

SHIFTING CULTIVATION EFFECTS ON BRAZIL NUT (*Bertholletia excelsa*)
REGENERATION

By

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To my parents, who made it all possible.

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TABLE OF CONTENTS

	<u>page</u>
ACKNOWLEDGMENTS	4
LIST OF TABLES	8
LIST OF FIGURES	9
ABSTRACT	10
CHAPTER	
1 INTRODUCTION	12
2 SHIFTING CULTIVATION EFFECTS ON BRAZIL NUT (<i>Bertholletia excelsa</i>) REGENERATION	17
Introduction.....	17
Species Description	19
Study Area	20
Methods	21
Plot Installation and Sampling Scheme	21
Regeneration Environments by Forest Type	22
Seedling and Sapling Densities	24
<i>B. excelsa</i> Survival and Growth	24
Data Analysis.....	25
Results.....	28
Regeneration Environments by Forest Type	28
Seedling and Sapling Densities	29
<i>B. excelsa</i> Survival and Growth	29
Seedlings	29
Saplings	30
Discussion.....	31
Densities Explained.....	31
Seed sources and dispersal	31
Seedling survival and growth.....	33
Sapling survival and growth.....	36
Greater Ecological and Management Implications	37
3 CONCLUSION.....	39
APPENDIX	
A TRANSECT CREATION	46
B SCHEMATIC OF PLOT INSTALLATION AND SAMPLING SCHEME.....	47

LIST OF REFERENCES.....	48
BIOGRAPHICAL SKETCH.....	55

LIST OF TABLES

<u>Table</u>		<u>page</u>
2-1	Mean (\pm sd) soil properties observed within fallows and mature forest plots in RESEX Chico Mendes and PAE Chico Mendes.	43
2-2	Mixed model results based on <i>B. excelsa</i> seedling and sapling data subsets.	44
2-3	Comparison of <i>B. excelsa</i> seedling and sapling characteristics in fallow and mature forest	45

LIST OF FIGURES

<u>Figure</u>		<u>page</u>
2-1	Location of study sites PAE Chico Mendes and RESEX Chico Mendes in Acre, Brazil.....	41
2-2	Mean (\pm SE) PPFD at four times of day in four fallows and two mature forest plots.....	41
2-3	<i>Bertholletia excelsa</i> seedling and sapling densities (means \pm SE) in fallow and mature forest.	42
2-4	Relationship between <i>B. excelsa</i> seedling height and photon flux density (PPFD) measured in 2005	42
2-5	Relationship between <i>B. excelsa</i> seedling total leaf area and photon flux density (PPFD) measured in 2005	43
B-1	Mature forest and fallow plot design	47

Abstract of Thesis Presented to the Graduate School
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SHIFTING CULTIVATION EFFECTS ON BRAZIL NUT (*Bertholletia excelsa*)
REGENERATION

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Brazil nut (*Bertholletia excelsa*), has emerged as the cornerstone of the extractive economy in much of the Amazon, but the debate continues as to whether or not current harvest levels have a detrimental effect on Brazil nut seedling recruitment. Regeneration studies to date have been conducted solely within mature forest, but my study provides further insight into current Brazil nut regeneration dynamics, with a unique first look at regeneration in swidden fallows within two multiple-use areas in Acre, Brazil. Recruitment of individuals ≤ 10 cm dbh was evaluated within 25 x 25 m and 10 x 10 m subplots in four 9 ha mature forest plots and six fallows (0.5-1.0 ha each), respectively. Individuals ≤ 10 cm dbh were grouped into two size classes: seedlings (individuals < 1.5 m in height) and saplings (individuals between 1.5 m in height and 10 cm dbh). General linear mixed model analyses revealed higher densities of *B. excelsa* in fallow than mature forest. Survival and growth of young *B. excelsa* individuals appear to be enhanced by higher light levels found in fallows. Greater light availability is positively related to seedling height and height growth, seedling leaf number and leaf area, and seedling survival, and may indirectly enhance sapling growth and survival. This enhanced survival and growth likely contributes to the observed higher densities of seedlings and saplings in fallows. Not only can anthropogenic disturbance, in the form of shifting cultivation, play a positive role in Brazil nut

regeneration, it could explain current Brazil nut densities and distributions. Finally, in light of these findings, swidden fallows could potentially be managed for enhanced Brazil nut densities, which may provide an opportunity for greater income for extractive families while contributing to the sustainability of Brazil nut extraction in the long term.

CHAPTER 1 INTRODUCTION

Degraded and secondary forests are widespread throughout the tropics, representing 60% of remaining tropical forests (ITTO 2002). In the Brazilian Amazon alone, over 12% of the forest mosaic is classified as degraded and secondary forest (ITTO 2002). As these forests undergo succession they are capable of conferring significant environmental and livelihood benefits. Secondary forests provide people with food resources, timber and non-timber forest products, including fuelwood, and quality hunting sites (ITTO 2002). They also regulate water regimes, protect soils from erosion, store carbon, and serve as biological corridors and refuges for species (ITTO 2002). In addition, regenerating secondary forests are especially important in the life histories of a number of tropical plant species, including some that are of particular socioeconomic and ecological importance, such as *Cedrela spp.* and *Swietenia spp.* (Whitmore 1989). Similarly, two other valued species, *Astrocaryum murumuru* and *Dipteryx micrantha*, benefit from seed dispersal to treefall gaps (Cintra and Horna 1997). All four of these species exhibit gap-opportunistic traits, achieving enhanced growth in higher light conditions found in canopy openings or young regenerating forest environments.

Brazil nut (*Bertholletia excelsa*, H.B.K.) is another highly valued tropical tree reported to be a gap-opportunistic species (Mori and Prance 1990, Myers *et al.* 2000), benefiting from canopy openings during early stages of its life history. Brazil nut has emerged as the cornerstone of the extractive economy in much of the Amazon (Clay 1997), and the seeds, commonly referred to as nuts, are used for a variety of products, including raw and dried nuts, oils, flour, medicines, and personal care products (Ortiz 1995), making Brazil nut a versatile and valuable non-timber forest product (NTFP). To assess recruitment status as related to long-term harvest sustainability of this valuable species, several regeneration studies have been conducted in recent

years (Viana *et al.* 1998, Zuidema and Boot 2002, Peres *et al.* 2003, Serrano 2005), yielding differing reports on the impact of nut harvest on Brazil nut population structures. However, studies to date have been conducted solely within mature forest sites. The modern Amazonian landscape consists of a mosaic of mature forest, regenerating secondary forest, swidden fallow, and pasture; therefore, in light of the increasing extent of secondary forests in the region, the role of these sites in critical economic and conservation species recruitment and regeneration processes should not be underestimated.

In Acre, Brazil, local extractivists report relatively high levels of Brazil nut recruitment in regenerating swidden fallows, which may be due to specific biotic and abiotic characteristics associated with these sites, including differences in seed disperser activity (Clay 1997, personal obs.), light availability (Kainer *et al.* 1998, Myers *et al.* 2000, Zuidema 2003), and nutrient availability (Kainer *et al.* 1998), as well as increased resistance to pathogens in higher light environments (Augspurger 1984b). The aim of my study is to assess to what extent swidden fallows constitute favorable regeneration environments for *B. excelsa*. Although various studies have assessed the performance of tropical seedlings in natural gaps (Popma and Bongers 1991, Cintra and Horna 1997, Myers *et al.* 2000), typically formed by treefalls, conclusions regarding recruitment, survival and growth in these canopy openings should not be applied to all cases of canopy disturbance. For the purpose of this study, I highlight some characteristics unique to secondary fallow forests, in comparison with treefall gaps, as well as other regenerating forest types, which may each contribute considerably different influences on *B. excelsa* regeneration.

Fallows forests differ from treefall gaps in many ways. To begin with, the most common treefall gap size is $< 20 \text{ m}^2$ (Brokaw 1982), while swidden plots average 2 hectares (equivalent to $20,000 \text{ m}^2$) (Fujisaka *et al.* 1998). Abiotic conditions, including light and temperature levels,

vary within gaps (Denslow *et al.* 1990). As a result, one might observe a larger range of light and temperature levels in larger gap areas, such as swidden plots. Also, herbivore activity may differ as a result of this difference in gap size (Janzen 1990), as some vertebrates prefer secondary forest environments (Peña-Claros and De Boo 2002), but others avoid crossing large clearings (da Silva *et al.* 1996).

