

THE EFFECTS OF HARVEST ON THE POPULATION STRUCTURE OF
ASTROCARYUM MEXICANUM AND ITS POTENTIAL FOR UNDERSTORY
CULTIVATION

A THESIS SUBMITTED TO THE GRADUATE DIVISION OF THE
UNIVERSITY OF HAWAII IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

IN

BOTANY

DECEMBER 2007


By
Dana Crompton

Thesis Committee:

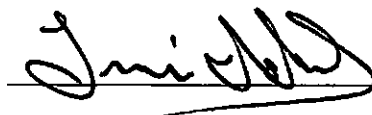
Tamara Ticktin, chairperson
Lawren Sack
Travis Idol

We certify that we have read this thesis and that, in our opinion, it is satisfactory in scope and quality as a thesis for the degree of Master of Science in Botany.

THESIS COMMITTEE



Chairperson



ACKNOWLEDGEMENTS

I would like to first thank my committee, Tamara Ticktin, Travis Idol and Lawren Sack. They provided helpful guidance and feedback throughout every step of the process. I am especially grateful to my academic advisor, Tamara, for her invaluable encouragement and support.

Thank you to the many people who helped me in Mexico. First, I extend my gratitude to everyone at El Proyecto Sierra Santa Marta, especially Oswaldo Graciano Porras, Daniel Tehuitzil Valencia and Susana Cruz. They provided not only logistical support, but also friendship. Special thanks to Oswaldo for proposing the project. I am grateful to the many residents of Magallanes, Venustiano Carranza, and Guadalupe Victoria for their hospitality and assistance. I must thank the families of Juana Gutiérrez and Simplicio Mateo, as well as Isabel Málaga and Victor Chapol Xoca for taking such good care of me and for the wonderful homemade tortillas. Thank you to Rubén Mateo, Leobardo Gutiérrez, Apolinar Gutiérrez, and their families for all their help and kindness. Most importantly, I thank Victor Chapol Xoca for all his field work and advice. Without his help, this project would not have been possible.

Finally, I thank my friends and family for their unlimited patience and support. And, I would like to take this opportunity to thank my father for his love of nature and sense of adventure.

ABSTRACT

Astrocaryum mexicanum is a native, understory palm of the tropical rainforests of the Sierra Santa Marta in southeastern Mexico. Local residents have traditionally harvested *A. mexicanum*, relying on its edible inflorescences as a food source as well as a trade commodity. Harvest pressure has increased drastically in recent years as a result of expansion of the local market, as well as habitat loss due to deforestation. This study assessed the current harvest intensity of *A. mexicanum* inflorescences and evaluated its effects on population structure. Seedling growth and inflorescence production were compared in the continuum of light conditions of forest environments subject to different management practices. We found that the structure of *A. mexicanum* populations subject to harvest differed significantly from that of unharvested populations. Seedling growth and inflorescence production were greater in the higher light environments. As a result of this study, *A. mexicanum* is recommended for understory cultivation in the secondary forests that are prevalent throughout the region.

TABLE OF CONTENTS

Acknowledgments.....	iii
Abstract.....	iv
List of Tables.....	vii
List of Figures.....	viii
Chapter I. Introduction.....	1
Objectives.....	4
Literature Review.....	5
Non-timber Forest Products.....	5
The Effects of Light Variation on Growth and Reproduction of Understory Plants.....	7
Understory Palms and the Effects of Light Variation on Growth and Reproduction.....	9
Factors Affecting Seed Germination in the Tropics.....	11
The Effects of Flower and Fruit Harvest on Population Structure and Dynamics.....	13
Biosphere Reserves.....	16
Study Species.....	17
Study Site.....	19
Literature Cited.....	25
Chapter II. The Effects of Inflorescence Harvest on Population Structure of <i>Astrocaryum mexicanum</i> in the Sierra Santa Marta.....	30
Introduction.....	30
Objectives.....	32
Methods.....	32
Results.....	38
Discussion.....	41
Conclusion.....	45
Literature Cited.....	46
Chapter III. Growth, Productivity and Germination of <i>Astrocaryum mexicanum</i> its Potential for Understory Cultivation.....	48
Introduction.....	48
Objectives.....	50
Methods.....	51
Results.....	60
Discussion.....	72
Conclusion.....	76
Literature Cited.....	78
Chapter IV. Conclusions.....	80
The Effects of Human Management on NTFP species and their Environments.....	80
Growth and Productivity in Different Forest Sites and Implications For Understory Cultivation.....	81

Implications for Forest Conservation and Economic Development	82
Appendix A. Poisson Regression table for Chapter III.....	85
Appendix B. Relationship of Original Number of Leaves and New Leaves Produced.....	86
Appendix C. Final Weights of Out-planted Seedlings.....	87

LIST OF TABLES

<u>Table</u>		<u>Page</u>
2.1	Correlations of Ranked Harvest Intensity and Size-Class Proportions	40
3.1	Mean Canopy Cover and Light Transmittance.....	61
3.2	Growth of Out-planted Seedlings.....	66

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1.1 Map of Study Site	24
2.1 Size-Class Densities	39
2.2 Population Densities	40
3.1 Light Transmittance for Wet and Dry Seasons.....	61
3.2 Light Transmittance versus Canopy Cover	62
3.3 Leaf Production in the Three Forest Sites	63
3.4 Light Transmittance and Leaf Production	64
3.5 Relative Growth Rate of Seedlings	65
3.6 Increase in Dry Mass of Seedlings.....	66
3.7 Increase in Shoot Mass	67
3.8 Increase in Root Mass	67
3.9 Root: Shoot Ratios	68
3.10 Root Mass Fractions	68
3.11 Inflorescence Production	70
3.12 Percent Germination per Treatment.....	71
3.13 Time until Germination.....	72

CHAPTER I

Introduction

Tropical forests worldwide provide for the basic subsistence and economic needs of their rural inhabitants. Other than timber, products extracted from forests include: fruit, seeds, leaves, fiber, resin, roots, and bark. Collectively these are known as non-timber forest products (NTFP). Approximately 80% of the developing world depends on these resources for food, medicine and shelter. The trade of NTFP furthermore provides a valuable source of income for several million households worldwide (e.g., Anderson 1990, Balick 1986, Cunningham 2001, Elevitch 2004, Endress et al. 2006, FAO 1995, Plotkin and Famolare 1992).

Conservationists have recognized the potential of NTFP extraction as a strategy for environmental conservation that may at the same time augment local economies. The cultural and economic value of NTFP for local people provides an incentive to conserve these resources and the environment in which they grow. Given the potential to generate income from the sustainable extraction of these theoretically renewable resources, NTFP extraction poses a workable alternative to deforestation (e.g., Anderson 1990, Plotkin and Famolare 1992, Vasquez and Gentry 1989). Often for large-scale commercial agriculture or cattle ranching, deforestation destroys millions of hectares of tropical forests annually (Mayaux 2005). This results in the loss of biodiversity and forest resources as well as the impoverishment of local people who rely on them (e.g., Anderson 1990, Gomez-Pompa and Kaus 1990). In contrast, the extraction of NTFP, particularly understory species, can allow for the forest overstory to be maintained (Elevitch 2004).

Although promoted as a conservation strategy, many NTFP species are themselves threatened as a result of overexploitation. In many cases, unsustainable exploitation is attributed to a lack of understanding of species ecology and of harvest practices (Boot and Gullison 1995, Hall and Bawa 1993). The ecological impacts of NTFP harvest are unknown in most cases despite concerns of over-exploitation (Endress et al. 2006). Increased harvesting pressure occurs as a consequence of human population expansion, increasing market demands and the loss of habitat (e.g. Perez et al. 2003, Olmsted and Alvarez-Buylla 1995, Sinha and Bawa 2002, Soeharto and Newton 2000).

The majority of NTFP are harvested from the wild; however in some cases cultivation is a viable alternative that may reduce harvest pressure on wild populations. Cultivation has the potential to increase yields, although it also requires a greater investment of labor and time. Consumer demand must therefore be great enough to provide economic incentive for cultivation instead of the continued wild harvest. As not all species are easily domesticated, spatial and temporal patterns of growth, productivity and their implications for cultivation should be assessed (Ticktin et al. 2003).

The Sierra Santa Marta of Mexico is a region where people depend on NTFP for both their subsistence and economic needs. The Proyecto Sierra Santa Marta (PSSM) is a non-governmental organization that advocates the sustainable use and conservation of natural resources, while contributing to the socioeconomic development of the communities of the Sierra Santa Marta. This organization, like others around the world, promotes the cultivation of native, understory NTFP under the canopies of primary and secondary forests (Ticktin et al. 2003).

The Sierra Santa Marta is located within the Los Tuxtlas Biosphere Reserve in southern Veracruz, Mexico. Primarily a result of intensive cattle ranching beginning in the late 1950s, the region has suffered massive deforestation. Between 1950 and 1991 77% of the existing forest cover was lost. Deforestation for cattle grazing continues in the buffer zones (Dirzo and Garcia 1992, Durand and Lazos 2004). The residents of Santa Marta are characterized by extreme poverty with the majority surviving on subsistence farming and the leasing of their land for cattle grazing (Paré and Velazquez 1997).

For as long as residents have lived in the Sierra Santa Marta, they have harvested a native understory palm, *Astrocaryum mexicanum*. They have relied on it as a food source as well as a trade commodity (Durand and Lazos 2004). The flowers, fruit and youngest leaf shoot are all edible; however, it is the immature inflorescence that is of greatest value to local people. In recent years, harvest intensity has increased drastically due to the expansion of the local market, as well as the loss of *A. mexicanum* populations resulting from forest destruction. In some communities, people have discontinued cultivation of traditional crops and have begun to trade *A. mexicanum* for staples such as corn. Demand is particularly high in the communities where the resource is no longer available due to the loss of primary forest habitat. As a result of the rise in demand and the decrease in availability of this important resource, there is increasing interest in the potential for its cultivation.

Astrocaryum mexicanum, known locally as “chocho”, is a shade-tolerant palm common in the understories of the remaining patches of primary forest in the Sierra Santa Marta. Studies have demonstrated that understory species are chronically light-limited

and have increased rates of growth and reproductive output in environments of greater light availability such as forest gaps (e.g., Martinez-Ramos and Alvarez-Buylla 1995, Popma and Bongers 1991, Svenning 2002). The results of these studies suggest an opportunity for the enhanced growth and flower production of understory species in the varied light environments of secondary forests, “managed” or partially cleared primary forests and in homegardens. This information has important implications for the cultivation of understory species in regions where secondary and managed forests are common.

OBJECTIVES

My objectives for this study were to (1) assess the harvest intensity of *A. mexicanum* in the Sierra Santa Marta and its effect on plant population structure and to (2) identify potential and optimal conditions for understory cultivation. In Chapter II, I examined harvest intensity through field documentation of inflorescence harvest and interviews with local harvesters. Population structure of *A. mexicanum* was compared between the protected, unharvested populations of the UNAM Biological Research Station at Los Tuxtlas Biosphere Reserve and the harvested populations in the communities of the Sierra Santa Marta. In Chapter III, I assessed potential conditions for cultivation by quantifying light transmittance beneath the canopies of three common forest settings in the Sierra Santa Marta: closed-canopy primary forest, “managed” or partially-cleared-canopy primary forest and homegardens. Seedling growth and inflorescence production were compared in the three settings. Finally, the effects of pre-treatment of *A. mexicanum* seeds on the percent and rate of germination were assessed.

