Machaerium scleroxylon	-	-	70.0(5.0)	-	-	-
Phyllostylon rhamnoides	14.0(2.27)	-	15.0	0.8	0.03	0.86
Piptadenia viridifolia	69.0(6.2)^{b}	-	140.0(19.1)^{a}	54643	12.51	0.001
Sweetia fruticosa	58.0(17.2)	110.0	120.0	2552	1.23	0.36
Tabebuia impetiginosa	44.5(36.8)	90.0(52.0)	116.9(11.4)	10001	1.85	0.17

Table 3-6. Mean (± 1SE) heights of trees ≤ 2 m tall that were root sprouts, stem sprouts, or seedlings grouped by ecological guild. Different letters indicate significant differences between ecological groups using Tukey *post hoc* comparisons at the 95% confidence level.

Origin types	Light-demanding pioneer	Long-lived pioneer	Partially shade tolerant	Shade tolerant	Mean Square	F	P
Root sprout	149.1 (3.9)^{a}	116.9 (10.7)^{b}	64.6 (8.2)^{c}	46.7 (7.3)^{c}	323997	66.8	< 0.0001
Stem sprout	86.4 (13.0)^{ab}	90.0 (34.5)^{a}	64.0 (7.3)^{ab}	43.7 (5.7)^{b}	9593	4.1	0.009
Seedling	44.7 (2.0)^{a}	44.5 (20.1)^{a}	35.9 (2.8)^{a}	18.5 (2.9)^{b}	30298	18.6	< 0.0001

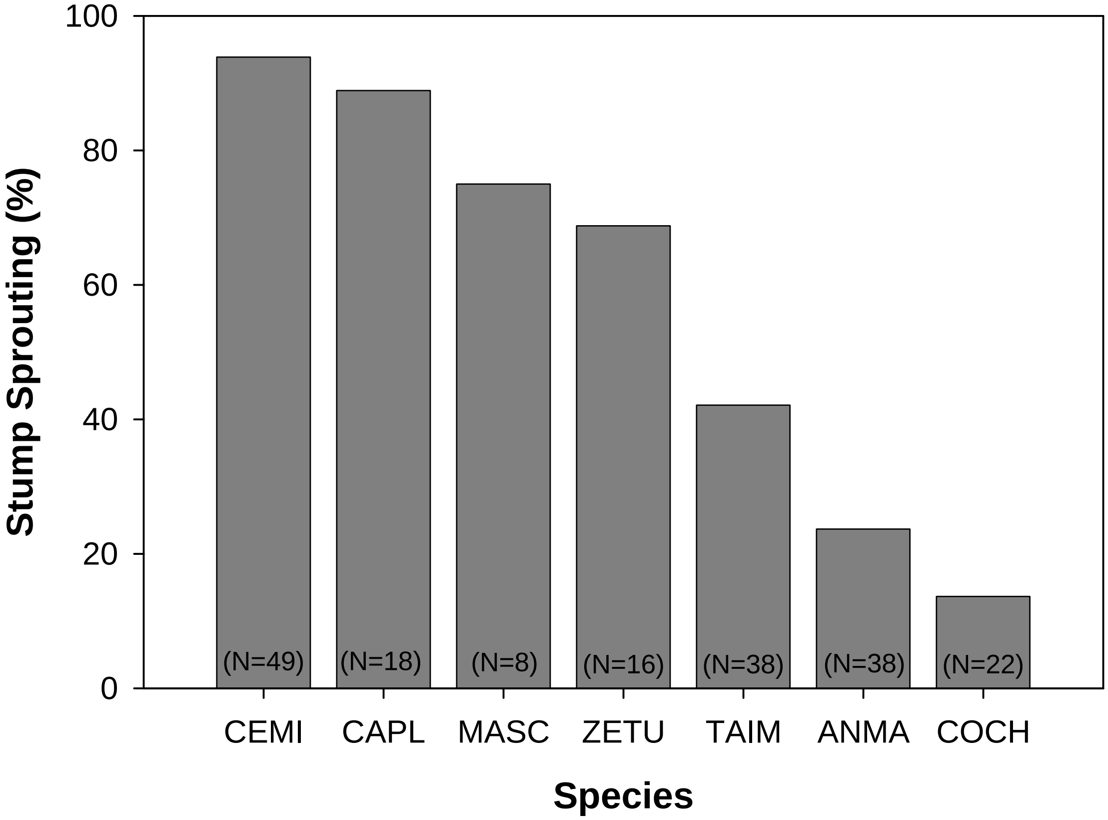

Figure 3-1. Proportions of stumps of commercial timber species that resprouted (number of stumps noted in parenthesis). CEMI = *Centrolobium microchaete*, CAPL = *Caesalpinia pluviosa*, MASC = *Machaerium scleroxylon*, TAIM = *Tabebuia impetiginosa*, ANMA = *Anadenanthera macrocarpa*, COCH = *Copaifera chodatiana*.