What may differentiate fallows most from other secondary forests is the influence of land use history on succession and regeneration (Uhl *et al.* 1988, Guariguata and Ostertag 2001, Mesquita *et al.* 2001). In general, swidden fallows develop after 2 to 4 years of cultivation, and are left to regenerate for a period of 5 to 15 years (Montagnini and Mendelsohn 1997). In fields which have been subjected to little burning, *Cecropia spp.* are often the dominant pioneers to establish in young fallows, however, where burning has been more frequent, *Vismia spp.* often dominate (Borges and Stouffer 1999). The dominance of these early pioneers directly influences subsequent vegetation succession (Nascimento *et al.* 2006). For example, in *Cecropia*-dominated areas heavy litterfall and increased shading can inhibit seedling establishment (Mesquita 1995, cited in Nascimento *et al.* 2006). As succession proceeds, differences in forest structure, stem density, and species composition can be observed. Fujisaka *et al.* (1998) found species richness to be higher in 3 – 5 year old fallows than in 1 – 2 year old fallows, and higher in fallows than in pasture sites. Also, vines were more abundant in mature forest and fallows of 3 – 5 years than in cultivated sites and pasture (Fujisaka *et al.* 1998). Furthermore, grass and weed dominance was reduced in fallows, compared to pasture and agroforestry sites, resulting in less competitive suppression (Ferguson *et al.* 2003). More shrub species were found in cropped and fallow sites than in mature forest and pasture (Fujisaka *et al.* 1998), and herbaceous plants were most common in cropped fields and pasture. Finally, as a result of burning and crop

harvesting, nutrient availability may be significantly altered in young fallows (Uhl and Jordan 1984).

After a few years of succession, large regenerating clearings may harbor increased numbers of vertebrates due to greater food availability for certain species than that of mature forest (Janzen 1990). Composition of seed dispersers may also differ between gap types, as a result of hunting activities that often coincide with crop cultivation (Janzen 1990).

In large man-made clearings, new recruitment is dependent upon seed dispersal (Ferguson *et al.* 2003), if cropping activities are carried out such that adults of desired species are removed or avoided, and no seeds are present in the seed bank. In this case, nearby patches of mature forest are required for forest trees to colonize abandoned plots (Uhl *et al.* 1982). On the other hand, recruitment may result from both dispersal and adult seed rain in a treefall gap. Although swidden fallows are often surrounded by other fallows or secondary forests of varying ages (Ferguson *et al.* 2003), recruitment processes may not be drastically compromised relative to those in treefall gaps, since mature forest is often left intact along at least a portion of the swidden edge (personal obs.). All of the aforementioned differences associated with forest gap type are relevant to any analysis of recruitment and regeneration processes of species such as *B. excelsa* in disturbed areas.

My study offers a new look at the seedling ecology of a valuable NTFP, through a focused study on the post-germination phase of *B. excelsa* regeneration within two multiple-use areas in the southeastern portion of Acre, Brazil. I predicted that densities of *B. excelsa* individuals ≤ 10 cm diameter at breast height would be greater in fallow than mature forest for two main reasons: 1) local extractivists report relatively high agouti seed dispersal in fallows (Clay 1997), and 2) survival and growth of young *B. excelsa* individuals is reported to be enhanced in the

presence of higher light availability in forest gaps (Mori and Prance 1990, Myers *et al.* 2000). In addition to evaluating seeding and sapling densities, light levels, soil nutrient content, leaf herbivory level, and number of nearby seed sources were evaluated in both fallow and mature forest to determine their respective influences on *B. excelsa* survival and growth. Chapter 2 is presented as a single, independent chapter ready for submission to a peer-reviewed journal. Relevant conclusions and management implications are presented in Chapter 3.

CHAPTER 2
SHIFTING CULTIVATION EFFECTS ON BRAZIL NUT (*Bertholletia excelsa*)
REGENERATION

Introduction

Brazil nut (*Bertholletia excelsa*, H.B.K.), has emerged as the cornerstone of the extractive economy in much of the Amazon (Clay 1997), which has given rise to the debate over whether or not current harvest levels have a detrimental effect on Brazil nut seedling recruitment. Some scholars report that current harvest levels have minimal to no detrimental effect on seedling recruitment in selected Brazil nut populations (Viana *et al.* 1998, Zuidema and Boot 2002), while others report that regeneration is rare or nonexistent in over-exploited populations (Peres *et al.* 2003, Serrano 2005). All previous Brazil nut regeneration studies have been conducted solely within mature forest, however, species regeneration is not limited to this forest type. The modern Amazonian landscape is a mosaic of mature forest, regenerating secondary forest, swidden fallow, and pasture; which comprise a continuum of microhabitat suitability for *B. excelsa* recruitment and regeneration. An evaluation of Brazil nut regeneration ecology is needed across the entire mosaic of forest types in order to provide an accurate picture of current *B. excelsa* population structures.

Bertholletia excelsa may regenerate more successfully in secondary than mature forest, based on reports that it is a gap-opportunistic species (Mori and Prance 1990, Myers *et al.* 2000). *Bertholletia excelsa* is one of a number of shade-tolerant species which experience enhanced seedling survival and growth in canopy openings, characterized by higher light levels (Brokaw 1985, Whitmore 1989, Molofsky and Fisher 1993, Cintra and Horna 1997). According to Myers *et al.* (2000), *B. excelsa* seedlings not only benefit from forest gaps, they require a minimum gap size of $> 95 \text{ m}^2$ or $> 10.4\%$ global site factor in order to reach sapling size. One large-scale disturbance yet unexplored for *B. excelsa* recruitment is that of recent anthropogenic secondary

forests, which, in addition to being widespread throughout Amerindian history (Denevan 1992, Heckenberger *et al.* 2003), are becoming increasingly common in the Amazonian landscape (ITTO 2002).

In Acre, Brazil, landholders annually clear 0.5 – 2 ha patches of older secondary or mature forest for swidden agriculture. When agricultural sites are abandoned, unique secondary forests succeed in fallow sites, which may constitute particularly favorable regeneration environments for *B. excelsa*. Local extractivists describe fallows as having greater *B. excelsa* recruitment than mature forest, associated with a relatively higher incidence of agouti seed dispersal to these disturbed sites. In addition, seedling survival may also be enhanced in fallow, due to decreased vulnerability to pathogens in higher light environments (Augsburger 1984b). Subsequent establishment and growth of *B. excelsa* may be greater in fallows because of high light levels (Kainer *et al.* 1998, Myers *et al.* 2000, Zuidema 2003) and greater nutrient availability (Kainer *et al.* 1998).

An evaluation of the potential of fallow sites to provide favorable *B. excelsa* regeneration environments will complement previous assessments of tropical seedling performance in other disturbed sites, specifically natural gaps (Popma and Bongers 1991, Cintra and Horna 1997, Myers *et al.* 2000). Although both types of disturbance increase forest light availability, fallows represent ecologically unique microhabitats which may differentially affect seedling recruitment, survival and growth. As a result of the shifting cultivation process, which often includes the application of fire, fallow forests may be characterized by significantly different nutrient stocks (Uhl and Jordan 1984), plant assemblages (Fujisaka *et al.* 1998, Ferguson *et al.* 2003), and vertebrate activity (Schupp 1988, Cintra and Horna 1997, Peña-Claros and de Boo 2002).

This study directly tests the hypothesis, based upon aforementioned scientific evidence and extractivist observations, that *B. excelsa* seedling and sapling densities are greater in fallows than mature forest, by assessing the post-germination phase of *B. excelsa* recruitment. To understand some of the mechanisms behind observed recruitment, effects of light, nutrient availability and proximity of seed sources are also assessed. In addition, one-year survivorship and growth rates of young individuals, seedling leaf production, and seedling herbivory, which further shape *B. excelsa* recruitment, are compared between fallow and mature forest.

Species Description

Bertholletia excelsa is a monospecific member of the Lecythidaceae family, found in unflooded (terra firme) forests across the Amazon basin and the Guianas (Mori and Prance 1990). This canopy emergent can reach up to 50 m in height (Mori and Prance 1990), and some individuals have been recorded at almost 1000 years of age (Vieira *et al.* 2005). In the two landholdings surveyed in my study (Filipinas and Cachoeira), densities of Brazil nut trees ≥ 10 cm diameter at breast height (dbh) were 1.4 individuals ha^{-1} (Wadt *et al.* 2005) and 2.5 individuals ha^{-1} (Serrano 2005), respectively, which are representative of densities reported by Peres *et al.* (2003) elsewhere in the study region. Although some authors report that *B. excelsa* occurs in groves of 50 – 100 individuals, with each grove separated from another by distances of up to 1 km (Mori and Prance 1990), Wadt *et al.* (2005) reported no existence of groves in my study area.