LITERATURE REVIEW

Non-timber forest products (NTFP)

For millennia people have depended upon forest species for non-timber products such as fruit, seeds, leaves, fiber, resin, oils, and bark for their subsistence and economic needs. However, it has been over the last couple of decades that the harvest of these non-timber forest products (NTFP) has attracted considerable attention from conservationists due to the potential for environmental conservation and rural economic development. Hundreds of millions of people worldwide depend on NTFP for financial income (Endress et al. 2004 and 2006, FAO 1995, Vantomme 1997). The value of these theoretically renewable resources provides economic incentive to rural residents to conserve forests. As opposed to the often-permanent loss of biodiversity caused by logging and cattle grazing, NTFP extraction is a potentially sustainable source of income (e.g. Anderson 1990, Goody and Bawa 1993, Mohd. Ali and Mohmod 1997, Plotkin and Famolare 1992, Vasquez and Gentry 1989).

The success of NTFP exploitation as a strategy for conservation and development is dependent on both the ecological and economic sustainability of harvest. In ecological terms, extraction is considered sustainable if harvest has no long-term deleterious effects on the reproduction and regeneration of harvested populations (Hall and Bawa 1993). Although frequently neglected, the impacts on the structure and function of the larger ecosystem should be considered (Boot and Gullison 1995, Ticktin 2004).

Unfortunately, in many cases NTFP are not being exploited sustainably, resulting in the decline of many species (e.g. Hall and Bawa 1993, Olmsted and Alvarez-Buylla 1995, Peres et al. 2003, Sinha and Bawa 2002, Soeharto and Newton 2000, Vasquez and

Gentry 1989). According to Boot and Gullison (1995), there are “few if any examples of demonstrably sustainable extraction”. The pressure on wild populations increases as a result of human population expansion, increased market demands, and the loss of habitat (Cunningham 1993, Haeruman 1997).

The sustainability of exploitation depends on the understanding of both the harvest practices and the ecology of the resource (Cunningham 2001, Haeruman 1997, Peres et al. 2003, Singha and Bawa 2002, Vasquez and Gentry 1989). Unsustainable harvest of NTFP species is frequently a result of the lack of quantitative information in both areas (e.g. Boot and Gullison 1995, Endress et al. 2004, Gould 1998, Soeharto and Newton 2000). In order to determine the sustainability of harvest, knowledge of the species’ natural distribution and abundance, population dynamics, as well as of variations in growth and productivity is imperative. Growth and yield data are often lacking for NTFP species, which makes it impossible to determine the impacts of harvest (Gould 1998). Information on product demand is likewise necessary in determining the sustainability of harvest (Cunningham 2001, Hall and Bawa 1993, Ticktin et al. 2003).

Cultivation of NTFP can in some circumstances provide relief of harvesting pressure on wild populations. It may be expected to increase yields, although it also requires a greater investment of labor and time. Consumer demand must be great enough to provide economic incentive for cultivation as opposed to the continued wild harvest. As not all species are easily domesticated, ecological studies on the spatial and temporal patterns of growth and productivity are required (Ticktin et al. 2003). Comparisons should be made between wild and cultivated plants, under different harvesting regimes, and in different forest types and anthropogenic habitats. The suitability of the crop must

be assessed in terms of ecological as well as socioeconomic information (Cunningham 1993, Ticktin et al. 2003).

The cultivation of shade-tolerant understory species in particular has important conservation and economic implications. NTFP species that grow beneath the canopy of primary and secondary forests provide added incentive for the conservation of these areas. Harvest yield of the cultivated understory species may be increased, while the biodiversity of the forest may potentially be maintained (Elevitch 2004, Ticktin and Nantel 2004).

The effects of light variation on the growth and reproduction of understory plants

Light is known to be an important limiting factor for growth and reproduction of many tropical understory plants. Studies have demonstrated the increased growth rates of individual understory plants in response to greater levels of irradiance. For example, studies have recognized the enhanced growth of seedlings and understory species that occurs in primary forest gaps (e.g. Martinez-Ramos and Alvarez-Buylla 1995, Pompa and Bongers 1991, Svenning 2002).

Variation in the light environment has been shown to influence reproduction in understory plants by such means as increasing the quantity of flowers produced (e.g., Chazdon 1984, Cunningham 1997). Understory palms, in particular, “notoriously enhance seed production after they are exposed to canopy gaps” (Martinez-Ramos and Alvarez-Buylla 1995). Studies have furthermore demonstrated that crown illumination and canopy openness have strong demographic effects on species such as understory palms, a consequence of the increased growth and fecundity under higher illumination (Svenning 2002).

Forest structure and its associated light variability furthermore have important implications for the sustainability of understory species harvest. For example, leaf harvest of the understory palm *Geonoma macrostachys* Mart. was determined to be unsustainable in the closed canopy of primary forest, while semi-open and disturbed forest conditions provided a better environment for sustainable harvest (Svenning and Macia 2002). The capacity for re-growth after harvest of the understory bromeliad *Aechmea magdalenae* was found to be greater in secondary forests than in old-growth forests (Ticktin and Nantel 2004).

These observations have implications for the cultivation of understory NTFP species. As a result of the deforestation of tropical lands, regeneration has led to the increasing prevalence of secondary forests (Ticktin and Nantel 2004, Pulido et al. 2007). Secondary forests in varying stages of succession provide habitat heterogeneity and a diversity of light levels dependent on the degree of canopy closure. Many such areas may provide light conditions that induce cultivated species to grow and produce at improved rates. Furthermore “managed” forest sites are also common in tropical countries as the regulation of shade provided by overstory trees is important in the management of shaded-perennial agroforestry systems. Many farmers manipulate shade levels by partially clearing and thinning the forest canopy (Bellow and Nair 2003). The observed effects of light variation on the growth and reproduction of understory plants has important implications for cultivation in regions where secondary and managed forests are common.

Understory palms and the effects of light variation on growth and reproduction

The palm family (Arecaceae) is one of the most important plant families for rural people in the tropics as it is the most widely used for NTFP such as food, beverages, fibers, thatch, house construction material, medicine, domestic artifacts and handicrafts. All parts of the palm may be used including the leaves, fruit, petioles, trunk, palm heart and sometimes the roots (Balick 1986, Silva-Matos and Watkinson 1998, Scroth et al. 2004, Svenning and Macia 2002). Many palms have the ability to thrive on low-quality soil generally considered unfit for agriculture, and certain species form large and dense populations, a quality that promises greater economic potential (Kahn 1988).

According to Balick (1986), the recognition of the role that agroforestry can play as an alternative to cattle ranching or monoculture of tropical lands has resulted in the need for additional economically attractive multi-use tree species, and palms fit this role. Although most understory palms are able to survive for prolonged periods in deeply shaded environments, light is nevertheless an important limiting factor for growth and reproduction (e.g., Endress et al. 2004, Piñero and Sarukhán 1982, Svenning 2002). Ecophysiological studies of understory palm species support the interpretation that growth patterns are due to light limitation. For example, carbon gain in seedlings has been shown to be light limited along a gradient of light availability from closed understory conditions to small gap centers (Chazdon 1986). Slow, continuous leaf production and long-lived leaves are characteristics of understory palms and represent adaptations to light restriction and temperatures, respectively (Ataroff and Scwarzkopf 1992).

Energetic restrictions influence reproductive patterns. Longer reproductive cycles may be an answer to the energetic problem for plants that produce costly fruits (Ataroff and Scwarzkopf 1992). The probability of fruiting was found to increase with the age (height) of the palm, *Astrocaryum mexicanum*, and the authors suggested that access to light that was the important variable in fruiting cycles (Piñero and Sarukhán 1982).

Two canopy parameters, crown illumination and canopy openness, were found to affect all aspects of the demography of the understory palm, *Geonoma macrostachys*, including growth, reproduction, survival and recruitment. Although this species is shade tolerant, light limitation was demonstrated to influence growth and reproductive rates in the population. The rate of leaf length increase and new leaf production increased with increasing illumination. Early seedling growth rates were greater under higher illumination, although the germination rate remained unaffected. The probability of reproduction, the number of spikes and spike length all increased with increasing illumination. Matrix models suggested that closed-canopy population levels would decline towards extinction were it not for the spatio-temporal heterogeneity created by gap dynamics (Svenning and Macia 2002).

The potential for cultivation was assessed for the understory palm, *Astrocaryum tucuma*, the fruit of which is a locally important trade commodity in Brazil. The required burning of the seeds for germination has allowed this species to become common in disturbed areas. Reproductive output of this palm was found to vary widely among areas such as secondary forest of different ages, fallows, open fields and homegardens. The homegardens and open fields had the highest yield and the highest percentage of

productive palms. Shading in the other environments reduced fruit yield and delayed the onset of fruit production (Scroth et al. 2004).

Factors affecting seed germination in tropical forests

The light requirements for seed germination are an important criterion for distinguishing early and late successional species in tropical forests (Baskin and Baskin 2001). Light-demanding pioneer species germinate, establish and grow to maturity only in canopy gaps, while non-pioneer species germinate and establish primarily in the shade, but often attain maturity when juveniles are released from suppression (Swaine and Whitmore 1988). Although shade and gaps are generally optimal for the germination of non-pioneer and pioneer species, respectively, the opposite is true for some species (Baskin and Baskin 2001.) Studies on the environmental conditions required for the germination of seeds of late successional species have been conducted by comparing germination of seeds sown in shaded and non-shaded conditions. Results vary according to species: some exhibit higher percentages of germination in the shade, others in the non-shaded environment. Results of similar comparative studies on pioneer species more consistently demonstrate higher percentages of germination under non-shaded conditions (Raich and Khoon 1990).

Seed size is another important difference between pioneer and non-pioneer species. (Baskin and Baskin 2001). The large seeds of shade-tolerant species are thought to be of adaptive value because they contain relatively large amounts of food reserves that can be used for seedling establishment in the reduced light levels on the forest floor (Baskin and Baskin 2001). Dispersal syndromes have furthermore led to the selection for and production of different seed sizes (Khurana and Singh 2001).

An adequate amount of water must be available in the soil for imbibition and subsequent germination of seeds (Khurana and Singh 2001). Furthermore, many rainforest species produce seeds that are recalcitrant. This type of seed exhibits little or no dormancy and cannot be dried below critical moisture contents. High moisture conditions are therefore required for germination of recalcitrant seeds (Baskin and Baskin 2001). Germination of such seeds may be prevented in gaps due to increased temperatures (Raich and Khoon 1990) and, consequently, a decrease in water availability (Baskin and Baskin 2001).

The accumulation of leaf litter on the soil surface may be crucial for some water demanding species by reducing evaporation from the soil. Leaf litter may influence seed germination by moderating the amount of light that reaches the seeds, modifying the soil temperature and chemical environment, or by potentially hiding seeds from predators (Becerra et al. 2004).

The most common type of dormancy in seeds of rainforest trees is physiological dormancy, which is caused by an inhibiting mechanism of the embryo that prevents radicle emergence. Such mechanisms include covering structures (such as endosperm, seed or fruit coats) that impede the entry of water and oxygen, or restrict growth of the embryo. Germination of seeds with physiological dormancy may be induced by exposure to high temperatures, low temperatures, to light, dark or by hydration (Baskin and Baskin 2001).

Other rainforest tree species have morphological dormancy, a result of underdeveloped embryos. The majority of palms display morphophysiological dormancy, or underdeveloped embryos that have physiological dormancy. In order for

seeds with morphophysiological dormancy to germinate, the embryo must grow to a species-specific critical size and the physiological dormancy must be broken.

Environmental conditions, such as a change in temperature are responsible for each of these events (Baskin and Baskin 2001).

Palm seeds are notorious in the nursery trade for their slow and uneven patterns of germination. This is often attributed to their hard, impermeable seed coats that restrict the entry of water and oxygen and impede the emergence of the cotyledon. Germination studies of such species have shown that many respond to a number of different pre-treatments that promote faster and more uniform germination. For example, scarification, either mechanical or chemical, has been shown to increase the rate of germination of palm species with hard seed coats. Similarly, seeds soaked in water for a few days have also been shown to have a much higher rate of germination than did untreated seeds. (Moussa et al. 1998, Potvin et al. 2003).