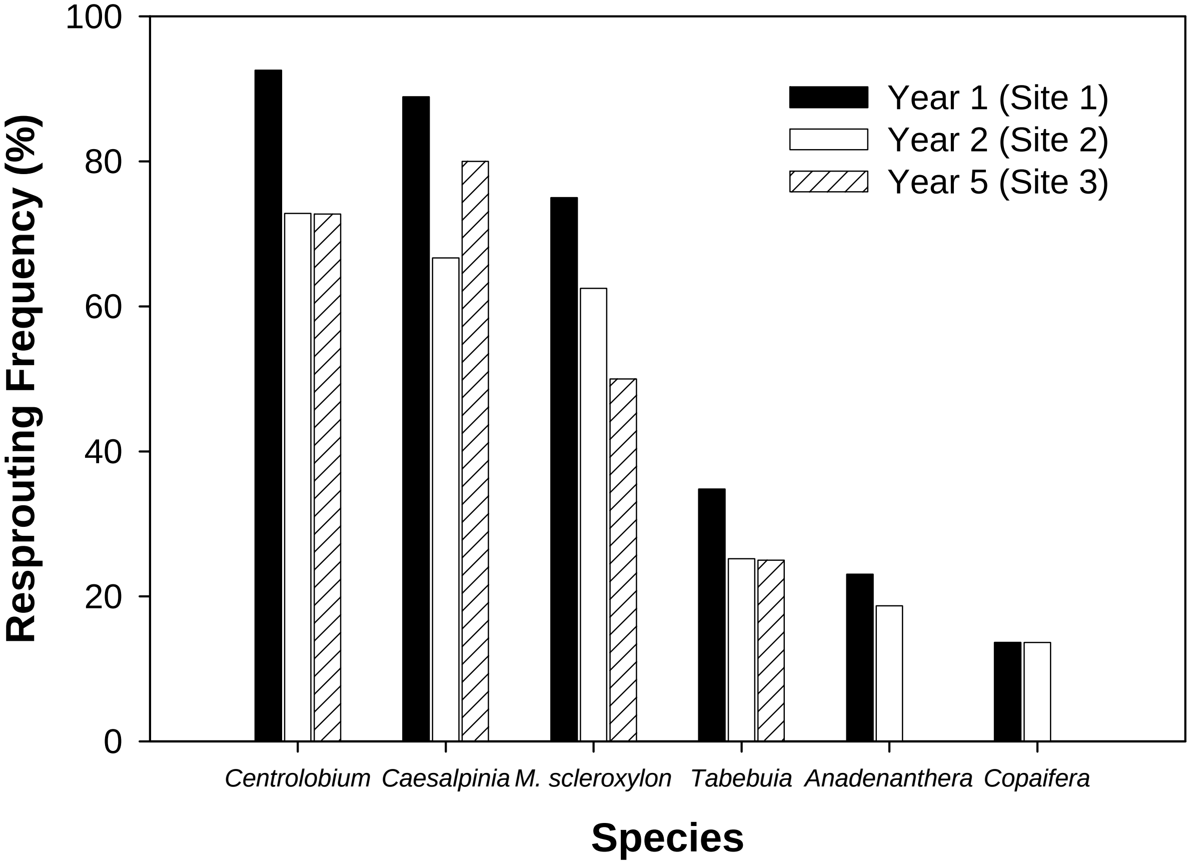

Figure 3-2. The proportions of stumps with live sprouts over time since logging. For complete species names see Table 3-1.