Mammal communities play a critical role in the regeneration of many large-seeded tropical tree species (Sork 1987, Asquith *et al.* 1997, Sánchez-Cordero and Martínez-Gallardo 1998, Forget *et al.* 2000, Jansen 2003), via seed dispersal and seed predation. Brazil nut is no exception, as the regeneration of *B. excelsa* is highly dependent upon the presence of agoutis (*Dasyprocta spp.*), the primary dispersers of Brazil nut seeds (Huber 1910, Prance and Mori

1978). Agoutis have been observed burying seeds at clearing edges (Peres and Baider 1997) and in young secondary forest (Forget *et al.* 2000), and extractivists have often observed agoutis carrying seeds to fallows (Clay 1997, personal obs.). Agoutis may prefer fallow sites because of the protection provided against predators by regenerating vegetation (Cintra and Horna 1997). These reports suggest a possibility of comparable or greater seed dispersal to fallows than mature forest. Recruitment of *B. excelsa* in both mature forest and fallows may also depend upon density and proximity of reproductive adults, as the proportion of seeds that arrive at a certain point in the forest should decline with distance from parent tree (Janzen 1970). Agoutis have been observed dispersing *B. excelsa* seeds as far as 100 m from seed sources, with the majority of seeds being dispersed within 25 m (Peres and Baider 1997). Normal seed shadows can be extended by secondary dispersal, when seeds are unearthed by seed predators and reburied even further from the adult tree (Mori and Prance 1990, Peres *et al.* 1997).

Study Area

Fieldwork was carried out in the southeastern portion of Acre Brazil, between 10° and 11° south of the equator in Acre, Brazil. The region has undulating topography, vegetation classified as humid, moist tropical forest (Holdridge 1978), and a pronounced three month dry-season from June to August. Average annual rainfall is from 1600-2000 mm (IMAC 1991). Soils of the region are classified under the Brazilian classification system as Argissolos (ZEE 2000), which correspond roughly to U.S. Soil Taxonomy System Ultisols. Recruitment of *B. excelsa* was evaluated within RESEX Chico Mendes and the Chico Mendes Agro-Extractive Settlement Project (PAE Chico Mendes), multiple use areas of 976,570 ha and 24,898 ha, respectively, separated by 30 kilometers (Fig. 2-1). Extractivists in the two study sites subsist on agricultural and cattle production, rubber tapping and Brazil nut collection (Gomes 2001), and some timber extraction in PAE Chico Mendes (personal obs.).

In my study sites, 0.5 – 1.5 ha of mature or older secondary forest found in close proximity to households was manually cleared of large trees to initiate the shifting cultivation cycle. Clearings were created either in areas void of valuable Brazil nut and rubber (*Hevea brasiliensis*) trees, or great care was taken to protect individuals of these species. Clearings were burned once, first cultivated for corn and rice, followed the next year by beans, and then manioc. After a cultivation period of two to three years, agricultural sites were abandoned, and regenerating secondary forests formed in situ. Young secondary forests such as these are typically characterized by lower stand basal area than surrounding mature forest (Saldarriaga *et al.* 1988). Although these swidden fallows are often surrounded by other fallows or secondary forests of varying ages, mature forest bordered at least one length of each fallow border studied. Thus, the study landscape consisted of a forest matrix with small fallows and pastures embedded within mature forest expanses.

Methods

Plot Installation and Sampling Scheme

Mature forest plots (300 x 300m or 9 ha each) in RESEX Chico Mendes and PAE Chico Mendes were originally demarcated and delineated in 2002 (Serrano 2005) using transects opened every 25m and extending for 300m (Appendix A). Transects produced 25 x 25m grids of 9-hectare survey plots (Fig. B-1[A]). From May to July 2005, transects within three of these original plots in RESEX Chico Mendes were reopened to evaluate all *B. excelsa* individuals > 10cm dbh by searching to the right and left of systematically placed parallel lines spaced 25m apart. To survey 25 % of the area of each mature forest plot for recruitment, four mature forest subplots (25 x 25 m each) were randomly selected within each hectare. Thus randomization was restricted to each one-hectare plot, generating a total of 36 subplots (Fig. B-1[A]).

Six fallows formed in RESEX Chico Mendes (0.5 – 1.0 ha each), and two in PAE Chico Mendes (1.0 – 1.5 ha each), were also delineated in 2005 (Fig. B-1[B]), using transects opened every 10m. Fallow ages ranged from 5 to 12 years, based upon year of abandonment of the agricultural site and, due to their variable sizes and shapes, were delineated and demarcated with a Garmin 12XL3 GPS unit. All individuals > 1.5 m in height were located in fallows by searching to the right and left of parallel lines spaced 10 m apart. Recruitment subplots in fallows (10 x 10 m) were randomly assigned across the extent of each fallow, and comprised approximately 25% of each fallow area (Fig. B-1[B]).

Regeneration Environments by Forest Type

To evaluate the influence of seed sources on recruitment, all *B. excelsa* individuals > 10 cm dbh were tallied within each 9 ha mature forest and 0.5 – 1.5 ha fallow, as well as within a 50m border strip of each plot. Dbh, XY coordinates, and reproductive status were recorded for each individual.

To compare understory light availability among 2 mature forest plots and 4 fallows in 2005, photosynthetically active radiation (PAR) was estimated by averaging photosynthetic photon flux density (PPFD) measurements taken at 10 equidistant sample points running through the center of each plot, from one plot edge to the opposite edge (Appendix B). Measurements were taken every 30 m in mature forest plots and measurement spacing varied in fallow sites, due to variation in fallow size. To capture daytime variations, PPFD was measured in each plot every 2.5h from 7:30 to 15:00 (ie. four times per day) for three days. PPFD was measured using 10 gallium arsenide phosphide (GaAsP) photocells mounted on a 10-cm disk and connected to a multimeter (Micronta LCD Digital Multimeter 22-185A; Tandy Corporation, Fort Worth, Texas). Sensors were calibrated with a standard LI-COR quantum sensor (model LI190SA) and a Campbell CR10x data logger.

To determine soil properties within each fallow and mature forest plot, soil samples were collected in 2005 below the litter layer at two depths (0 – 20 cm and 20 – 40 cm). In the fallows, soil cores were collected at two depths within one randomly selected subplot in each of the four corners of the fallow, as well as the center-most subplot, to create one composite of five soil cores for each depth (Appendix B). In the 9 ha mature forest plots, soil cores were collected within the four hectares located at the corners of each plot, as well within the center-most hectare (Appendix B). Within each of these five sampled hectares, a composite of five soil cores was created for each depth, using the same sampling scheme described for soil collection in the fallows. Two replicates of each composite were dried for 4 days at 65°C, and passed through a 2 mm stainless steel sieve. Soil pH was measured at a 1:2.5 soil to water ratio. Extractable P and K were processed using a dilute double acid extraction (Mehlich-1), with concentrations of P determined colorimetrically using the molybdate blue method (Murphy and Riley 1962), and K concentrations were determined using flame emission spectrophotometry. To determine total potential acidity, H⁺ and Al³⁺ were extracted with a buffered solution of calcium acetate at pH 7, and then titrated with a 0.1 N NaOH. Oxidizable organic carbon was determined on soils passed through a 1 mm screen, ground in a porcelain mortar, and then digested in a potassium dichromate acid medium with external heat. All soil analyses were conducted at the Soils Laboratory of Embrapa-Acre, Brazil (EMBRAPA 1997).

The temperature and moisture environment in fallow and mature forest were evaluated between July 2005 and June 2006. Mean monthly temperature and percent relative humidity were determined for two fallow sites and one mature forest site based on measurements taken at 30 minute intervals using HOBO ProSeries data loggers.

Seedling and Sapling Densities

Seedling densities were assessed within all subplots installed in mature forest and fallows. Sapling densities in mature forest also were assessed within subplots. Due to the ease of locating saplings in fallow, however, sapling densities were assessed over entire fallow areas, rather than in subplots only. Individuals < 1.5 m in height were defined as seedlings and individuals between 1.5 m in height and 10 cm dbh were defined as saplings. This classification scheme was selected not to differentiate between those individuals still using their seed reserves for growth and those individuals relying on environmental resources, but rather to look at general classes of recruitment. Within each subplot, XY location coordinates, height, seedling basal diameter, and sapling dbh were recorded for all individuals.