In an extensive study of the factors affecting the germination of the palm *Hyphaene thebaica*, Moussa et al. (1998) found that freshly collected seeds exhibited a substantially higher rate of germination than did seeds that had been stored for one year. Furthermore, by collecting the seeds directly from the trees, it was possible to minimize the degree of infestation by insect larvae particularly that of bruchid beetles (Marcus and Banks 1999, Potvin et al. 2003).

The effects of flower and fruit harvest on population structure and dynamics

The harvesting of flowers and fruit is often assumed to have less of an impact on plant populations than harvesting of the stem, bark, roots or the removal of the entire plant. However the sustainability of harvest depends on the frequency, intensity and

manner of the harvest as over time it may impact population dynamics such as seedling recruitment (e.g. Cunningham 2001, Peres et al. 2003).

General predictors of resiliency or vulnerability of NTFP species to harvest include: geographic distribution, habitat specificity, local population size, part of plant used, growth rate, reproductive biology and the variety of uses of the plant. In terms of flower and fruit harvest, species that annually produce many small flowers have a greater opportunity for sustainable harvest than those that produce a few large flowers, those that are serotinous or those that exhibit mast fruiting. Monoecious species furthermore possess a greater degree of resiliency to harvest than do dioecious species (Cunningham 2001).

Fruit and flower harvests that have proven to be unsustainable often involve destructive harvesting techniques. In some cases, the harvest of fruit and flowers is achieved by the lopping off of branches or the felling of entire trees. This often occurs in an effort to maximize the short-term gain and minimize the investment of time and labor. In such situations where the target species is damaged or killed during the process of harvest, NTFP extraction is rarely sustainable (e.g. Cunningham 2001, Singha and Bawa 2002, Soehartono and Newton 2000, Vasquez and Gentry 1989).

Harvest of reproductive structures such as flowers and seeds that does not involve destructive harvesting techniques may still have dramatic influences on the targeted population by affecting regeneration. Ensuring adequate regeneration is one of the biggest challenges for designing sustainable extraction systems. It is imperative for the maintenance of the population as well as the future availability of the harvested product. (Boot and Gullison 1995, Zuidema and Boot 2002).

The recruitment history of a species is reflected by the size class distribution of individuals within the population (Freckleton 2003). Populations with large numbers of juveniles relative to adults (a negative slope in a plot of size class proportions) are often considered to indicate that a population is stable or perhaps growing (Condit et al. 1998). In some cases the harvest of species with abundant fruiting proved unsustainable based upon marked reduction in recruitment and changes in size structure profiles (e.g. Boot and Gullison 1995, Peters 1994).

The history and intensity of harvest are major determinants of population size structure. A study of the size-class distributions of *Pterocarpus angolensis* populations harvested for timber in Tanzania revealed that small as well as large size classes were missing. This was attributed to the uncontrolled logging of the largest trees and the significant relationship between tree size and seed production. Based on this study, the authors concluded that current harvest practices were unsustainable (Schwartz, et al. 2002).

An alternative scenario is illustrated by a size-class profile of *Sclerocarya birrea* subspecies *caffra* harvested for seeds in South Africa. Comparisons of harvested and unharvested populations proved that the low proportion of seedlings was not due to over-harvesting-but rather a result of the unequal number of years the individuals spend in each class as well as the highly episodic regeneration characteristic of the species (Emanuel et al. 2005).

Factors other than recruitment history may affect the size distribution. Lower growth rate of juveniles and lower survival at any stage produce more steeply declining distributions. Faster growing species will have fewer juveniles than slower growing

species, even when population growth is equal. An empirical evaluation of 216 tree populations showed that juvenile growth was the strongest predictor of the size distribution. Growth was found to correlate with size distribution-but only weakly and only in understory species. Size distribution did not correlate with survival-or with growth of canopy species (Condit et al. 1998).

Population structure surveys represent static information that may not serve to make predictions for further population trends. However, they may provide insight into population stability and regeneration potential. Furthermore, they can be powerful tools used to assess the impacts of harvest by comparing the size distribution between harvest and unharvested populations (Lawes and Obiri 2003).

Biosphere Reserves

Biosphere reserves are established to promote and demonstrate a balanced relationship between humans and the biosphere. They represent an international network of protected areas initiated by UNESCO's Man and Biosphere Programme in the early 1970's. The proposed functions of biosphere reserves include: (i) conservation of landscapes, ecosystems, as well as species and genetic variation. (ii) socio-economic development which is culturally and ecologically sustainable, and (iii) logistical support for demonstration projects, environmental education, as well as research and monitoring related to issues of conservation and sustainable development (Tangley 1988, UNESCO 2005).

Biosphere reserves consist of three distinct zones. The core area is region of strict preservation devoted to long-term protection. In the surrounding buffer zone or zones a variety of activities, such as traditional land uses, are permitted as long as they are

compatible with the protection of the core area. Beyond the buffer zone is the reserve's outer transition area where in theory, sustainable resource management practices are promoted and developed in local communities (Tangley 1988, UNESCO 2005).

However, a considerable gap exists between the theory and the reality of biosphere reserves. For example, the activities practiced in many designated buffer zones are not always sustainable, such as large-scale monoculture and cattle ranching. Despite the value of the biosphere reserve concept, their overall effectiveness is often debated (Duffy 2001, Tangley 1988).

STUDY SPECIES

Astrocaryum mexicanum, Liebm. ex Mart. (Arecaceae) is a monoecious, understory palm of the tropical rainforest, with a natural range extending from Veracruz, Mexico to the Atlantic coast of Honduras (Eguiarte et al. 1993). Long-term studies on the demography and population ecology of *A. mexicanum* beginning in 1975 at Los Tuxtlas Biological Field Station of the Instituto de Biología, Universidad Autónoma Nacional de México (18°36'N, 95°07'W) Veracruz have provided much of the information known about this species (e.g. Martinez-Ramos and Alvarez-Buylla 1995, Piñero et al. 1977, Piñero and Sarukhán 1982, Sarukhán 1978 and 1980). *A. mexicanum* often dominates the forest understory and may attain population densities of more than 1,000 mature individuals per hectare (Martinez Ramos and Alvarez-Buylla 1995). This long-lived palm (oldest ages recorded about 130 years) has an average mature height of 1-4 meters. The trunk, petioles, flowers and fruit are covered with sharp, flat, black spines 3-5 cm in length (Martinez-Ramos and Alvarez-Buylla 1995, Martinez-Ramos, et al. 1988).

A. mexicanum flowers in mid-April following a short, 4-5 week dry season. Both female and male flowers are present on the inflorescence. Individuals are self-compatible, but self-pollinators produce lower fruit set than out-crossed individuals and there is a high out-crossing rate. Long-distance cross-pollination is performed by several species of beetles (Eguiarte et al. 1993).

In the primary forest of the Los Tuxtlas Biological Field Station, *A. mexicanum* was observed to have a mean probability of reproduction (proportion of adults bearing flowers) of 41%. An average of 1.6 infructescences is produced per tree, with an average of 25 fruit per infructescence (Brewer and Webb 2001, Piñero and Sarukhán 1982). Information on the mean number of inflorescences produced is not available. Maturation occurs mostly between late September and late October. Fruits are one-seeded nuts (technically a nuculanium) 3-5cm long and densely covered with spines (Brewer 2001, Piñero and Sarukhán 1982). The edible endosperm is solid and white. The age of first reproduction is reported to be approximately 22 years (Mendoza et al. 1987, Piñero and Sarukhán 1982).

Primary dispersal of seeds is through gravity. A variety of mammals are responsible for both seed dispersal and predation. The spiny pocket mouse (*Heteromys desmarestianus*) and the Mexican deer mouse (*Peromyscus mexicanus*) are common predators/dispersers (Brewer and Webb 2001, Sanchez-Cordero and Martinez-Gallardo, 1998). Heavy seed predation by squirrels while fruit is still attached to the palm has also been reported (Martinez-Ramos and Alvarez- Buylla 1995). Insect predation may occur even before fruit is mature and beetle infestation is common in fruit on the ground (Brewer and Webb 2001). Most reports suggest germination occurs after approximately

6 months on the forest floor. (Brewer and Webb 2001, Martínez Ramos and Álvarez-Buylla 1995).

Both growth and reproduction of *A. mexicanum* are light-limited (e.g. Piñero and Sarukhán and Piñero et al. 1982). In forest gaps where the amount and/or quality of light are higher, both immature and mature palms grow significantly faster in gap than in mature forest (Martínez-Ramos et al. 1988).

Fecundity in forest gaps is twice that under closed canopy, as both the probability of reproduction, and the reproductive output are greatly enhanced (Martínez-Ramos and Álvarez-Buylla 1995, Martínez-Ramos et al. 1988).

Although both growth and fecundity increase under gap conditions, the finite population growth rate of *A. mexicanum* varies from under-equilibrium in gaps to above-equilibrium in mature forest sites (Martínez-Ramos et al. 1988). In gaps the palms double their fecundity, pre-dispersal seed predation is reduced, and recruitment is greater, yet seedling mortality increases significantly. The authors attributed this to high intraspecific competition (Martínez-Ramos and Álvarez-Buylla 1995, Martínez-Ramos et al. 1988).

STUDY SITE

The Sierra Santa Marta is located in buffer zone of the Los Tuxtlas Biosphere Reserve in the south of the Mexican state of Veracruz, on the Gulf of Mexico coast. This reserve, established by the federal government 1998 is comprised of 334,002 hectares of protected area. A total of 29,720 hectares of highly preserved core zones where no human activity is permitted are located at: San Martín Tuxtla, Sierra Santa Marta and the San Martín Pajapan. The buffer and transition zones are comprised of 125,402 hectares

and 178,880 hectares, respectively. The field station of the Institute of Biology of UNAM is located in the Los Tuxtlas Reserve (Guevara-Sada et al. 2000).

The region is considered the northern limit of the tropical rainforest in America (Durand and Lazos 2004). Altitudes within the area range from 0-1,500 meters, and three volcanoes-the Yohualtajapan, the Santa Marta, and the San Martín Pajapan-are conspicuous features of the landscape. The great heterogeneity of topography and climate gives rise to a diversity of environments and an equally impressive array of biological diversity. The dominant ecosystem is tropical rainforest, though tropical moist deciduous forests, mesic forests, mangroves and savannahs also exist. The region is home to over 3,000 higher plant and 1,149 animal species. At least 20 of the plant species are endemic to the area (Durand-Smith 2000, Durand and Lazos 2004).

This region is characterized by not only biological, but also cultural richness. The buffer zone hosts 288 communities, many of which are Nahua and Popoluca indigenous groups. The residents of these communities represent some of the most economically marginalized in the country. Approximately 90% of the population survives on *milpa* subsistence agriculture. Due to drastic environmental and social changes, much of the self-sufficiency of this traditional agricultural system has been lost (Paré and Velazquez 1997).

Primarily a result of intensive cattle ranching beginning in the late 1950s, the region has suffered massive deforestation. Between 1950 and 1991 77% of the existing forest cover was lost. Deforestation for cattle grazing continues in the buffer zones to this day, and the area is considered one of the major deforestation fronts in Latin America (Duran and Lazos 2004).

In addition to deforestation, the introduction of modern agricultural technology has contributed to soil degradation, river pollution and the occurrence of devastating forest fires (Paré and Velazquez 1997). The traditional *milpa* agriculture is characterized by slash and burn cultivation, which involves a critical fallow period for croplands. The introduction of modern agricultural techniques has involved a transformation to monoculture, loss of the fallow period, and a reliance on artificial inputs. Consequently, cultivation, 90 percent of which is for subsistence, has become unsustainable (Paré and Velazquez 1997).

Environmental degradation has furthermore resulted in a loss of nutritional resources including protein (such as fish, agouti and peccary) and wild harvested forest goods. In conjunction with the decreased sufficiency of crops, the population has experienced a reduction in the quality of their nutrition. For many residents, their diet is restricted to corn and sometimes beans (Paré and Velazquez 1997).