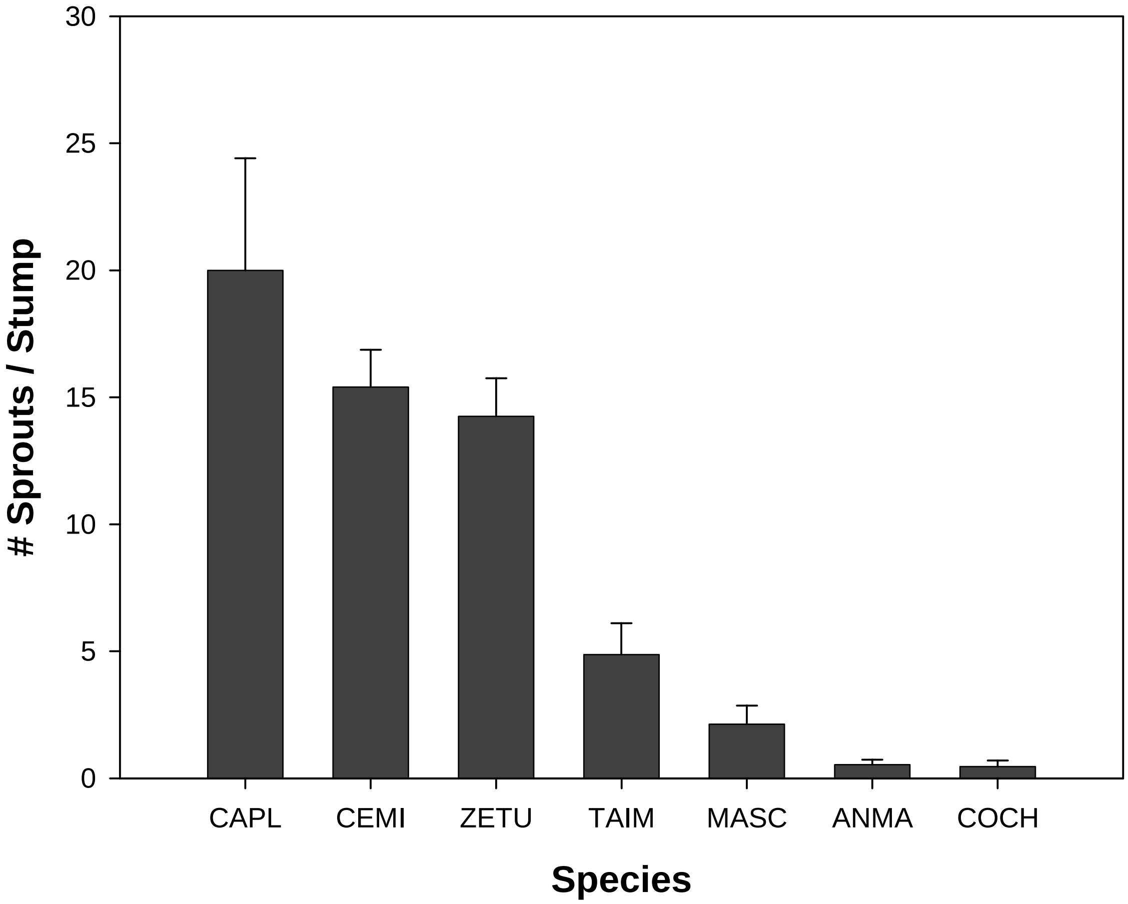

Figure 3-3. Mean (± 1SE) numbers of sprouts/stump for the most frequent sprouting species. CEMI = *Centrolobium microchaete*, CAPL = *Caesalpinia pluviosa*, MASC = *Machaerium scleroxylon*, TAIM = *Tabebuia impetiginosa*, ANMA = *Anadenanthera macrocarpa*, COCH = *Copaifera chodatiana*.