***B. excelsa* Survival and Growth**

Survival and annual growth (seedling height and basal diameter and sapling dbh) were evaluated from June to July 2006. To evaluate the effect of PAR on seedling survival and growth, PPF_D was measured directly above seedlings in two mature forest plots and four fallows. To capture daytime variations and to measure the full complement of all seedlings in each selected plot, seedling PPF_D was sampled on a rotating basis every 2.5h from 6:45 to 16:45 (ie. five sampling times per day) for three days. To assess the influence of photosynthetic capacity on survival and growth of all seedlings, leaf area was evaluated for seedlings in three mature forest plots and four fallows. When leaf number totaled ≤ 5 , all observed leaves were sampled, which was the case for the majority of seedlings. In all other cases, 5 leaves were sampled, representing the full range of leaf sizes. To avoid destructive sampling, leaves were traced in the field, and average leaf area was measured in Gainesville, Florida, with a LiCor, Inc. Model 3000A Leaf Area Meter with Transparent Conveyor Belt Accessory (LiCor, Inc., Lincoln,

Nebraska). Total leaf area was then estimated by multiplying total number of leaves per seedling by average leaf area.

The influence of invertebrate herbivory on seedling survival and growth was also assessed by quantifying the percentage of leaves per plant that showed signs of attack in 2005. Vertebrate leaf herbivory was not assessed because it was not possible to observe or account for the significant portion of predation which is comprised of leaves that are completely removed by this type of herbivore.

Data Analysis

All statistical analyses were performed using SAS software (Version 9.1, SAS Institute), excepting Student's t-tests, which were performed using SPSS software (Version 10.0, SPSS Inc.). Mature forest plots and fallows were treated as statistical blocks for all analyses, and seedling and sapling densities were determined on a per hectare basis. Average soil values were included as random effects, with plot nested within forest type, and soil nested within plot, for all analyses. PPF values were log transformed prior to all analyses to improve normality and homoscedasticity of residuals, which were evaluated visually. PPF levels were compared between forest types using a repeated measures ANOVA, and soil nutrients were compared between forest types using a two-way ANOVA. All soil nutrient values were averaged on a plot basis, and average soil pH, potassium, and percent organic carbon at two depths (0 – 20 cm and 20 – 40 cm) were included in explanatory density and growth models. Correlation analysis, using the PROC CORR procedure, revealed high correlations between the two depths for phosphorous and potential acidity (H^+Al^{3+}), therefore these soil nutrient values were collapsed into one depth for inclusion in the explanatory models.

Since *B. excelsa* densities demonstrated a Poisson distribution, they were modeled using a general linear mixed model and the GLIMMIX procedure. Two-way correlations were

calculated between relevant variable pairs using PROC CORR in order to determine relationships which merited inclusion in the model. I explored model building by conventional methods of sequentially dropping non-significant interactions and covariates based on p-values. In this case, I used a less restrictive significance level ($\alpha = 0.10$) than the usual arbitrary 0.05 level (Johnson 1999, Burnham and Anderson 2002) to allow all possible significant effects to remain for the purpose of building the best explanatory model (Bancroft 1968). Because a primary purpose of data analysis was to evaluate differences between mature forest and fallow, the indicator variable for forest type was considered fundamental and, therefore, retained in the density models without regard to its significance level (Bancroft 1968). Densities were first compared for all plots, with forest type (mature versus fallow) as the only retained fixed effect.

Seedling and sapling densities of mature forest plots previously surveyed in 2004 in PAE Chico Mendes (Serrano 2005) were included in the comparative density analysis to increase my sample size. These data were collected using the same sampling scheme described herein, and it was assumed that no event had occurred that significantly affected these seedling and sapling densities in this mature forest site (PAE Chico Mendes) between 2004 and 2005. To test this assumption, 2004 seedling and sapling density data collected mature forest in RESEX Chico Mendes, using the same sampling scheme, were compared with my 2005 seedling and sapling density data from this same forest and plots and no statistical differences were detected ($p = 0.57$). Finally, no site (PAE Chico Mendes versus RESEX Chico Mendes) interaction was found when comparing *B. excelsa* densities; therefore, observations from both sites were included in the analysis, with site dropped as a fixed effect from the model.

To explain observed densities, a subset of data (2 mature forest plots and 4 fallows) was analyzed. Tested fixed effects included forest type, number of reproductive adults within 50 m

of each subplot, all plot soil content averages, and plot PPFD averages; insignificant variables were sequentially removed from the final model. All possible predictor variables were included in the final model to provide the best explanatory model; however, residuals were not well distributed.

Student's t-tests were used to compare initial height, initial basal diameter, height and basal diameter growth, number of leaves, total leaf area, and leaf herbivory between fallow and mature forest for all seedlings; all data were normally distributed. Sapling diameter growth, which was likewise normally distributed, was also compared using a t-test. Logistic regression was used to analyze differences in seedling survival; tested fixed effects included initial height, initial diameter, height growth, diameter growth, forest type, all plot soil content averages, PPFD, number of leaves per seedling, total leaf area, and percent leaf herbivory. Insignificant variables were sequentially removed from the final model. Initial seedling height and diameter were highly correlated with total leaf area, therefore, interactions were explored between total leaf area and initial seedling size.

The GLIMMIX procedure was used to test seedling and sapling growth. Growth values, some of which were negative, were log transformed ($\log_{10} [1+x]$) prior to analyses to improve normality and homoscedasticity of residuals, which were observed visually. Because data related to more mechanistic causes of growth (ie. light observed directly above seedlings) were available, the forest type variable was intentionally excluded from the seedling growth analysis. However, because these data were unavailable for saplings, forest type was retained for analysis in the sapling diameter growth model. Tested fixed effects included in initial seedling growth models were initial height or diameter, forest type, all plot soil content averages, PPFD, number of leaves per seedling, total leaf area, and percent leaf herbivory, while initial sapling diameter

growth models included initial dbh, forest type, all plot soil content averages, and plot PPFD averages. Again, all possible predictor variables were included in the final models to provide the best explanatory models of growth, and insignificant variables were sequentially removed from the final model; residuals were fairly well distributed. Sapling height growth could not be compared between forest types, as sapling heights were estimated visually.

Differences in seedling leaf herbivory percentage were analyzed with the GLIMMIX procedure, accounting for a log-normal distribution of data. Leaf herbivory percentages were arcsin transformed prior to analysis in order to improve the normality of the response variable. Tested fixed effects included initial height or diameter, forest type, all plot soil content averages, PPFD, number of leaves per seedling, total leaf area; insignificant variables were sequentially removed from the final model. Normality and homoscedasticity of residuals were observed visually and the residuals were fairly well distributed.

Results

Regeneration Environments by Forest Type

Of all variables measured to characterize regeneration environments (plot light levels, density of nearby seed sources, temperature and relative humidity, and soil nutrient stores), only light levels differed significantly between the two forest types. A repeated measures ANOVA revealed higher average PPFD levels in fallow than mature forest ($p = 0.02$) (Fig. 2-2). There were no significant differences between forest types in number of adults within 50 m of evaluated subplots, nor in observed daily temperature and percent relative humidity monitored in two fallows and one mature forest site between July 2005 and June 2006. Mean monthly temperature in the three sites ranged between 23.5 and 24.2°C and mean relative humidity ranged between 90.3 and 92.7%. Although two-way ANOVAs revealed no soil property

differences between forest types (Table 2-1), soil P was significantly different by depth ($p = 0.0006$).

Seedling and Sapling Densities

Observed mean seedling densities of 12.7 and 5.3 trees ha^{-1} in fallow and mature forest (Fig. 2-3), respectively, were different at $p = 0.07$, according to the general linear mixed model. Mean sapling densities of 5.2 and 1.3 trees ha^{-1} in fallow and mature forest (Fig. 2-3), respectively, were also different, again at $p = 0.07$. Based upon an analysis of the data subset, seedling density differences were somewhat explained by the number of adults within 50m of each subplot ($p = 0.06$), such that seedling densities increased with number of adults, while sapling densities were best explained by percent organic carbon at the 0 – 20 cm depth ($p = 0.02$) (Table 2-2).

***B. excelsa* Survival and Growth**

Seedlings

After one year, 26% of surveyed seedlings in fallow and 19% in mature forest (21% of all seedlings) were either dead or unable to be located, with no survivorship differences between these two forest types (Table 2-3). Seedling survival was possibly explained by total leaf area ($p = 0.08$) and an interaction between percent leaf herbivory and PPFD ($p = 0.08$) (Table 2-2); improved survival was associated with greater leaf area and higher leaf herbivory.