Three small villages in the northeast of the Sierra Santa Marta, Magallanes, Venustiano Carranza and Guadalupe Victoria are the focal communities of this study. These communities were formed in the 1960's and 1970's when most of the region was colonized. The environment at the time of colonization was dense, uninhabited tropical rainforest, extremely isolated from other settlements. The Mexican government approved occupation of the land and both communities formed *ejidos*, a Mexican type of land tenure system.

Magallanes is a community of Popluca indigenous people who first arrived to the area in 1960. They came from Ocotac Chico, an area in the lowlands of the Sierra Santa Marta looking for land on which to continue their traditional *milpa* agriculture. However,

the new environment and its poor quality soils produced low harvest yields. The colonists supplemented their diet by hunting and gathering, yet soon turned to commercial agriculture and logging in order to satisfy their basic needs. Commercial agriculture proved profitable for a short time, yet as yields diminished residents began to convert their land to cattle pasture. Cattle-ranching was encouraged by the Mexican government, and residents were provided with financial incentives for further forest clearance. Since 1960, approximately 94% of the original forest cover pertaining to Magallanes has been lost to deforestation and wildfires.

The community of Venustiano Carranza was first colonized in 1967 by landless, *mestizo* peasants mostly from the region of Los Tuxtlas. Like the residents of Magallanes, settlers describe the colonization as a time of great suffering. Colonists relied upon forest products such as *Astrocaryum mexicanum* as a means of survival. Failed agricultural endeavors resulted in the introduction of cattle ranching in 1974. Between 1967 and 1999, approximately 86% of the original forest cover of Venustiano Carranza was cleared (Durand-Smith 2000).

Like Magallanes, Guadalupe Victoria is community of Popoluca indigenous people. Settlers from the nearby community of Piedra Labrada founded this community in 1973. Guadalupe Victoria was one of the last to be communities to be established in the Sierra Santa Marta, and is considered to have some of the most inhospitable terrain. This community is marked by a history of land disputes, including the expropriation of land when the Los Tuxtlas Biosphere Reserve was established in 1998. Approximately half of the land pertaining to this community has been converted to pasture since the mid 1980's (Graciano-Porras, unpublished).

For all communities, cattle-ranching has been an extensive and low profit activity. Deforestation has promoted soil erosion, changes in climactic conditions and the disappearance of wild plants and animals that were once important food resources. Although the villages of Magallanes and Venustiano Carranza now have roads, electricity, running water, as well as access to schools and health clinics, most residents continue to live in poverty (Durand and Lazos 2004).

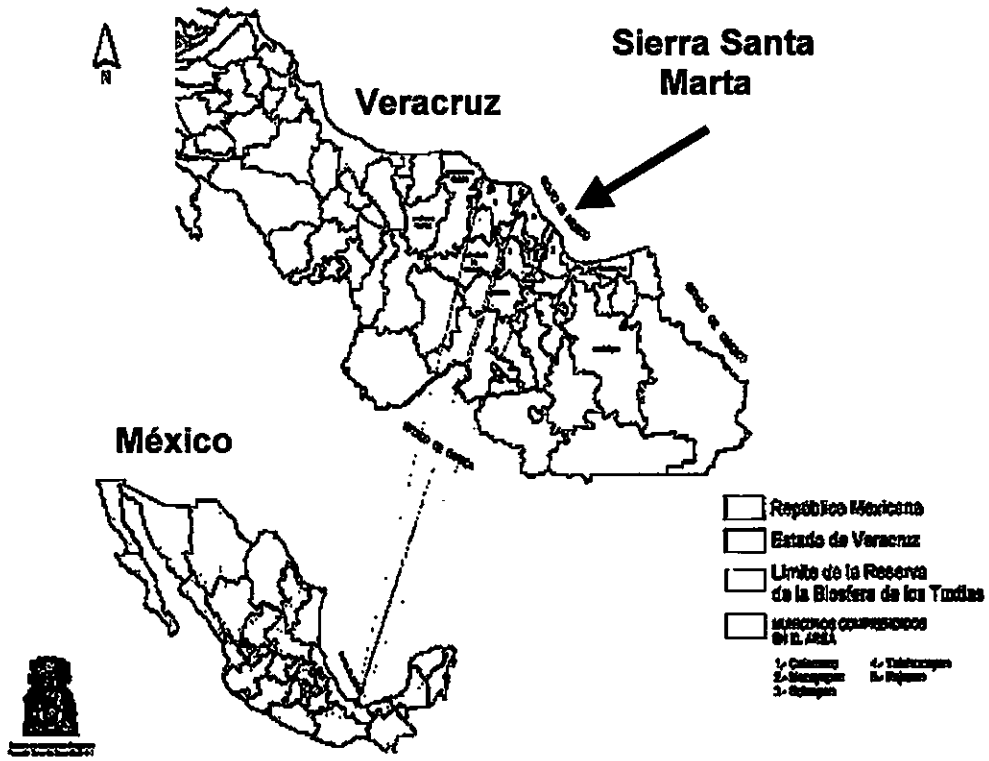


Figure 1.1. Map of study site.

LITERATURE CITED

- Anderson, A.B. 1990. Alternatives to Deforestation: Steps Toward Sustainable Use of the Amazon Rainforest. Columbia University Press, New York.
- Ataroff, M. and T. Schwarzkopf, 1992. Leaf production, reproductive patterns, field germination and seedling survival in *Chamaedorea bartlingiana*, a dioecious understory palm. *Oecologia* 92(2): 250-256
- Balick, M.J. 1986. The Palm-Tree of Life: Biology, Utilization and Conservation. Advances in Economic Botany Volume 6. The New York Botanical Garden, Bronx, New York.
- Baskin, Carol C. and Jerry M. Baskin. 2001. Seeds: Ecology, Biogeography, and Evolution of dormancy and germination. Academic Press San Diego, California.
- Becerra, P.I., J.Celis-Diez and O. Bustamante-Ramiro. 2004. Effects of leaf litter and precipitation on germination and seedling survival of the endangered tree *Beilschmiedia miersii*. *Applied Vegetation Science* 7: 253-257.
- Bellow, J.G. and P.K.R. Nair. 2003. Comparing common methods for assessing understory light availability in shaded-perennial agroforestry systems. *Agroforestry and Forest Meteorology* 114: 197-211.
- Boot, R.G. A. and R.E. Gullison. 1995. Approaches to developing sustainable extraction systems for tropical forest products. *Ecological Applications* 5(4): 896-903.
- Brewer, S.W. and M.A.H. Webb. 2001. Ignorant seed predators and factors affecting the seed survival of a tropical palm. *Oikos* 93: 32-41.
- Chazdon, R. 1986. Light variation and carbon gain in rainforest understory palms. *Journal of Ecology* 74: 995-1012.
- Chazdon, R. And N. Fetcher. 1984. Photosynthetic light environments in a lowland tropical rainforest in Costa Rica. *Journal of Ecology*. 72: 553-564
- Condit, R., R. Sukumar, R.Hubbell, P. Stephen and R.B. Foster. 1998. Predicting population trends from size distributions: a direct test in a tropical tree community. *The American Naturalist* 152(4): 495-509.
- Cunningham, A.B. 2001. Applied Ethnobotany: People, Wild Plant Use, and Conservation. Earthscan Publications Ltd, London and Sterling, VA.
- Cunningham, S.A. 1997. The effects of light environment, leaf area, and stored carbohydrates on inflorescence production by a rainforest understory palm. *Oecologia* 111: 26-44.
- Dirzo, R. and M.C. Garcia. 1990. Rates of deforestation in Los Tuxtlas, a Neotropical area in southeast Mexico. *Conservation Biology* 6: 84-90.
- Duffy, S.B., M.S. Corson and W.E. Grant.. Simulating land-use decisions in La Amistad Biosphere Reserve in Costa Rica and Panama. *Ecological Modelling* 140: 9-29.
- Durand, L. And E. Lazos. 2004. Colonization and tropical deforestation in the Sierra Santa Marta, Southern Mexico. *Environmental Conservation* 31(1): 11-21.
- Durand-Smith, L. 2000. La colonización en la Sierra Santa Marta: Perspectivas ambientales y deforestación en una región de Veracruz. PhD. Thesis. UNAM.
- Eguiarte, L.E., A. Burquez, J. Rodriguez and M. Martinez. 1993. Direct and indirect estimates of neighborhood and effective population size in a tropical palm, *Astrocaryum mexicanum*. *Evolution* 47(1): 75-87.

- Elevitch, C.R. 2004. *The Overstory Book: Cultivating Connections With Trees*. 2nd Edition. Permanent Agriculture Resources. Holualoa, Hawaii, USA.
- Emanuel, P.L., C.M. Shackleton and J.S. Baxter. 2005. Modeling the sustainable harvest of *Sclerocarya birrea* subspecies *caffra* fruits in the South African lowveld. *Forest Ecology and Management* 214: 91-103.
- Endress, B.A., D.L. Gorchov and E.J. Berry. 2006. Sustainability of a non-timber forest product: Effects of alternative leaf harvest practices over 6 years on yield and demography of the palm *Chamaedorea radicalis*. *Forest Ecology and Management* 234 (1-3): 181-191
- Endress, B.A., D.L. Gorchov, and R.B. Noble. 2004. Non-timber forest product extraction: effects of harvest and browsing on an understory palm. *Ecological Applications* 14(4): 1139-1153.
- FAO 1995. Non-wood forest products for rural income and sustainable forestry. FAO technical papers, Non-Wood Forest Products Series. FAO, Rome, Italy
- Freckleton, R.P., D.M Silva-Matos, M.L.A. Bovi, and A.R. Watkinson. 2003. Predicting the impacts of harvesting using structured population models: the importance of density dependence and timing of harvest for a tropical palm tree. *Journal of Applied Ecology* 40: 846-848.
- Goody, R.A. and K.S. Bawa. 1993. The economic value and the sustainable harvest of plants and animals from the tropical forest: Assumptions, hypotheses, and methods. *Economic Botany* 47(3): 215-219.
- Gómez-Pompa, A. and A. Kaus. 1990. Traditional management of tropical forests in Mexico. In *Alternatives to Deforestation: Steps Toward Sustainable Use of the Amazon Rainforest*. Columbia University Press, New York.
- Gould, K., A.F. Howard and G. Rodriguez. 1998. Sustainable production of non-timber forest products: Natural dye extraction from El Cruce Dos Aguadas, Peten, Guatemala. *Forest Ecology and Management* 111: 69-82
- Graciano-Porras, O. (unpublished thesis) Luchando por la tierra y por la vida: Las estrategias de subsistencia y manejo de recursos naturales en una comunidad indígena en la Reserva de la Biosfera de los Tuxtlas, Veracruz. Universidad Autónoma Metropolitana, Mexico City, Mexico.
- Guevara-Sada, S., J. Laborde-Dovali and G. Sanchez-Rios. 2000. La Reserva Biosfera Los Tuxtlas. Documentos de Trabajo, Programa de Cooperación Sur-Sur Sobre Desarrollo Socioeconómico Ambientalmente Adecuado en los Trópicos Húmedos. UNESCO, Paris, France.
- Haeruman Js, Herman. 1997. Non-wood forest products: exploitation and the environment. In Nair, M.N.B, et al. 1998. *Sustainable Management of Non-Wood Forest Products*. University Putra Malaysia Press. Serdang.
- Hall, P. and K. Bawa. 1993. Methods to assess the impact of extraction of non-timber tropical forest products on plant populations. *Economic Botany* 47(3): 234-247.
- Kahn, F. 1988. Ecology of economically important palms in Peruvian Amazonia. *Advances in Economic Botany* 6: 42-49.
- Khurana E. and J.S. Singh. 2001. Ecology of tree seed and seedlings: Implications for tropical forest conservation and restoration. *Current Science (Banglore)* 80(6): 748-757.