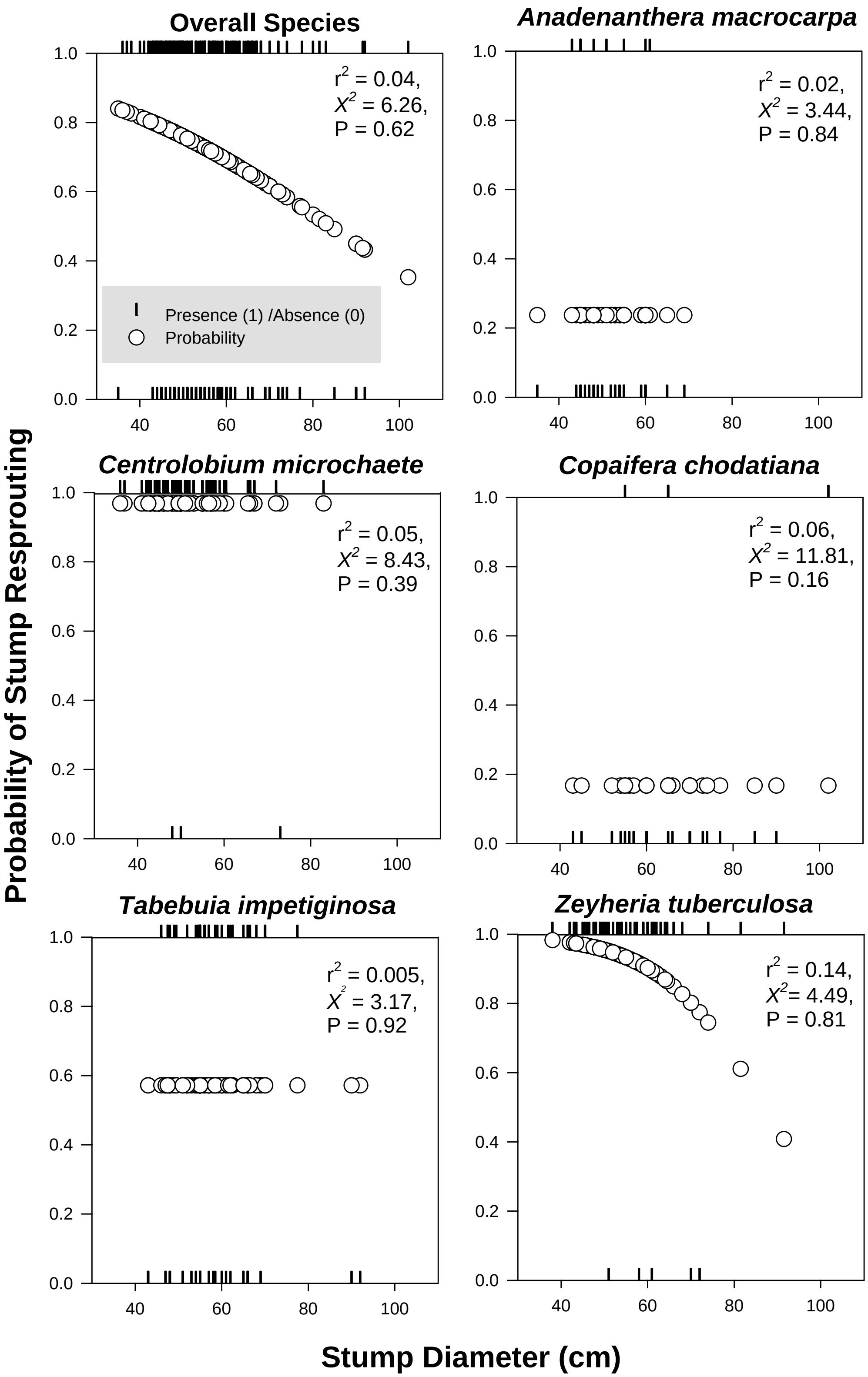

Figure 3-4. Probabilities of stump sprouting as a function of stump diameter for the most frequently sprouting commercial tree species (curves fit by logistic regression).