Initial seedling height was not significantly different between forest types (Table 2-3), and, across forest types, seedling height in 2006 was best explained by PPFD measured in 2005 ($p = 0.0009$) (Fig. 2-4); seedling height increased with PPFD increase. Seedling height growth was best explained by an interaction between percent leaf herbivory and PPFD ($p = 0.02$) and percent leaf herbivory alone ($p = 0.02$) (Table 2-2). Height growth increased with PPFD, and increased with herbivory decrease. Seedling growth appeared to increase more with PPFD at

intermediate herbivory levels. A t-test revealed no significant difference in initial seedling basal diameter between forest types (Table 2-3), however, basal diameter growth was greater in fallow than mature forest ($p = 0.05$), according to a t-test. According to the general linear mixed model, seedling basal diameter growth was best explained by total leaf area ($p = 0.05$) (Table 2-2), such that seedlings with more leaf area grew more. Seedling height and diameter growth demonstrated positive relationships to all tested factors except percent leaf herbivory.

Total leaf area was highly correlated with seedling height, diameter and number of leaves and, as a result, less significant variables sequentially fell out of the growth models. Total leaf area was strongly related to PPF (D) ($p = 0.0004$) (Fig. 2-5). Observed herbivory level was much higher in mature forest than fallows ($p < 0.0001$) (Table 2-3). The mixed model corroborated that percent seedling leaf herbivory was explained by forest type alone ($p = 0.05$) (Table 2-2), but also showed that herbivory was best explained by an interaction between forest type and number of leaves ($p = 0.006$) (Table 2-2), such that herbivory decreased with leaf number in mature forest, but increased with leaf number in fallow.

Saplings

Estimated mean sapling heights were 5.51 and 2.99 m, in mature forest and fallow, respectively, which was significantly different ($p = 0.02$) (Table 2-3). Initial sapling dbh was also greater in mature forest than fallow ($p = 0.05$) (Table 2-3). Maximum dbh values were 9.5 cm in mature forest and 7.0 cm in fallow. Nearly 100% sapling survival was observed in both forest types (only one sapling died in a single fallow site), and therefore no significant difference in sapling survival between forest types was detected. Sapling dbh growth was much greater in fallow than mature forest ($p = 0.02$), and was potentially explained only by forest type ($p = 0.07$) (Table 2-2).

Discussion

Densities Explained

Bertholletia excelsa seedling densities were over two times greater in anthropogenically-disturbed fallows than mature forest, and sapling densities were four times greater in fallow (Fig. 2-3). Many factors influence establishment, survival, and growth of young individuals, including proximity and density of seed sources (Janzen 1970), seed disperser and predator behavior (Sork 1987, Forget 1994, Molofsky and Fisher 1993, Asquith *et al.* 1997), light availability (Augspurger 1984a, Augspurger 1984b, Poorter 1999), and nutrient availability (Ceccon *et al.* 2003), some of which may be related to microhabitat, or forest type. My data suggest that the influence of density and proximity of seed sources and light levels, at various stages in the *B. excelsa* recruitment process, play a significant role in shaping the observed densities of young *B. excelsa* individuals. Differences in densities between forest types, however, could also be a reflection of additional factors not measured, such as seed dispersal. These factors, which affect species establishment to differing degrees at various stages in the recruitment process, will be discussed below.

Seed sources and dispersal

Based on a deeper analysis of a subset of data, which included number of seed sources within 50m of surveyed subplots, seedling densities were mildly related to the number of nearby seed sources ($p = 0.06$). These findings are consistent with scientific evidence that seedling densities decline with increased distance from parent trees (Janzen 1970). Therefore, higher recruitment would be expected in fallows that either contain adult *B. excelsa* trees or are located adjacent to mature forests with high adult densities, compared to those with no adults nearby. Although density of nearby adults explained relative densities, seedlings and saplings were often found in areas with neither a reproductive adult within 50m, nor traces of potential seed sources

that may have suffered mortality prior to my study, confirming seed dispersal distances well beyond the typical dispersal maximum of 25m (Peres and Baider 1997). These dispersal distances may be explained by secondary dispersal (Mori and Prance 1990, Peres *et al.* 1997).

Residuals in these explanatory density models were poorly distributed, with high density observations being grossly underestimated, suggesting that relevant factors have not been included in the models. These underestimations could be due to a clumped, and possibly directed, seed dispersal pattern that has not been accounted for. *Bertholletia excelsa* seed dispersal beyond the adult crown is determined nearly entirely by agouti scatterhoarding behavior (Prance and Mori 1978), and local extractivist reports suggest that agouti dispersal behavior may be non-random. Extractivists report preferential seed dispersal in fallow environments (Clay 1997, personal obs.). These accounts are corroborated by observations of seed burial at clearing edges (Peres and Baider 1997) and in young secondary forest (Forget *et al.* 2000), perhaps related to agouti predator avoidance in areas composed of limb and vine tangles (Cintra and Horna 1997). Agouti scatterhoarding activity may potentially increase the proportion of seeds in favorable microenvironments (Jansen and Zuidema 2001), which has been proposed as a more critical influence on regeneration than post-dispersal predation escape or successful germination (Rey and Alcántara 2000). The importance of disperser site preference and directed dispersal has been demonstrated for species other than *B. excelsa* (Uhl *et al.* 1981, Schupp *et al.* 1989, Forget 1994). Although disperser behavior was not tested in this study, it likely had a significant effect on seed availability for recruitment in fallow and mature forest. Equally important is the influence of differential seed removal rates (due to retrieval and predation) between different forest types, which may further affect observed *B. excelsa* densities. Some authors report higher seed removal rates of various tropical species in gap environments

(Schupp 1988, Schupp and Frost 1989, Cintra and Horna 1997), while Sanchez-Cordero and Martinez-Gallardo (1998) report greater tropical seed removal in mature forest than gaps.

Tabarelli and Mantovani (1996), did not find seed removal of *B. excelsa* to be different between treefall gaps and undisturbed forest, however, clearings created by anthropogenic disturbances were not assessed. It is clear that seed disperser and seed predator activities are essential factors to include in future density evaluations.

Seedling survival and growth

Once seeds are dispersed and young seedlings establish, individuals may demonstrate differential growth (Augspurger 1984a, Popma and Bongers 1991, Brown and Whitmore 1992, Poorter 1999) and/or survival (Augspurger 1984b, Cintra and Horna 1997, Brown and Whitmore 1992) in different forest types, which are often differentiated in the literature between understory and gap environments. In my study, however, forest type explained only sapling diameter growth (sapling height growth could not be evaluated). Other measured variables, some of which may be associated with forest type, demonstrated stronger influences on observed survival and growth of *B. excelsa* seedlings.

To begin with, total leaf area, which is correlated with leaf number, was a mild indicator of seedling survival ($p = 0.08$). Leaves facilitate the acquisition of carbon by means of photosynthesis; an enhanced carbon gain, due to greater leaf area, may confer relatively higher fitness (and ultimately survival) to seedlings by various means, including the provision of more structural material and energy, an increase in nutrient content, and a better tolerance to environmental stresses (Chabot and Hicks 1982). PPFD, although not highly significant on its own, may contribute to increased seedling survival, as PPFD was strongly positively correlated with total leaf area ($p = 0.0004$), which did explain seedling survival at $p = 0.08$. Although some studies have demonstrated greater seedling survival in gaps than understory for some species

(Augspurger 1984b, Cintra and Horna 1997), my results do not directly support these conclusions, as I found one-year *B. excelsa* survivorship to be no different between mature forest and fallow. Kainer *et al.* (1998) also found no relationship between seedling survival and comparative light levels in pasture, forest gap, and shifting cultivation sites (Kainer *et al.* 1998). The positive effect of leaf herbivory on survival is not so easily explained. Contrary to my findings, numerous studies demonstrate the negative effect of leaf herbivory on seedling survival (Howe 1990, Hulme 1996, Vasconcelos and Cherrett 1997). In this study, the influence of herbivory level on survival may be coincidental. Invertebrate herbivory was not unusually high in either forest type, and is probably not sufficient to lead to seedling mortality under normal conditions. In addition, it was not possible to quantify vertebrate herbivory on seedling survival in this study. Nevertheless, it is likely that a greater percentage of mortality was represented by completely uprooted seedlings (Ortiz 1995, Zuidema 2003, personal obs.), resulting from seed predators unearthing and consuming seeds at the base of the plant. Furthermore, only 14 of 94 total seedlings died, therefore concrete differences between factors relating to seedling survivorship were difficult to detect. Although forest type was not a significant factor in survival probability, in light of other analyzed effects, it is possible that the forest type variable was partially masked by other variables such as percent leaf herbivory or PPFD (due to multiple colinearity), which were both significantly different by forest type (PPFD was higher in fallow and leaf herbivory was lower in fallow than mature forest). If forest type is partially included in one of these variables, it may play an undetected role in determining seedling survival probability.