- Lawes, M.J. and J.A.F. Obiri. 2003. Using spatial grain of regeneration to select harvestable tree species in subtropical forests. *Forest Ecology and Management* 184: 105-114.
- Marcus, J. and K. Banks. 1999. A practical guide to germinating palm seeds. *Palms (formerly Principes)* 43(2).
- Martinez-Ramos, M. and E.R. Alvarez-Buylla. 1995. Seed dispersal and patch dynamics in tropical rain forests: A demographic approach. *Ecoscience* 2 (3): 223-229.
- Martinez-Ramos, M., M.J. Sarukhán and D. Piñero. 1988. The demography of tropical trees in the context of forest gap dynamics: the case of *Astrocaryum mexicanum* at Los Tuxtlas tropical rainforest. In: *Plant Population Ecology* (D.J. Davy, M.J. Hutchings & A.R. Watkinson, eds.) Blackwell, Oxford, England.
- Mayaux, P., P. Holmgren, F. Achard, H. Eva, H.J. Stibig and A. Branthomme. 2005. Tropical forest cover change in the 1990's and options for future monitoring. *Philosophical Transactions of the Royal Society B-Biology Sciences* 360(1454): 373-384.
- Mendoza, A., D. Piñero, and J. Sarukhán, 1987. Effects of experimental defoliation on growth, reproduction and survival of *Astrocaryum mexicanum*. *Journal of Ecology* 75: 545-554.
- Mohd-Ali, A. R. and A.L. Mohmod. 1997. Non-wood forest resources and products: management and research considerations. In Nair, M.N.B, et al. 1998. *Sustainable Management of Non-Wood Forest Products*. University Putra Malaysia Press. Serdang.
- Moussa, H., H.A. Margolis, P.A. Dube, J. Odongo. 1998. Factors affecting the germination of doum palm (*Hyphaene thebaica* Mart.) seeds from the semi arid zone of Niger, West Africa. *Forest Ecology and Management* 104: 27-41.
- Olmsted, I. and E.R. Alvarez-Buylla. 1995. Sustainable harvesting of tropical trees: Demography and matrix models of two palm species in Mexico. *Ecological Applications* 5(2): 484-500.
- Pare L. and E. Velasquez. 1997. In: L. Pare and E. Velasquez, Editors, *Gestión de recursos naturales y opciones agroecológicas para la Sierra de Santa Marta*, Institución de Investigaciones Sociales y UNAM, Mexico.
- Peres, C.A., C. Baider, P.A. Zuidema, L.H.O. Wadt, K.A. Kainer, D.A. P. Gomes-Silva, R.P. Salomão, L.L. Simões, E.R. N. Franciosi, F.C. Valverde, R. Gribel, G.H. Shepard, Jr., M. Kanashiro, P. Coventry, D.W. Yu, A.R. Watkinson and R.P. Freckleton. 2003. Demographic threats to the sustainability of Brazil Nut exploitation. *Science* 302(5653): 2112-2114.
- Peters, C.M. 1994. *Sustainable Harvest of Non-Timber Forest Plant Resources in Tropical Moist Forest: an ecological primer*. Biodiversity Support Program, Washington, D.C.
- Piñero, D. and J. Sarukhán. 1982. Reproductive behavior and its individual variability in a tropical palm, *Astrocaryum mexicanum*. *Journal of Ecology* 70: 461-472.
- Piñero, D., J. Sarukhán, and E. González. 1977. Estudios demográficos en plantas-*Astrocaryum mexicanum* estructura de las poblaciones. *Boletín de la Sociedad Botánica de México* 37: 69-118.

- Plotkin and Famolare, 1992. Plotkin, M., Famolare, L. (Eds.), 1992. Sustainable Harvest and Marketing of Rain Forest Products. Island Press, Washington, DC.
- Pompa J. and F. Bongers. 1991. Acclimation of seedlings of three Mexican tropical forest tree species to a change in light availability. *Journal of Tropical Ecology* 72: 777-795.
- Potvin, C., R. Cansari, J. Hutton, I. Caisamo and B. Pacheco. 2003. Preparation for propagation: understanding germination of giwa (*Astrocaryum standleyanum*), wagara (*Sabal mauritiiformis*), and eba (*Socratea exorrhiza*) for future cultivation. *Biodiversity and Conservation* 12: 2161-2171.
- Raich, J.W. and G.W. Khoon. 1990. Effects of canopy openings on tree seed germination in a Malaysian dipterocarp forest. *Journal of Tropical Ecology* 6: 203-217.
- Sanchez-Cordero, V. and R. Martinez-Gallardo. 1998. Post dispersal fruit and seed removal by forest dwelling rodents in a lowland rainforest in Mexico. *Journal of Tropical Ecology* 14(2): 139-151.
- Scroth, G., V.H.F. Moraes and M.S.S Mota. 2004. Extractive use, management and in situ domestication of a weedy palm, *Astrocaryum tucuma* in the central Amazon. *Forest Ecology and Management* 202: 161-179.
- Schwartz, M.W., T.M. Caro and T. Banda-Sakala. 2002. Assessing the sustainability of harvest of *Pterocarpus angolensis* in Rukwa Region, Tanzania. *Forest Ecology and Management* 170: 259-269.
- Silva-Matos, D.M. and A.R. Watkinson. 1998. The fecundity, seed, and seedling ecology of the edible palm *Euterpe edulis* in Southeastern Brazil. *Biotropica* 30(4): 595-603.
- Sinha, A. and K.S. Bawa. 2002. Harvesting techniques, hemiparasites and fruit production in two non-timber forest species in south India. *Forest Ecology and Management* 168: 289-300.
- Soehartono, T. and A.C. Newton. 2000. Conservation and sustainable use of tropical trees in the genus *Aquilaria* II. The impact of gaharu harvesting in Indonesia. *Biological Conservation* 97: 29-41.
- Svenning, J.C., 2002. Crown illumination limits the population growth rate of a neotropical understorey palm (*Geonoma macrostachys*, Arecaceae). *Plant Ecology* 159:185-199.
- Svenning, J.C. and M.J. Macía. 2002. Harvesting of *Geonoma macrostachys* Mart. leaves for thatch: an exploration of sustainability. *Forest Ecology and Management* 167: 251-262.
- Swaine, M.D. and T.C. Whitmore. 1988. On definition of ecological species groups in tropical forests. *Vegetatio* 75: 81-86.
- Tangley, L. 1988. A new era for biosphere reserves. *Bioscience* 38(3): 148-155.
- Ticktin, T., T. Johns, and V. Chapol-Xoca. 2003. Patterns of growth in *Aechmea magdalenae* (Bromeliaceae) and its potential as a forest crop and conservation strategy *Agriculture, Ecosystems and Environment* 94: 123-139.
- Ticktin, T. and P. Nantel. 2004. Dynamics of harvested populations of the tropical understorey herb *Aechmea magdalenae* in old-growth versus secondary forests. *Biological Conservation* 120: 461-470.

- Ticktin, T. 2004. The ecological impacts of harvesting non-timber forest products. *Journal of Applied Ecology* 41(4): 11-21.
- UNESCO. 2005 (online access: www.UNESCO.org) World Network of Biosphere Reserves. The MAB program. UNESCO. Paris, France.
- Vantomme, P. 1997. Non-wood forest products for rural income and sustainable forestry. In Nair, M.N.B, et al. 1998. Sustainable Management of Non-Wood Forest Products. University Putra Malaysia Press. Serdang.
- Vasquez, R. and A.H. Gentry. 1989. Use and misuse of forest-harvested fruits in the Inquitos area. *Conservation Biology* 3(4): 350-361.
- Velasquez-Runk, J. 1998. Productivity and sustainability of a vegetable ivory palm (*Phytelephas aequatorialis*, Arecaceae) under three management regimes in northwestern Ecuador. *Economic Botany* 52(2): 168-182.
- Zuidema, P.A. and R.G.A. Boot. 2002. Demography of the Brazil nut tree (*Bertholletia excelsa*) in the Bolivian Amazon: impact of seed extraction on recruitment and population dynamics. *Journal of Tropical Ecology* 18: 1-31.

CHAPTER II

The Effects of Inflorescence Harvest on Population Structure of *Astrocaryum mexicanum* in the Sierra Santa Marta

INTRODUCTION

Tropical forests worldwide provide for the basic subsistence and economic needs of their rural inhabitants. Approximately 80% of the developing world depends on non-timber forest products (NTFP) for food, medicine and shelter (Elevitch 2004, FAO 1995). The trade of NTFP furthermore provides a valuable source of income for several million households worldwide (e.g., Anderson 1990, Cunningham 2001, Elevitch 2004, FAO 1995).

The extraction of NTFP has been recognized as a strategy for environmental conservation that may at the same time augment local economies. The cultural and economic value of NTFP for local people provides an incentive to conserve these resources and the environment in which they grow. Given the potential to generate income from the sustainable extraction of these theoretically renewable resources, NTFP extraction poses a workable alternative to deforestation (e.g., Anderson 1990, Vasquez and Gentry 1989). Often for large-scale commercial agriculture or cattle ranching, deforestation destroys millions of hectares of tropical forests annually (Mayaux 2005). This results in the loss of biodiversity and forest resources as well as the impoverishment of local people who rely on these resources (e.g., Anderson 1990, Gomez-Pompa and Kaus). In contrast, the extraction of NTFP can allow for the forest overstory to be maintained (Elevitch 2004).

Although promoted as a conservation strategy, many NTFP species are themselves threatened as a result of overexploitation. Increased harvesting pressure occurs as a consequence of human population expansion, increasing market demands and the loss of habitat (e.g., Olmsted & Alvarez-Buylla 1995, Perez et al. 2003, Sinha and Bawa 2002, Soehartono and Newton 2000). In many cases, unsustainable exploitation is attributed to a lack of understanding of species ecology and of harvest practices (Boot and Gullison 1995, Hall and Bawa 1993). The harvest of flowers and fruit is often considered to have less of an impact on plant populations than the harvest of vegetative structures or removal of the entire plant. However, harvest of reproductive structures can significantly impact target populations by reducing regeneration (Boot and Gullison 1995, Cunningham 2001, Zuidema and Boot 2002).

The Sierra Santa Marta, located within the buffer zone of the Los Tuxtlas Biosphere Reserve in southern Veracruz, Mexico, is a region where people depend on NTFP for both their subsistence and economic needs. For as long as residents have lived in the region, they have harvested a native understory palm, *Astrocaryum mexicanum* Liebm. ex Mart. (Arecaceae). They have relied on it as a food source as well as a trade commodity (Durand and Lazos 2004). Known locally as “*chocho*”, this palm is shade-tolerant and common in the understories of the remaining patches of primary forest. The flowers, fruit and youngest leaf shoot are all edible; however, it is the immature inflorescence that is of greatest value to local people. In recent years, harvest intensity has increased drastically due to expansion of the local market, as well as the loss of *A. mexicanum* populations resulting from deforestation and forest fires. Furthermore, in some communities, people have discontinued cultivation of traditional crops and have

begun to trade *A. mexicanum* for staples such as corn. Due to rising demand and decreasing availability, there is growing interest in assessing the current status of this important resource and understanding the potential effects of its harvest on population structure in the hopes of promoting the ecological sustainability of harvest.

OBJECTIVES

My objectives were to assess the current harvest intensity of *A. mexicanum* in the Sierra Santa Marta and investigate the impact of flower harvest on population structure. In order to evaluate harvest intensity, we interviewed local harvesters and documented the fate of all inflorescences produced in study plots. I conducted population structure surveys and compared the size-class distributions of harvested populations of the Sierra Santa Marta with unharvested populations at Los Tuxtlas Biological Research Station.