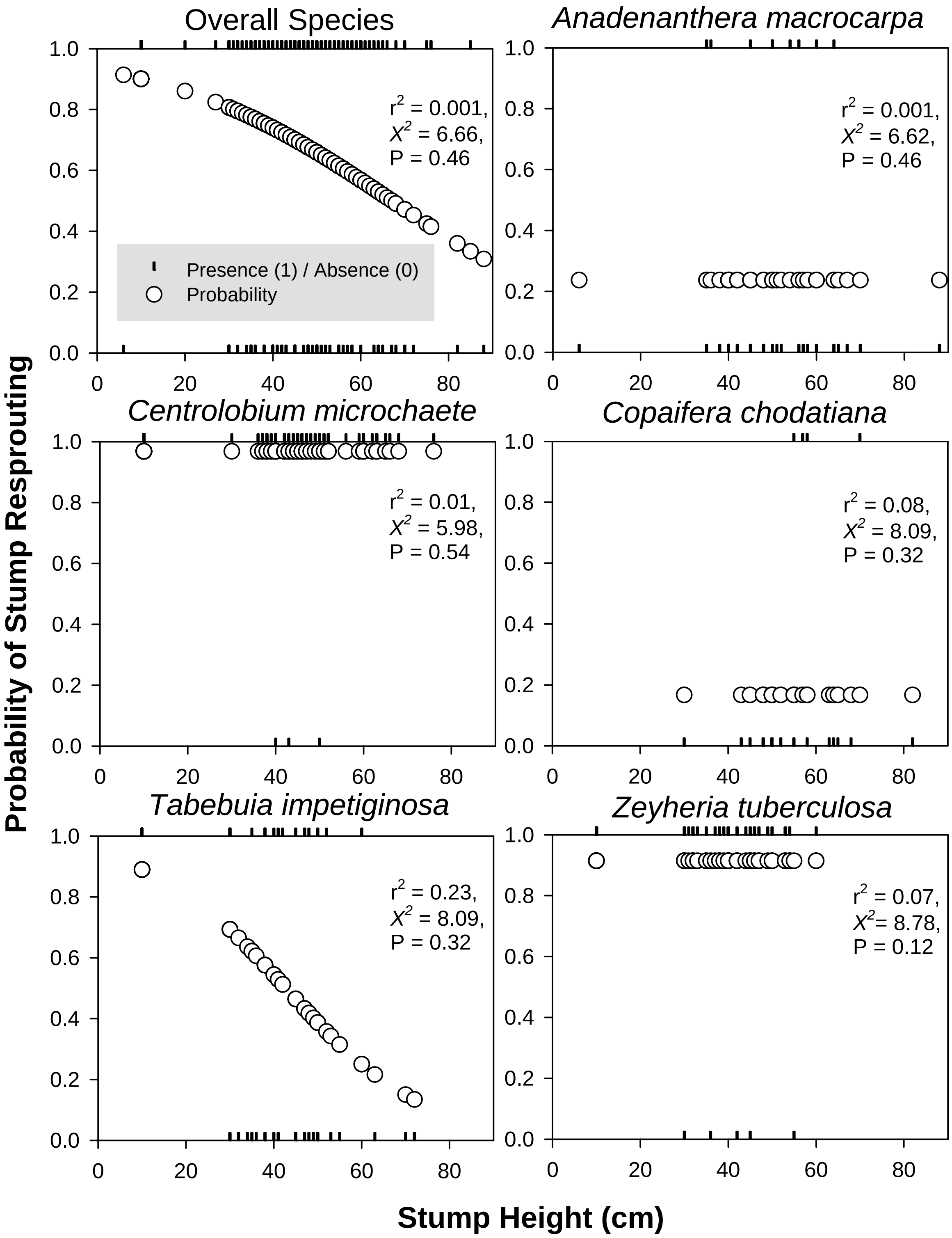

Figure 3-5. Probabilities of stump sprouting as a function of stump height for the commercial tree species that most frequently sprouted (curves fit by logistic regression).