Seedling heights in 2006 were highly positively correlated with PPFD levels measured directly above seedlings in 2005, which implies a significant advantage to height growth in

higher light environments. In my study, one-year seedling height growth was influenced by an interaction between PPFD and percent leaf herbivory ($p = 0.02$), such that height growth declined with increased leaf herbivory and, while generally increasing with PPFD, was greatest at intermediate light levels. Previous studies have shown a positive relationship between seedling height growth and light availability in the tropics (Augspurger 1984a, Denslow *et al.* 1990, Popma and Bongers 1991), and similar results have been reported for *B. excelsa* (Poorter 1999, Zuidema 2003), again, with highest growth rates at intermediate light levels.

Uhl and Jordan (1984) found that soil nutrient concentrations did not vary significantly between agricultural sites and mature forest 5 years after cutting and burning. Similarly, I found no difference in soil nutrient availability between mature forest and fallows. As a result, soil nutrients did not explain *B. excelsa* survival and growth as well as other measured variables, such as light availability.

Numerous studies have described the negative effects of herbivory on seedling growth (Marquis 1984, Howe 1990, Hulme 1996, Vasconcelos and Cherrett 1997). In my study, seedling leaf area did not differ significantly by forest type, but was highly correlated with seedling height, and the two variables exhibited a significant interaction effect for seedling height growth. Height growth was positively related to both variables, similar to other studies which have demonstrated increased growth with greater initial height (Zuidema 2003) and leaf area (Poorter 1999). Similar to height growth, seedling diameter growth was explained by total leaf area ($p = 0.05$), and possibly by an interaction between leaf herbivory and PPFD ($p = 0.07$), with a positive relationship to each factor. Zuidema *et al.* (2003) report a similar relationship between *B. excelsa* biomass growth and light availability. Although not directly evaluated, seedling survival and growth in my study sites may also have been influenced by ant presence.

Leaf cutter ants (*Atta spp.*) are known to modify soil nutrient concentrations (Lugo *et al.* 1973, Haines 1978), which may directly influence the development of young *B. excelsa* individuals, as well as influence the competitive environment with other species. In addition, extractivists assert that leaf cutter ants preferentially predate both *B. excelsa* seeds and seedlings. The potential importance of leaf cutter ants in fallow environments is worth particular attention as leaf-cutting ant populations have been shown to increase after forest clearing (Vasconcelos and Cherrett 1995). Blanton and Ewel's (1985) findings suggest that leaf-cutting species continue to thrive as succession proceeds, representing the most important herbivore in the successional forests they studied. I found one of my six surveyed fallows was covered to a great extent in leaf cutter ant nests (species unknown). The relationship between forest type and ant density, intensity of ant seed and seedling predation in fallow and mature forest, and the effects of ant populations on soil composition all merit further consideration, to better understand the role of ant populations in *B. excelsa* recruitment and regeneration.

Sapling survival and growth

High sapling survival rates in both mature forest and fallow suggest that, once seedlings have been well-established, they develop and survive equally well in either forest type. Zuidema and Boot (2002) also found extremely low mortality rates (1%), over a two-year period, for *B. excelsa* individuals > 1 cm dbh. Initial sapling diameter was greater in mature forest, but this can be explained by the young age of the fallows (5 – 12 years), as fallow saplings have not had the opportunity to attain dbh sizes near 10cm within this time frame. No factor included in statistical analyses, aside from forest type, explained higher diameter growth rates in fallow. However, saplings in fallow may also be able to invest more in biomass growth than mature forest saplings, since height growth is greatly enhanced by higher light levels in fallow. Light is cited as the most frequently limiting resource for seedling growth (Kitajima 1996), a major component of

tropical plant regeneration processes (Chazdon *et al.* 1996). Increased light availability is likely one of the most significant advantages conferred upon well-established seedlings in fallow, as observed PPFD was significantly greater in fallow than mature forest ($p = 0.02$), and the benefits of light availability are likely great for individuals up to 10 cm dbh, which continue to compete to reach the canopy up to, and even beyond, this 10 cm limit.

Secondary forests are, by nature, dynamic and, as a result, are associated with an ever-changing microenvironment of vegetation, water, and soil nutrients. Therefore, the suitability for seedling and sapling growth and survival may vary with forest successional stage. However, the observed higher densities of young individuals in fallow indicate that this forest type, in general, constitutes a favorable microhabitat for both seedling and sapling development.

Greater Ecological and Management Implications

This research provides a new, and perhaps more accurate, depiction of current Brazil nut regeneration in tropical forest landscapes, as secondary forest environments have previously been ignored. The high densities of young Brazil nut individuals in secondary forests created through shifting cultivation (fallows) clearly demonstrate that Brazil nut regeneration may have been underestimated in previous studies which were conducted solely within mature forest.

In light of these findings, fallows could potentially be managed for enhanced Brazil nut densities, which may provide an opportunity for greater income for extractive families while contributing to the sustainability of Brazil nut extraction in the long term. In the past, some extractivists have experimented with small-scale Brazil nut enrichment plantings, as a means to economically enrich their landholdings (Kainer *et al.* 1998). The benefits of fallow management may also provide an additional incentive for extractivists to allow fallows to regenerate, rather than convert them to pasture, which is an increasingly common practice in much of the Amazon.

Shifting cultivation has previously been recognized for its role in shaping Amazonian ecosystems (Dufour 1990). Pre-Columbian human interventions, in the form of active planting, were previously considered by Posey (1985) and Balée (1989) as a possible explanation for the presence of Brazil nut “groves” in parts of the Amazon. Based on the results of this study, however, it is possible that higher densities are a result of less direct human interventions, such as shifting cultivation. Not only can anthropogenic disturbance, in the form of shifting cultivation, play a positive role in Brazil nut regeneration, it could explain current Brazil nut densities and distributions.

CHAPTER 3 CONCLUSION

The objective of this study was to compare *B. excelsa* recruitment and regeneration in regenerating swidden fallows and mature forest. My results suggest that fallows constitute favorable microhabitats for both seedling and sapling development. Perhaps most importantly, survival and growth of young *B. excelsa* individuals appear to be enhanced by the higher light levels found in fallow. Greater light availability is positively related to seedling height and height growth, seedling leaf number and leaf area, and seedling survival, and may indirectly enhance sapling growth and survival. This enhanced survival and growth likely contributes to the observed higher densities of seedlings and saplings in fallow sites.

At the conclusion of this study it became clear that seed dispersal and seed predation should be compared between forest types in future regeneration studies, in order to better assess the various recruitment advantages, and possibly disadvantages, associated with fallow environments. In addition, herbivore activity, and its effects on *B. excelsa* survival and growth, should be evaluated in greater detail, quantifying the proportion of herbivory exercised by both vertebrates and invertebrates, in both forest types. Leaf cutter ant behavior in regenerating fallow fields merits particular consideration. Future studies should also compare *B. excelsa* regeneration between different secondary forest types, as well as between fallows of varying ages, as various successional forest types and successional stages may contribute to differential survival and growth of young individuals. At the time of thesis submission, soil analyses were incomplete, therefore conclusions regarding the effects of soil content were limited. Upon publication of Chapter 3 in a scientific journal, the incorporation of additional soil data should yield further insights.

Although some significant factors in *B. excelsa* recruitment processes, such as disperser activity, were not evaluated in the study, the importance of the results should not be underestimated. My research focuses on a widespread forest type which has not previously been included in assessments of *B. excelsa* population dynamics therefore conclusions regarding regeneration in fallows may better explain current *B. excelsa* densities and distributions than other studies to date. An understanding of the role of fallows in *B. excelsa* regeneration may also provide insight into the regeneration requirements of other valuable gap-loving species, such as those in the *Cedrela* and *Swietenia* genera.