METHODS

Study Site:

The Sierra Santa Marta is located within the buffer zone of the Los Tuxtlas Biosphere Reserve in the south of the Mexican state of Veracruz, on the Gulf of Mexico coast. This reserve, established by the federal government 1998 is comprised of 334,002 hectares of protected area. A total of 29,720 hectares of highly preserved core zones where no human activity is permitted are located at: San Martín Tuxtla, Sierra Santa Marta and the San Martín Pajapan. The buffer and transition zones are comprised of 125,402 hectares and 178,880 hectares, respectively. The field station of the Institute of Biology of UNAM is located in the Los Tuxtlas Reserve (Guevara-Sada et al. 2000).

The region is considered northern limit of the tropical rainforest in America (Durand and Lazos 2004). Altitude within the area ranges from 0-1,500 meters. Three

volcanoes, the Yohualtjapan, the Santa Marta, and the San Martín Pajapan are conspicuous features of the landscape. The great heterogeneity of topography and climate gives rise to a diversity of environments and an impressive array of biological diversity.

The Sierra Santa Marta is characterized not only by biological, but also cultural richness. The buffer zone hosts 288 communities, many of which are Nahuatl and Popoluca indigenous groups. The residents of these communities represent some of the most economically marginalized in the country. Approximately 90% of the population survives on *milpa* subsistence agriculture. Due to drastic environmental and social changes, much of the self-sufficiency of this traditional agricultural system has been lost (Paré and Velazquez 1997).

As a result of intensive cattle ranching beginning in the late 1950s, the region has suffered massive deforestation. Between 1950 and 1991, 77% of the existing forest cover was lost. Deforestation for cattle grazing continues in the buffer zones to this day (Durand and Lazos 2004)

Environmental degradation has furthermore resulted in a loss of nutritional resources including protein and wild harvested forest goods. In conjunction with the decreased sufficiency of crops, the population has experienced a reduction in the quality of their nutrition. (Paré and Velazquez 1997).

Study Species:

Astrocaryum mexicanum, known locally as “chocho”, is a monoecious, understory palm of the tropical rainforest, with a natural range extending from Veracruz, Mexico to the Atlantic coast of Honduras (Eguiarte et al. 1993). Long-term studies on the

demography and population ecology of *A. mexicanum* beginning in 1975 at Los Tuxtlas Biological Field Station of the Instituto de Biología, Universidad Autónoma Nacional de México (18°36'N, 95°07'W) Veracruz have provided much of the information known about this species (e.g., Martínez-Ramos and Alvarez-Buylla 1995, Piñero et al. 1977, Piñero and Sarukhán 1982, Sarukhán 1978 and 1980,). *A. mexicanum* often dominates the forest understory and may attain population densities of more than 1,000 mature individuals per hectare (Martínez Ramos and Alvarez-Buylla, 1995). This long-lived palm (oldest ages recorded about 130 years) has an average mature height of 1-4 meters. The trunk, petioles, inflorescences and fruit are covered with sharp, 3-5 cm-long spines (Martínez-Ramos and Alvarez-Buylla 1995, Martínez-Ramos et al. 1988).

In Los Tuxtlas, *A. mexicanum* was observed to have a mean probability of reproduction (proportion of adults bearing flowers) of 41% (Brewer and Webb 2001, Piñero and Sarukhán 1982). Information on the mean number of inflorescences produced is not available. *A. mexicanum* flowers in mid-April following a 4-5 week dry season. There is an average of 28 female and 212 male flowers on each inflorescence (Sarukhán 1980). Individuals are self-compatible, but self-pollinators produce lower fruit set than out-crossed individuals, and there is a high out-crossing rate. Long-distance cross-pollination is performed by several species of beetles (Eguiarte et al. 1993).

The studies in Los Tuxtlas further observed that mature, adult trees produce an average of 1.6 infructescences, each producing an average of 25 fruit (Brewer and Webb 2001). Maturation occurs mostly between late September and late October. Fruits are one-seeded nuts (technically a nuculanium) (Brewer 2001, Piñero and Sarukhán 1982). The edible endosperm is solid and white. The age of first reproduction

is reported to be approximately 22 years (Mendoza et al. 1987, Piñero and Sarukhán 1982). The shortest trunk recorded for reproductive individuals is 1 meter in height (Mendoza et al. 1987).

To my knowledge, the structure of *A. mexicanum* populations subject to harvest has not been evaluated.

Population Structure Surveys

I conducted size-class surveys in three different locations: the Sierra Santa Marta communities of Venustiano Carranza and Guadalupe Victoria (harvested populations), and at the UNAM Biological Research Station in Los Tuxtlas (unharvested populations). The *ejido* land pertaining to the communities is divided into parcels with different owners. In Venustiano Carranza, parcels to be surveyed were selected completely randomly (7 total plots). In Guadalupe Victoria permission to enter parcels was only given for 3 parcels, all of which were surveyed. At Los Tuxtlas research station, there are two principal areas available for investigations. Two plots were randomly located within each area, for a total of four plots.

Within each selected parcel, I selected the first plot corner by randomly choosing a compass bearing and by walking a randomly chosen number of meters in that direction. The direction of the first side of the plot was determined based on a random compass bearing. The direction of the second side of the plot was chosen randomly. Plots measured 10 x 10 meters, accounting for slope in all directions.

I ranked harvest intensity in the plots based on discussions with landowners, harvesters and community members. The criteria I used in determining rankings involved accessibility, the estimated number of families that are known to harvest at that

site, how much they are known to harvest, and whether or not people from other villages harvest there. I also ranked the degree of canopy cover, proximity to villages, and proximity to streams were also ranked for each plot. I gave a score of “zero” to unharvested plots (only at the Research Station) and a score of “three” to the plots with the greatest intensity of harvest. I defined harvest intensity as the percentage of total inflorescences produced that were harvested by humans.

I assigned all *A. mexicanum* individuals within the plot to one of the following five size-classes:

1. 1-2 leaves, without an aboveground trunk.
2. 3-6 leaves, without an aboveground trunk.
3. 7 or more leaves, without an aboveground trunk
4. With a trunk of less than 1 meter in height.
5. With a trunk between 1-2m in height.
6. With a trunk of 2 meters or greater.

I determined the above size-classes based on life history traits.

Documentation of Inflorescence Harvest Intensity: Venustiano Carranza

In the study plots used for the growth and productivity experiments in Venustiano Carranza (see Chapter 3) I tagged, numbered and mapped all *A. mexicanum* individuals that were at least 1 meter in height. I recorded the height and number of leaves of each individual. Between November 2005 and June 2006, plots were monitored every two weeks by my field assistant for the emergence of inflorescences and their fate: fruit production, harvest, or loss due to predation. We were able to easily discern loss to

predation by the appearance of bite marks. I defined harvest intensity as the percentage of total inflorescences produced that were harvested by humans.

As part of a separate study on emigration of laborers out of the Sierra Santa Marta and its effects on NTFP extraction, I conducted structured interviews in the communities of Venustiano Carranza and Guadalupe Victoria. Both of these communities have remaining patches of primary forest where *A. mexicanum* may be harvested. I randomly selected twenty-three families in Venustiano Carranza and 10 families in Guadalupe Victoria for participation in the study.

As part of these interviews, I asked the following questions relating to the harvest of *A. mexicanum*:

1. Do you harvest *chocho*?
2. Do you harvest *chocho* for personal consumption or to sell?
3. How much do you harvest per week?
4. Where do you harvest?
5. Do you harvest more or less in recent years? Why?
6. Do you sell more or less in recent years? Why?
7. How mucho *chocho* do you sell per week?
8. How much do you sell *chocho* for?
9. Where do you sell *chocho*?

Data Analysis:

The density and the proportion of individuals belonging to each size class were calculated for each plot. I tested the independence of size-class distribution of *A.*

mexicanum and management type (harvested versus unharvested) using log-linear analysis (Sokal and Rohlf 1995).

$$\ln(y) = \mu + A_i + B_j + AB_{ij} + \epsilon_{ij}$$

y = the expected frequency in “row” i , column j of a two-way contingency table

μ = the mean of the logarithms of the expected frequencies

A_i = effect factor A, category i = Size-Class

B_j = effect factor b, category j = Harvested/Unharvested

AB_{ij} = interaction of the two variables = Dependence of Size-Class on management type

ϵ_{ij} = error

I tested the null hypothesis H_0 : No interaction-No relationship between size-class distribution and management type. Log-linear analyses were performed using the CATMOD Procedure in SAS[®] Enterprise Guide[®] 9.2.1 (2004) statistics software.

I compared the average population densities and the proportions of seedlings per reproductive adult between harvested and unharvested sites using non-parametric Mann-Whitney Wilcoxon tests of population medians. I used Spearman’s non-parametric correlations to examine the relationships between ranked harvest intensity and size-class proportions (Sokal and Rohlf 1995).

Harvest intensity was analyzed as the mean percent of inflorescences harvested in study plots. I compared the harvest intensity between the closed-canopy and managed-canopy plots using a paired t-test (Sokal and Rohlf 1995).

RESULTS

The size-class distributions of harvested ($n=10$) and unharvested ($n=4$) populations of *A. mexicanum* are represented by the mean densities of individuals in each

class (Figure 2.1). The distributions of both the harvested and the unharvested populations have roughly negative slopes, when excluding the lower proportions of the smallest size class. The salient difference between the harvested and the unharvested populations, as illustrated by the distributions, is the lack of the two middle size-classes in the harvested populations: individuals having 7 or more leaves without an above-ground trunk, and individuals having an above-ground trunk of less than 1 meter in height.

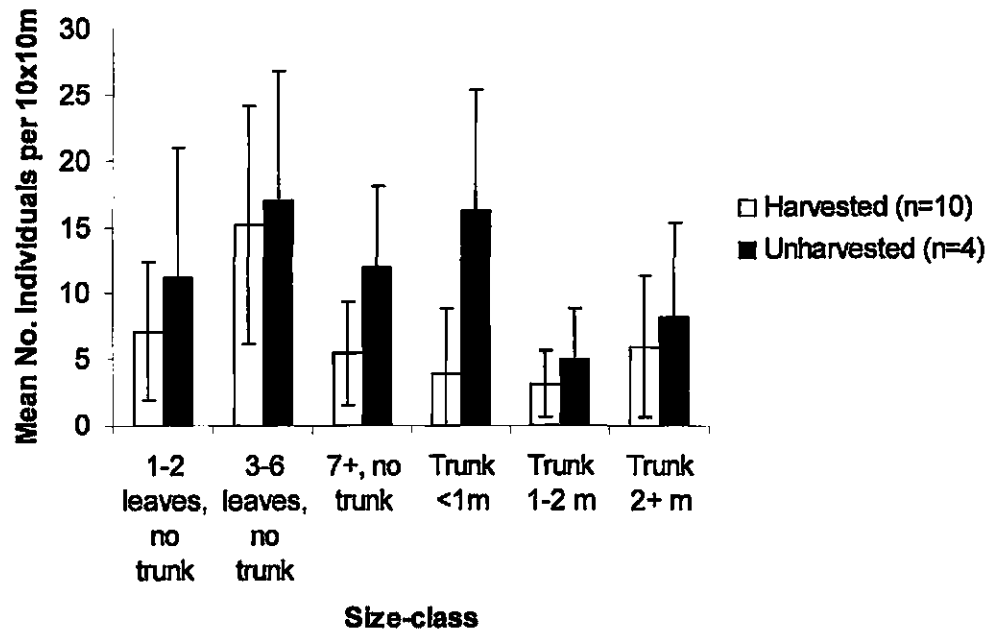


Figure 2.1. Mean size-class densities per 10x10m in harvested (n=10) and unharvested (n=4) populations of *A. mexicanum*. Error bars represent 1 standard deviation from the mean.