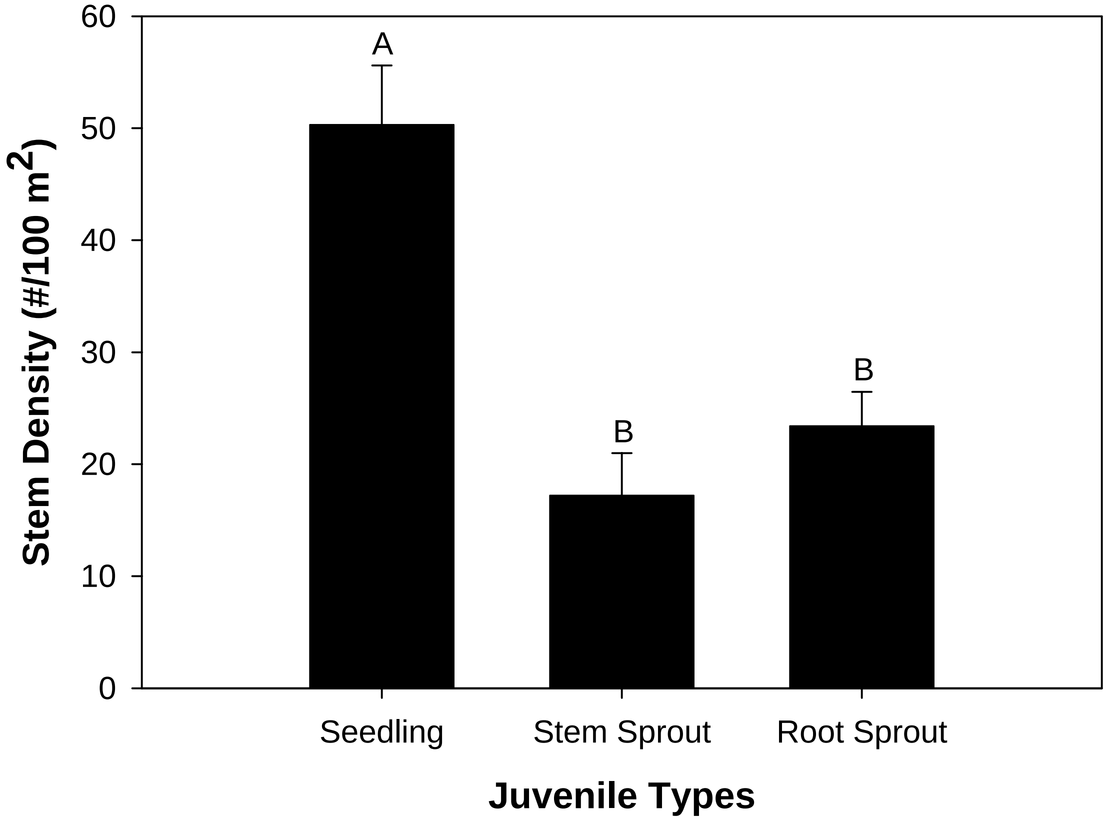

Figure 3-6. Mean (± 1SE) densities of juveniles < 2 m tall of commercial tree species that were true seedlings, stem sprouts, and root sprouts. Different letters indicate significant differences between origin types determined with Tukey *post hoc* comparisons with 95% confidence.

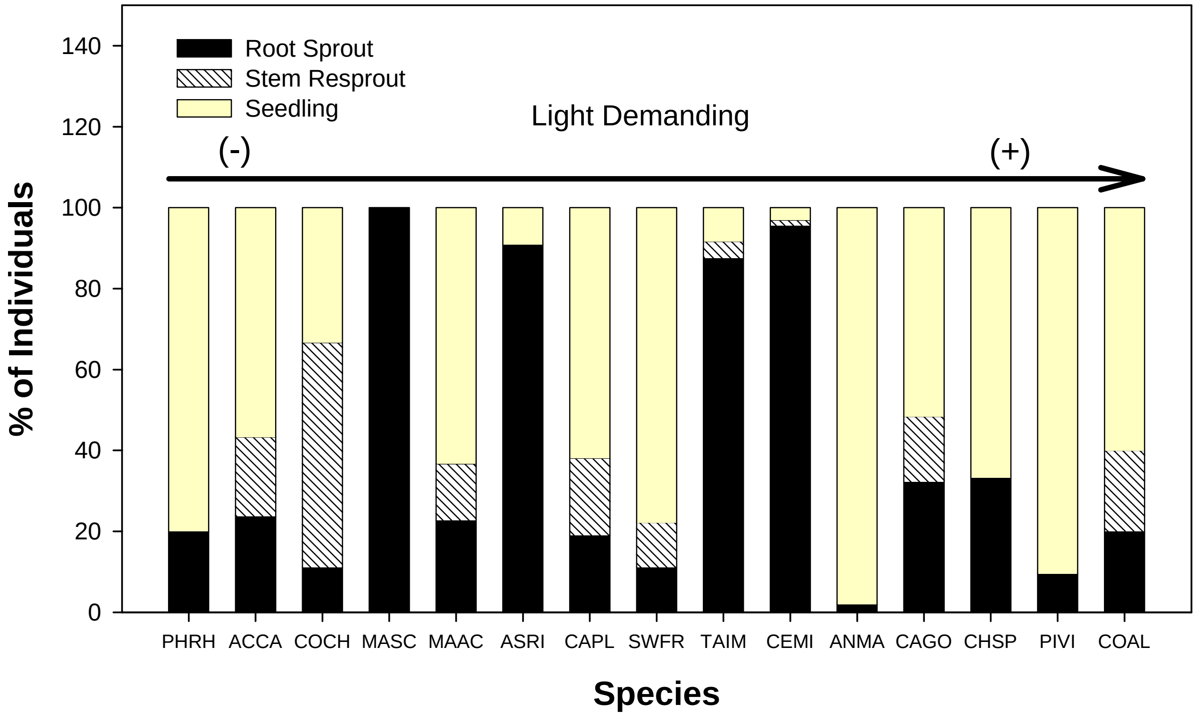

Figure 3-7. Percentage of juveniles < 2 m of different origins after logging (for each of 15 dry forest tree species) ordered by their light requirements.