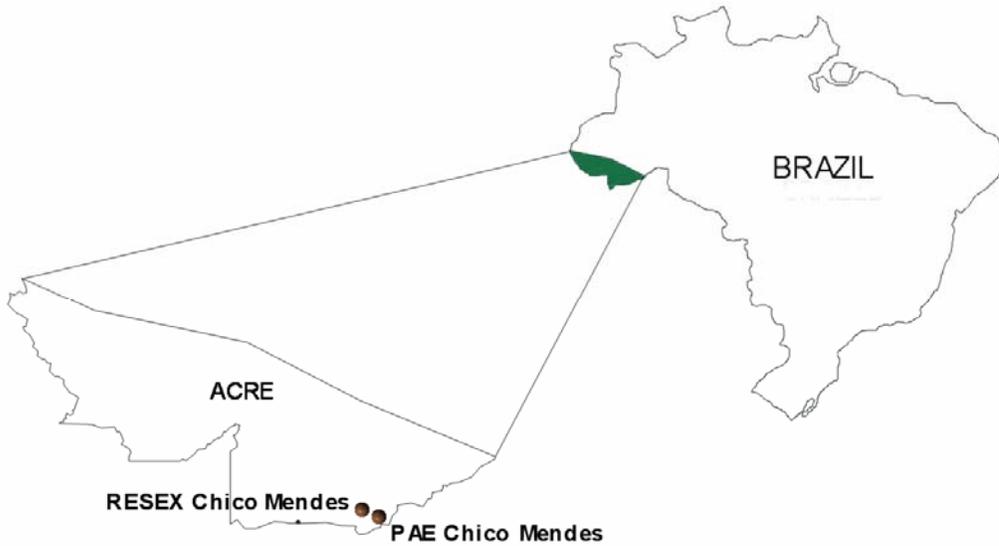


Figure 2-1: Location of study sites PAE Chico Mendes and RESEX Chico Mendes in Acre, Brazil (Figure adapted from Gomes 2001, with permission).

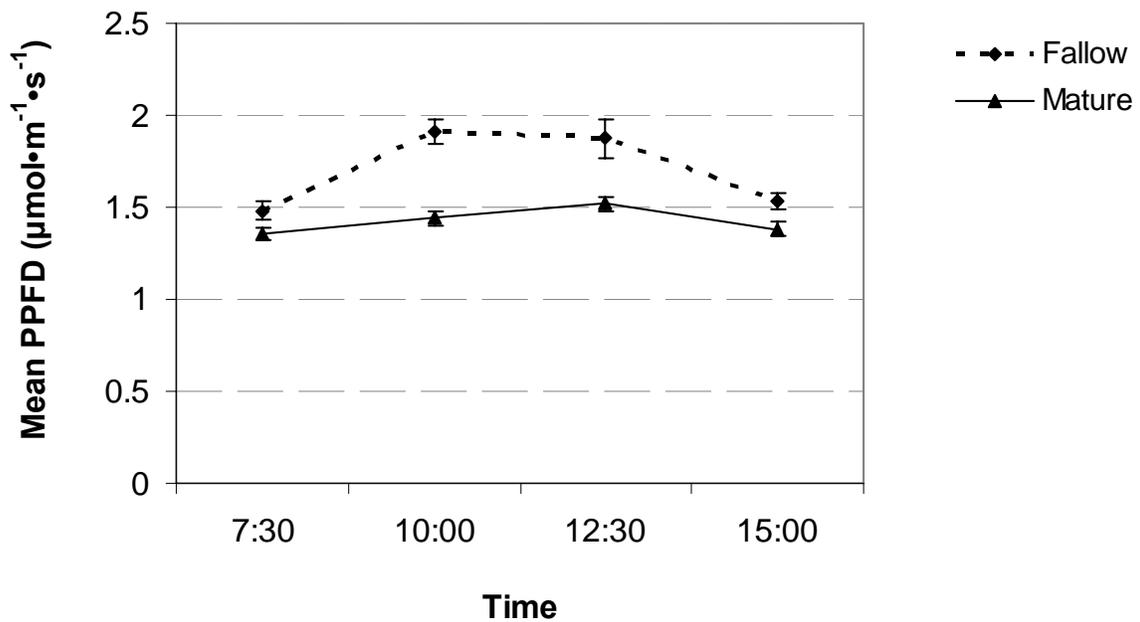


Figure 2-2: Mean (\pm SE) PPFD at four times of day in four fallows and two mature forest plots. Data are log transformed.

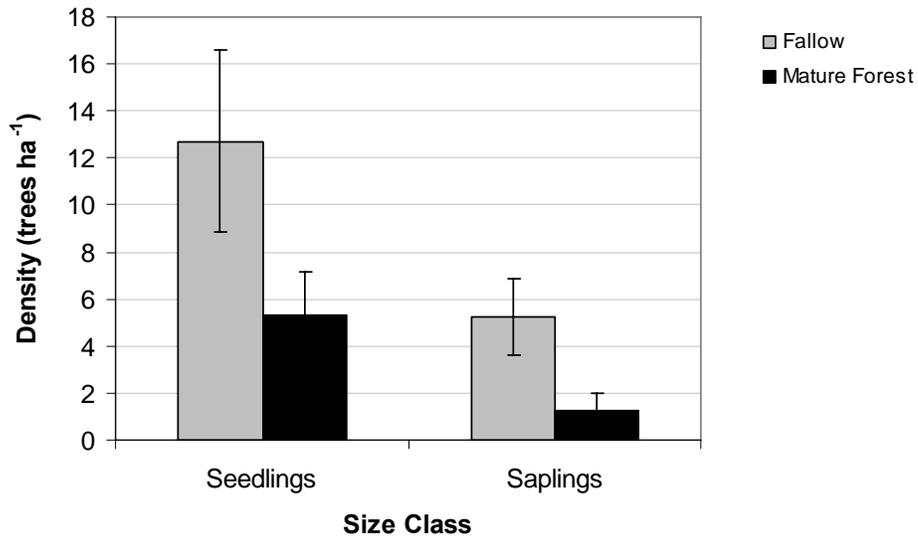


Figure 2-3: *Bertholletia excelsa* seedling and sapling densities (means \pm SE) in fallow and mature forest.

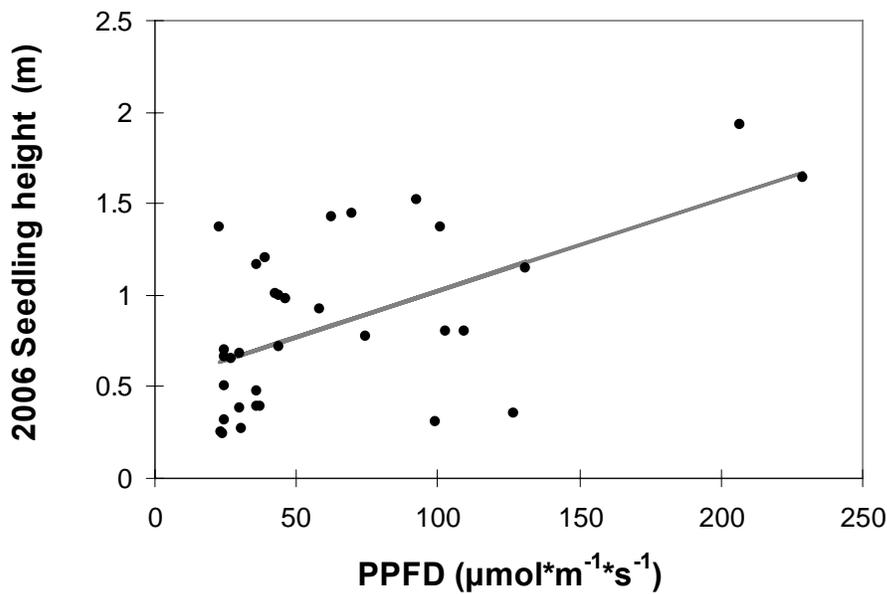


Figure 2-4: Relationship between *B. excelsa* seedling height and photon flux density (PPFD) measured in 2005. Each point represents one observed *B. excelsa* seedling. Regression line fitted: $y = 0.005x + 0.52$, $R^2 = 0.31$.

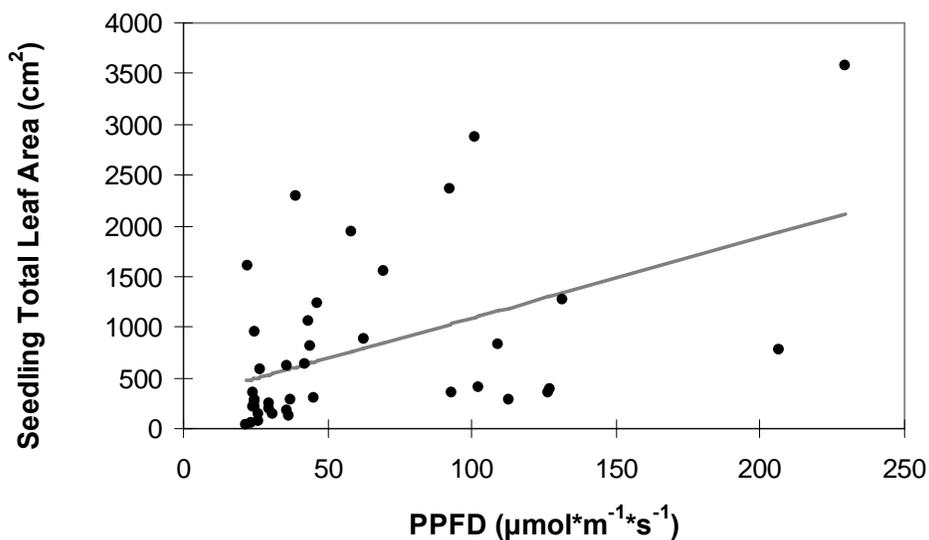


Figure 2-5: Relationship between *B. excelsa* seedling total leaf area and photon flux density (PPFD) measured in 2005. Each point represents one observed *B. excelsa* seedling. Regression line fitted: $y = 7.93x + 294.97$, $R^2 = 0.23$.