Log-linear analysis of the independence of size-class distribution of *A. mexicanum* and management type showed that the size-class distribution depends on whether or not the population is subject to harvest ($p < 0.001$, $df = 5$). Additionally, results

of the one-tailed, non-parametric Mann-Whitney Wilcoxon test that the unharvested populations have a greater median density was significant ($W=42$, $p=0.05$). (Figure 2.2).

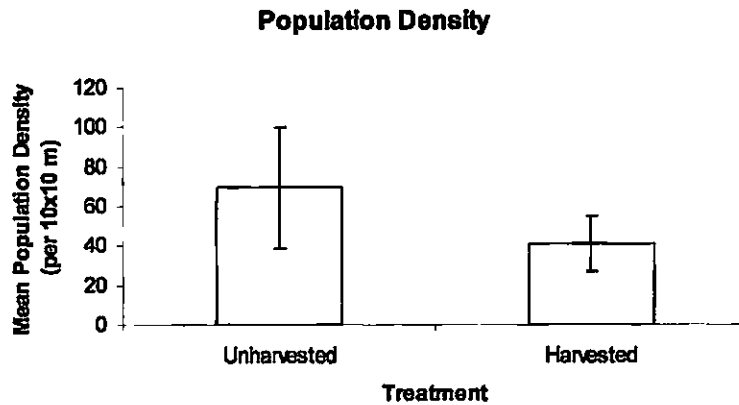


Figure 2.2. Mean population densities per 10x10m in harvested ($n=10$) and unharvested ($n=4$) populations of *A.mexicanum*. Error bars represent 1 standard deviation from the mean.

Size-classes 3 and 4 were the only ones that showed a significant relationship with variation in harvest intensity (Table 2.1). For these size-classes, the proportion and density of individuals were negatively correlated with harvest intensity across all plots.

Table 2.1. Correlations of ranked harvest intensity and size-class proportions

Size-class	r	p-value
(1) 1-2 leaves, no trunk	0.357	0.211
(2) 3-6 leaves, no trunk	0.230	0.429
(3) 7+ leaves, no trunk	-0.539	0.046
(4) Trunk <1 m	-0.587	0.027
(5) Trunk 1-2m	0.278	0.336
(6) Trunk 2+ m	0.309	0.282

The proportions of seedlings (Class 1) per reproductive adult (classes 5&6: with trunks of 1-2m and 2+meters) were not significantly different in harvested and unharvested populations (2-tailed test: $W=71$, $p= 0.9326$).

An average of 67% (SD=19%) of the inflorescences produced in the 8 study plots in Venustiano Carranza were harvested. Harvest intensity was significantly greater in the managed-canopy plots (83.85%, SD=12.74%) than the closed-canopy plots (54.77%, SD=14.74%) as revealed by the paired t-test. ($p=0.04$, $t=2.82$, $DF=6$).

Thirty-two of the 33 families interviewed in Venustiano Carranza and Guadalupe Victoria reported harvesting *A. mexicanum* from the wild. Of the families that harvest, 34% reported harvesting for the purpose of selling, in addition to personal consumption. On average, families reported harvesting approximately 84 inflorescences per week (SD=119.20, a range of 5 to 500 inflorescences per week). Forty-four percent of the families interviewed reported harvesting less chocho now than in the past (44% no change, 12% more), and 71% of these families attributed this to a decrease in availability. Sixty-one percent of all of the families reported a decrease in the abundance of *A. mexicanum*, and the principal reasons provided for this decline were over-harvest and deforestation.

DISCUSSION

Based on the information provided by the interviews as well as the documentation of inflorescence harvest in the study plots, I found the harvest of *Astrocaryum mexicanum* to be of considerable intensity. My results from Venustiano Carranza indicate that a mean of 67% of inflorescences produced are harvested and that ninety-seven percent of the families interviewed harvests *chocho*. If I extrapolate this proportion to represent the

number of families living in the two communities, I can estimate that there are approximately 87 families between the two communities that harvest chocho. Eight-seven families, harvesting an average of 84 inflorescences per week for the harvest season of approximately 16 weeks is approximately 116,928 inflorescences harvested in one season by the two communities. If I assume 70% of adult trees produce an average of 2.6 inflorescences each (see productivity data in Chapter 3), then 64,246 adult trees are needed to satisfy the harvest pressure of these two communities. I found an average of 41 *A. mexicanum* individuals per 10 x 10 m-plot, or 410 individuals per hectare. Based on these densities, I estimated that approximately 157 hectares of forest containing *A. mexicanum* are required to support current wild harvest.

I attribute the significantly lower degree of harvest in the closed-canopy plots compared to the managed plots to dense underbrush of the non-managed plots. These plots are considered more dangerous to harvesters because of the increased likelihood of venomous snakes (such as the “*Nauyaca*” *Bothrops asper*, and the “*Cora*” *Micruroides euryxanthus*) hiding in the underbrush, and are therefore often avoided.

The size-class distributions of harvested populations of *A. mexicanum* in the communities of the Sierra Santa Marta and unharvested populations in Los Tuxtlas Biosphere Reserve were similar, with generally negative slopes, although neither distribution peaked at the smallest size-class. Demographic studies of *A. mexicanum* conducted in Los Tuxtlas in the 1970s reported populations to have a “stable age structure” represented by the negative slope of the size-class distribution (Pifero et al. 1977). A greater proportion of juveniles relative to adults is often thought to indicate a population that is stable or growing. According to this theory, both the harvested and

unharvested populations of Chocho might be considered to be regenerating (Condit et al. 1998).

The overall population density of unharvested populations of *A. mexicanum* was significantly greater than that of the harvested populations, and log-linear analysis revealed the dependence of population structure on harvest. These results indicate an association between harvest and population structure, though not necessarily causality. There may be multiple confounding variables in the comparison between the Los Tuxtlas and Sierra Santa Marta sites. Both abiotic and biotic factors such as climate, soil, specific topography, and interactions with sympatric species may account for differences between the harvested and unharvested populations. Further studies should address these variables and their impacts on the population dynamics of *A. mexicanum* in an effort to better understand the role that harvest may play. In addition, there are abiotic and biotic factors apart from harvest that are also associated with the human-managed forests that may impact the *A. mexicanum* populations. These include, but are not limited to, the potential trampling of seedlings, the hunting of mammal predators/dispersers, as well as the modification of the canopy and/or understory.

Harvested populations of *A. mexicanum* had significantly lower proportions and densities of mid-size classes (both classes containing 7 or more leaves without an above-ground trunk, and with a trunk of less than one meter in height) than unharvested populations. Furthermore, the proportions of these 2 size-classes in the populations had significant negative correlations with ranked harvest intensity. Because harvest of reproductive structures such as flowers and seeds can reduce seedling recruitment (Boot and Gullison 1995, Zuidema and Boot 2002), we would expect that heavily harvested

populations might have lower proportions of seedlings. However, this was not the case in our study, as this size-class had similar proportions in both the harvested and unharvested populations.

There are various possible explanations for the lack of mid-size classes I observed in the harvested populations, and these are likely complex. One possibility is that harvest intensity was greater in the past, although this is inconsistent with local opinion. An alternative explanation may involve the extensive forest fires that occurred in the communities in 1997. These fires and the associated heat and smoke may have negatively affected this cohort at the flower, seed or seedling stage.

Based on the high degree of harvest intensity observed in this study, I hypothesize that the mostly likely explanation is that the lack of middle size classes in the communities is indeed a result of inflorescence harvest over the last few decades. The current similarities in the levels of seedling regeneration reflects the loss of mammal frugivores in the harvested regions, a consequence of the intensive hunting that has occurred in the communities of the Sierra Santa Marta. Previous studies in Los Tuxtlas Reserve found squirrels inflict 51% seed predation while seeds are still attached to the tree, and then a diverse guild of land-dwelling mammals inflict an additional 95% predation (Martinez-Ramos and Alvarez- Buylla 1995). Known seed predators of *A. mexicanum* include 2 species of squirrel, *Sciurus auroeogaster* and *Sciurus deppei*, (Sarukhán 1980) as well as land-dwelling mammals including agouti (*Agouti paca*) and peccary (*Tayassu pecari* (pers. comm. with local residents). Both agouti and peccary were intensely hunted in the past, though according to local residents hunting has declined drastically due to scarcity of the species. While squirrels are not hunted in the

Sierra, a decrease in their abundance was noted by numerous residents (pers. comm.). A study by Dirzo and Miranda (1990) attributed relatively high seedling densities of several canopy species in the Los Tuxtlas Reserve to the loss of mammal herbivores. Forest fragmentation was implicated as the principal cause of defaunation in the Reserve, a problem also evident in the forests of the Sierra Santa Marta. Based on this, and the occurrence of hunting in the Sierra, we might assume defaunation to be much more severe in these forests. Thus, the absence of mammal herbivores may allow for current higher proportions of seed and seedling survival in the harvested areas than in previous years. In order to test this hypothesis, it would be necessary to conduct comparative studies of *A. mexicanum* potential seed and seedling predators and seed fate/predation experiments in both Los Tuxtlas and the Sierra Santa Marta. Further investigation into the lack of the mid-size classes in the Sierra Santa Marta should also include future monitoring of the survival and transition rates of existing seedlings.

CONCLUSION

Based on the results of this study, particularly the very high current harvest intensity I documented, we believe further investigations into the ecological sustainability of harvest are warranted. I strongly encourage the enrichment planting of *A. mexicanum* that has already begun in a few of the communities of the Sierra Santa Marta. Ensuring adequate regeneration is one of the biggest challenges for designing sustainable extraction systems. However, action is imperative for the maintenance of the population as well as the future availability of the harvested product.

LITERATURE CITED

- Anderson, A.B. 1990. Alternatives to Deforestation: Steps Toward Sustainable Use of the Amazon Rainforest. Columbia University Press, New York.
- Boot, R.G. A. and R.E. Gullison. 1995. Approaches to developing sustainable extraction systems for tropical forest products. *Ecological Applications* 5(4): 896-903.
- Brewer, S.W. and M.A.H. Webb. 2001. Ignorant seed predators and factors affecting the seed survival of a tropical palm. *Oikos* 93: 32-41.
- Condit, R., R. Sukumar, R. Hubbell, P. Stephen and R.B. Foster. 1998. Predicting population trends from size distributions: a direct test in a tropical tree community. *The American Naturalist* 152(4): 495-509.
- Cunningham, A.B. 2001. Applied Ethnobotany: People, Wild Plant Use, and Conservation. Earthscan Publications Ltd, London and Sterling, VA.
- Dirzo, R. and A. Miranda. 1990. Contemporary neotropical defaunation and forest structure, function and diversity-a sequel to John Terborgh. *Conservation Biology* 4(4): 444-447.
- Durand, L. and E. Lazos. 2004. Colonization and tropical deforestation in the Sierra Santa Marta, Southern Mexico. *Environmental Conservation* 31(1): 11-21.
- Elevitch, C.R. 2004. The Overstory Book: Cultivating Connections With Trees. 2nd Edition. Permanent Agriculture Resources. Holualoa, Hawaii, USA.
- FAO 1995. Non-wood forest products for rural income and sustainable forestry. FAO technical papers, Non-Wood Forest Products Series. FAO, Rome, Italy.
- Gómez-Pompa, A. and A. Kaus. 1990. Traditional management of tropical forests in Mexico. In *Alternatives to Deforestation: Steps Toward Sustainable Use of the Amazon Rainforest*. Columbia University Press, New York.
- Guevara-Sada, S., J. Laborde-Dovali and G. Sanchez-Rios. 2000. La Reserva Biosfera Los Tuxtlas. Documentos de Trabajo, Programa de Cooperación Sur-Sur Sobre Desarrollo Socioeconómico Ambientalmente Adecuado en los Trópicos Húmedos. UNESCO, Paris, France.
- Hall, P. and K. Bawa. 1993. Methods to assess the impact of extraction of non-timber tropical forest products on plant populations. *Economic Botany* 47(3): 234-247.
- Martinez-Ramos, M. and E.R. Alvarez-Buylla. 1995. Seed dispersal and patch dynamics in tropical rain forests: A demographic approach. *Ecoscience* 2 (3): 223-229.
- Martinez-Ramos, M., M.J. Sarukhán and D. Piñero 1988. The demography of tropical trees in the context of forest gap dynamics: the case of *Astrocaryum mexicanum* at Los Tuxtlas tropical rainforest. In: *Plant Population Ecology* (D.J. Davy, M.J. Hutchings & A.R. Watkinson, eds.) Blackwell, Oxford, England.
- Mendoza, A., D. Piñero, and J. Sarukhán, 1987. Effects of experimental defoliation on growth, reproduction and survival of *Astrocaryum mexicanum*. *Journal of Ecology* 75: 545-554.
- Olmsted, I. and E.R. Alvarez-Buylla. 1995. Sustainable harvesting of tropical trees: Demography and matrix models of two palm species in Mexico. *Ecological Applications* 5(2): 484-500.