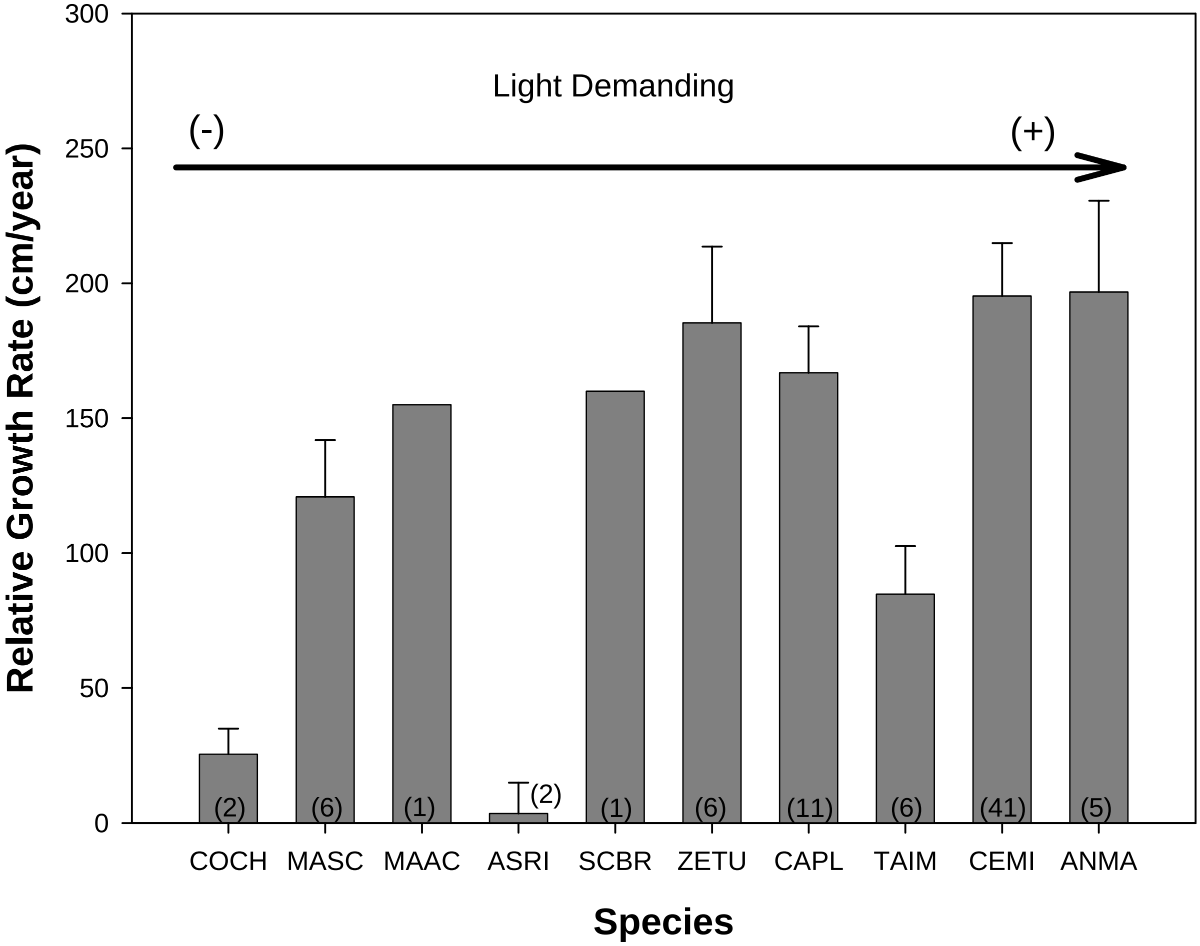

Figure 3-8. Relative growth rates (mean (± 1SE) of stump sprouts measured over the first two years after logging for commercial tree species in a tropical dry forest in Bolivia arranged by light requirements. Abbreviations of species are shown in Table 3-1.