Table 2-1: Mean (\pm sd) soil properties observed within fallows and mature forest plots in RESEX Chico Mendes and PAE Chico Mendes.

Soil property	Fallow	Mature Forest
pH	5.5 (\pm 0.2)	5.1 (\pm 0.3)
K (cmol*kg ⁻¹)	0.4 (\pm 0.03)	0.3 (\pm 0.1)
P (mg*kg ⁻¹)	2.0 (\pm 0.3)	2.7 (\pm 0.4)
Potential Acidity (H ⁺ Al ³⁺) (cmol*kg ⁻¹)	4.0 (\pm 0.7)	5.7 (\pm 1.0)
Organic Carbon (%)	0.5 (\pm 0.1)	0.6 (\pm 0.1)

Table 2-2: Mixed model results based on *B. excelsa* seedling and sapling data subsets.

Model fixed effects	F-statistic	p-value
<u>Seedlings</u>		
Density (ha⁻¹)		
Forest type	1.09	0.33
Number of adults within 50m of subplots	3.71	0.06
Survival		
Total leaf area	3.22	0.08
Percent leaf herbivory*PPFD	3.26	0.08
Height growth (cm)		
Initial height	4.99	0.08
Percent leaf herbivory	13.09	0.02
PPFD*Percent leaf herbivory	11.93	0.02
Potential acidity (0 – 40cm)	7.55	0.04
Soil K (0 – 20cm)	6.21	0.06
Basal diameter growth (cm)		
Total leaf area	4.26	0.05
Percent leaf herbivory	3.42	0.08
Percent leaf herbivory*PPFD	3.58	0.07
Percent leaf herbivory		
Forest type	6.96	0.05
Number of leaves*forest type	5.84	0.006
<u>Saplings</u>		
Density		
Forest type	1.80	0.23
Percent organic carbon	9.25	0.02
Growth (dbh)		
Forest type	4.55	0.07

Table 2-3: Comparison of *B. excelsa* seedling and sapling characteristics in fallow and mature forest (all p-values based upon t-tests, except one-year survivorship, which is based upon logistic regression).

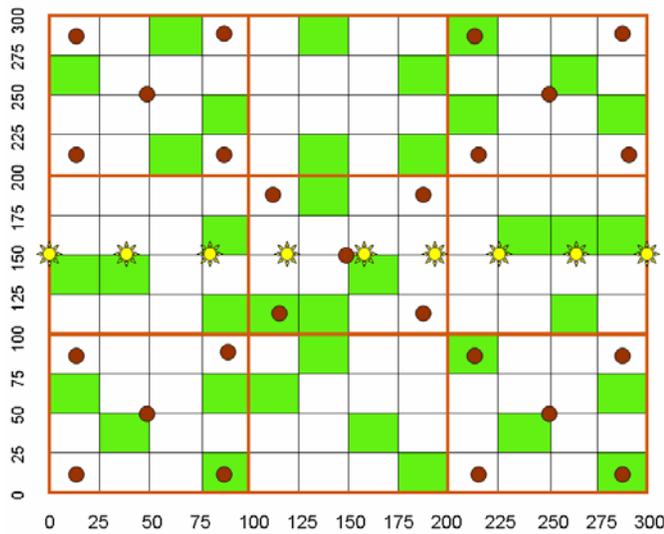
Characteristic	N	Fallow	Mature Forest	p-value
Seedlings				
Initial seedling height (m)	76	0.67 (± 0.42)	0.59 (± 0.38)	0.45
Initial seedling basal diameter (cm)	76	0.64 (± 0.34)	0.55 (± 0.21)	0.15
Seedling height growth (m)	62	0.14 (± 0.28)	0.12 (±0.22)	0.82
Seedling basal diameter growth (cm)	62	0.19 (± 0.25)	0.10 (±0.11)	0.05
Number of leaves per seedling	75	12.8 (± 9.4)	9.7 (±7.6)	0.13
Total leaf area (cm ²)	68	1003.4 (± 915.4)	710.5 (± 807.2)	0.20
Leaf herbivory (%)	74	16 (± 24)	58 (± 28)	< 0.0001
One-year survivorship (%)	66	74	81	0.79
Saplings				
Initial height (m)	31	2.99 (± 1.95)	5.51 (± 3.74)	0.02
Initial dbh (cm)	31	2.23 (± 2.07)	4.45 (± 3.32)	0.05
Dbh growth (cm)	25	0.47 (± 0.39)	0.11 (±0.32)	0.02

Data reported as means (± sd), excepting percentage data. Reported sapling heights are estimated.

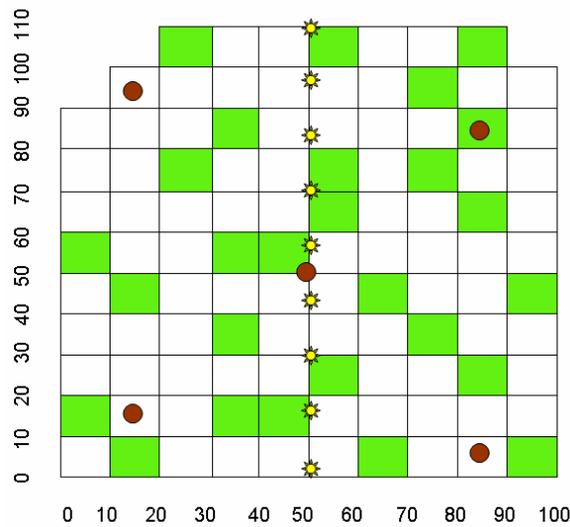
APPENDIX A TRANSECT CREATION

To open transects, a compass was placed on a level-cut branch. Next, two sapling poles were placed in the line of sight of the compass to begin a straight line. Field technicians and local assistants referred to this line in order to open a straight transect through the forest with a machete. Reference poles were placed no more than every 15 m apart, with poles placed closer together in hilly or overgrown areas. Distance was measured with a metric tape to create entire 300 m transects. Each transect was re-measured with metric tape after clearing was completed. This method facilitated searching and locating *B. excelsa* individuals over large areas.

APPENDIX B
SCHEMATIC OF PLOT INSTALLATION AND SAMPLING SCHEME



A



B

Figure B-1: Mature forest and fallow plot design. A) Nine ha plot of mature forest, with four 25 x 25m subplots randomly selected within each ha, for a total of 36 subplots B) 1.1 ha fallow with 27 10 x 10m subplots. Distance is indicated in meters. ■ represents recruitment subplot. Light environments within two mature forest plots and four fallows were characterized by photon flux density (PPFD) measurements; ☀ represents PPF measurement. Soil samples within each fallow and mature forest plot were collected below the litter layer at two depths (0-20 cm and 20-40 cm). Sampling scheme is depicted above for each forest type; ● represents soil sample.

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BIOGRAPHICAL SKETCH

Jamie Nicole Cotta was born and raised in Riverside, California, and began her career in tropical conservation at the University of California, San Diego, where she received a B.S. in Ecology, Behavior and Evolution. During her studies she conducted behavior observations of bonobo chimpanzees (*Pan paniscus*), at the San Diego Zoo, and pygmy lorises (*Nycticebus pygmaeus*), at the Center for Reproduction of Endangered Species. She next assisted a Cornell post-doc with behavioral research on orange-fronted parakeets (*Aratinga canicularis*) in Santa Rosa National Park, Costa Rica. Her undergraduate studies concluded with a semester of Tropical Biology in Monteverde, Costa Rica, where she first became interested in sustainable tropical forest management. She is most proud of her work as a research assistant for the School for Field Studies, in Yungaburra, Queensland, Australia, where she managed a tropical plant nursery and helped to design a restoration planting with a local community tree planting organization (TREAT). Her tropical research experiences fostered an interest in tropical ecology and forest restoration in the tropics, leading her to pursue a Masters of Science degree in Interdisciplinary Ecology at the University of Florida. Upon graduation she plans to apply her experience and education within an NGO setting, helping businesses and communities adopt more sustainable practices and lifestyles.