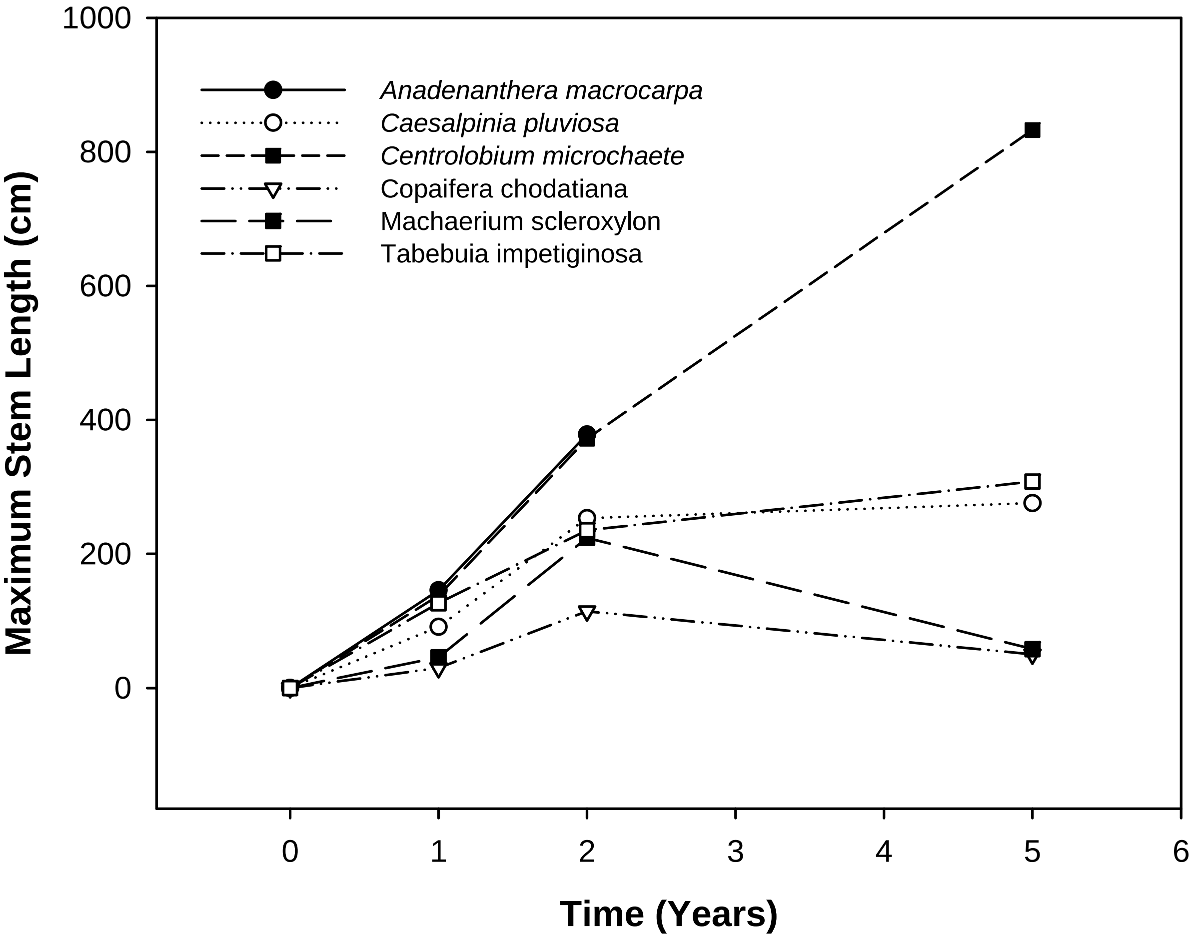

Figure 3-9. Mean growth rates of stump sprouts through time for the main commercial tree species as based on measurements of the tallest sprouts on different stumps 1, 2, and 5 y after creation.

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BIOGRAPHICAL SKETCH

Bonifacio Mostacedo was born in Sucre, Bolivia, and spent the first years of his life helping his father on their small family farm. For Bonifacio to further his studies beyond secondary school required a great deal of sacrifice and hard work for both him and his family. He studied agriculture at the Autonomous University Gabriel Rene Moreno (UAGRM) in Santa Cruz, Bolivia. While taking classes he became very interested in plant taxonomy and started working, first as a volunteer, at the Noel Kempff Mercado Natural History Museum. During that period of his life he had the opportunity to work with Robin Foster, from the Field Museum of Chicago and the late Alwin Gentry, from the Missouri Botanical Garden. Both of these world-renowned scientists and natural historians inspired him to keep working in botany and ecology. While associated with the Museum, he had many opportunities to visit remote parts of his native country and to become personally familiar with many of its ecological communities. He graduated from UAGRM as an Engineer in Agriculture in 1995. After his undergraduate training, he received a scholarship from BOLFOR Project to do his master's degree at the Autonomous National University of Mexico (UNAM), Mexico, from which he graduated in 1997 with a M.Sc. degree in ecology and environmental sciences. After graduating from UNAM, he worked for three years as Research Co-Coordinator for the BOLFOR Project and was appointed as a guest professor at UAGRM. The next stage in Bonifacio's educational career began in 2001 when he received a scholarship from BOLFOR to do his Ph.D. in the Department of Botany at the University of Florida. After taking classes in Gainesville he returned to Bolivia to simultaneously conduct his field research and work with the newly formed Instituto Boliviano de Investigación Forestal (IBIF), first as Research Coordinator and then as Executive Director. Upon graduation, he plans to return to Bolivia and to continue working with IBIF and UAGRM in Santa Cruz.