- Pare L. and E. Velasquez. 1997. In: L. Pare and E. Velasquez, Editors, *Gestión de recursos naturales y opciones agroecológicas para la Sierra de Santa Marta*, Institución de Investigaciones Sociales y UNAM, Mexico.
- Perez, C.A., C. Baider, P.A. Zuidema, L.H.O. Wadt, K.A. Kainer, D.A. P. Gomes-Silva, R.P. Salomão, L.L. Simões, E.R. N. Franciosi, F.C. Valverde, R. Gribel, G.H. Shepard, Jr., M. Kanashiro, P. Coventry, D.W. Yu, A.R. Watkinson and R.P. Freckleton. 2003. Demographic threats to the sustainability of Brazil Nut exploitation. *Science* 302(5653): 2112-2114.
- Piñero, D. and J. Sarukhán. 1982. Reproductive behavior and its individual variability in a tropical palm, *Astrocaryum mexicanum*. *Journal of Ecology* 70: 461-472.
- Piñero, D., J. Sarukhán, and Enrique González. 1977. Estudios demográficos en plantas-*Astrocaryum mexicanum* estructura de las poblaciones. *Boletín de la Sociedad Botánica de México* 37: 69-118.
- Sarukhán, J. 1978. Studies on the demography of tropical trees. In: *Tropical Trees as Living Systems* (P.B. Tomlinson, P.B. & M.H. Zimmermann, eds.), pp. 163-184. Cambridge University Press, London.
- Sarukhán, J. 1980. Demographic problems in tropical systems. In *Demography and Evolution in Plant Populations* (O. Solbrig, ed.) Blackwell Scientific Publications, Oxford: 161-188.
- Sinha, A. and K.S. Bawa. 2002. Harvesting techniques, hemiparasites and fruit production in two non-timber forest species in south India. *Forest Ecology and Management* 168: 289-300.
- Sokal, R.R. and F.J. Rohlf. 1995. *Biometry : the principles and practice of statistics in biological research*. 3rd edition. W.H. Freeman, New York.
- Soehartono, T. and A.C. Newton. 2000. Conservation and sustainable use of tropical trees in the genus *Aquilaria* II. The impact of gaharu harvesting in Indonesia. *Biological Conservation* 97: 29-41.
- Vasquez, R. and A.H. Gentry. 1989. Use and misuse of forest-harvested fruits in the Inquitos area. *Conservation Biology* 3(4): 350-361.
- Zuidema, P.A. and R.G.A. Boot. 2002. Demography of the Brazil nut tree (*Bertholletia excelsa*) in the Bolivian Amazon: impact of seed extraction on recruitment and population dynamics. *Journal of Tropical Ecology* 18: 1-31.

CHAPTER III

Growth, Productivity and Germination of *Astrocaryum mexicanum* and its Potential for Understory Cultivation

INTRODUCTION

It is estimated that over 80% of people in developing countries rely on non-timber forest products (NTFP) such as fruit, seeds, leaves, fiber, resin, oils, and bark for their subsistence and economic needs (Elevitch 2004, FAO 1995, Vantomme 1997). The potential of NTFP extraction as a strategy for environmental conservation is based on the concept that the cultural and economic value of NTFP for local people provides an incentive to conserve these resources and the environment in which they grow. (e.g., Anderson 1990, Plotkin and Famolare 1992, Vasquez and Gentry 1989). Although promoted as a conservation strategy, many NTFP species are themselves threatened as a result of over-exploitation.

The majority of NTFP are harvested from the wild; however in some cases cultivation, including cultivation in forest understories, provides an alternative that may reduce harvest pressure on wild populations (e.g., Cunningham 1993, Ticktin et al. 2003). As not all species are easily domesticated, ecological studies on the spatial and temporal patterns of growth and productivity are required (Ticktin et al. 2003). Comparisons should be made between wild and cultivated plants, under different harvesting regimes, and in different forest types and anthropogenic habitats. The suitability of the crop must be assessed in terms of ecological as well as socioeconomic information (Cunningham 1993, Ticktin et al. 2003).

The Sierra Santa Marta of Mexico is a region where people depend on NTFP for both their subsistence and economic needs. For as long as they have lived in the region, residents have harvested a native understory palm, *Astrocaryum mexicanum* Liebm. ex Mart. (Arecaceae) and have relied on it as a food source as well as a trade commodity (Durand & Lazos 2004). In recent years, harvest pressure has increased on extant populations as a result of expansion of the local market, as well as the loss of *A. mexicanum* populations due to forest destruction. In some communities, people have discontinued cultivation of traditional crops and have begun to trade *A. mexicanum* for staples such as corn. Demand is particularly high in the communities where the resource is no longer available due to loss of primary forest habitat. Due to rising demand and decreasing availability of this important resource, there is increasing interest into its potential cultivation.

Like many tropical regions worldwide, the Sierra Santa Marta has been devastated by deforestation; primarily a result of the intensive cattle ranching that began in the 1950s. Between 1958 and 1991, approximately 77% of the existing forest cover was lost due to deforestation for cattle and the occurrence of highly destructive forest fires (Durand and Lazos 2004). Consequently, the region is characterized by the prevalence of secondary forest in varying stages of forest succession.

Secondary forests in varying stages of succession provide habitat heterogeneity and a diversity of light levels dependent on the degree of canopy closure. Many such areas may provide light conditions that induce cultivated species to grow and produce at improved rates. Light is known to be an important limiting factor for growth and reproduction of many tropical understory plants (e.g., Endress et al. 2004, Piñero and

Sarukhán 1982, Svenning 2002, Ticktin and Nantel 2004). Studies have recognized the enhanced growth of seedlings and understory species that occurs in primary forest gaps (e.g., Martinez-Ramos and Alvarez-Buylla 1995, Popma and Bongers 1991, Svenning 2002). Although most neotropical understory palms are able to survive for prolonged periods in deeply shaded environments, light is nevertheless an important limiting factor for growth and reproduction (Svenning 2002). The prevalence of secondary forests has important implications for the potential cultivation of native, understory NTFP.

Germination studies of palm seeds have shown many species respond to a number of different pre-treatments that promote faster and more uniform germination. For example, scarification, either mechanical or by use of chemicals has been shown to increase the rate of germination palm species with hard seed coats (e.g., Moussa et al. 1998, Potvin et al. 2003).

OBJECTIVES

The objective of this study was to identify the potential and optimal conditions for the cultivation of the native understory palm, *Astrocaryum mexicanum*. Specifically, we addressed the following questions: (1) how does light transmittance differ in the three forest environments (closed-canopy primary forest, “managed” or partially cleared canopy primary forest and in homegardens)? (2) Is light transmittance significantly correlated with percent canopy cover in the three environments? (3) Does soil moisture content differ in the three environments? (4) Are there differences in *A. mexicanum* seedling growth among the three environments? (5) Does *A. mexicanum* inflorescence production differ in the three environments? (6) Does experimental pre-treatment of *A. mexicanum* seeds affect the percent and rate of germination?

To address these questions we focused on plants in existing wild populations of *A. mexicanum* in primary forests, under both closed-canopy and “managed” or partially cleared canopy and also in homegardens. Although a few small populations of *A. mexicanum* were identified in secondary forests, they were not abundant enough for our studies. However, their presence does suggest the ability of the species to survive in secondary forest conditions.

METHODS

Study Site:

The Sierra Santa Marta is located within the buffer zone of the Los Tuxtlas Biosphere Reserve in the south of the Mexican state of Veracruz, on the Gulf of Mexico coast. This reserve, established by the federal government 1998, is comprised of 334,002 hectares of protected area. A total of 29,720 hectares of highly preserved core zones where no human activity is permitted are located at: San Martín Tuxtla, Sierra Santa Marta and the San Martín Pajapan. The buffer and transition zones are comprised of 125,402 hectares and 178,880 hectares, respectively. The field station of the Institute of Biology of UNAM is located in the Los Tuxtlas Reserve (Guevara-Sada et al. 2000).

The region is considered the northern limit of the tropical rainforest in America (Durand and Lazos 2004). Altitude within the area ranges from 0-1,500 meters and three volcanoes, the Yohualtajapan, the Santa Marta, and the San Martín Pajapan are conspicuous features of the landscape. The great heterogeneity of topography and climate gives rise to a diversity of environments and an equally impressive array of biological diversity.

This region is characterized by not only biological, but also cultural richness. The buffer zone hosts 288 communities, many of which are Nahua and Popoluca. The residents of these communities represent some of the most economically marginalized in the country. Approximately 90% of the population survives on *milpa* subsistence agriculture. Due to drastic environmental and social changes, much of the self-sufficiency of this traditional agricultural system has been lost (Paré and Velazquez 1997).

As a result of intensive cattle ranching beginning in the late 1950s, the region has suffered massive deforestation. Between 1950 and 1991 77% of the existing forest cover was lost. Our studies were conducted in the communities of Venustiano Carranza and Magallanes, where more than 80% of the original forest was removed. Deforestation for cattle grazing continues in the buffer zones to this day (Durand and Lazos 2004).

Environmental degradation has furthermore resulted in a loss of nutritional resources including protein (such as fish, agouti and peccary) and wild harvested forest goods. In conjunction with the decreased sufficiency of crops, the population has experienced a reduction in the quality of their nutrition. (Paré and Velazquez 1997).

Study Species:

Known locally as “*chocho*”, *Astrocaryum mexicanum* is a monoecious, understory palm of the tropical rainforest, with a natural range extending from Veracruz, Mexico to the Atlantic coast of Honduras (Eguiarte et al., 1993). Long-term studies on the demography and population ecology of *A. mexicanum* beginning in 1975 at Los Tuxtlas Biological Field Station of the Instituto de Biología , Universidad Autónoma Nacional de México (18°36'N, 95°07'W) Veracruz have provided much of the information known

about this species (e.g., Martinez-Ramos and Alvarez-Buylla 1995, Piñero et al. 1977, Piñero and Sarukhán 1982, Sarukhán 1978 and 1980). *A. mexicanum* often dominates the forest understory and may attain population densities of more than 1,000 mature individuals per hectare (Martinez Ramos and Alvarez-Buylla, 1995). This long-lived palm (oldest ages recorded about 130 years) has an average mature height of 1-4 meters. The trunk, petioles, inflorescences and fruit are conspicuously covered with sharp, flat, black spines measuring 3-5cm in length (Martinez-Ramos and Alvarez-Buylla 1995, Martinez-Ramos et al. 1988).

In Los Tuxtlas, *A. mexicanum* has a mean probability of reproduction (proportion of adults producing flowers) of 41% (Piñero and Sarukhán 1982). Information on the average number of inflorescences produced is not available. Flowering begins in mid-April following a short, 4-5 week dry season. Individuals are self-compatible, but self-pollinators produce lower fruit set than out-crossed individuals and there is a high out-crossing rate. Long-distance cross-pollination is performed by several species of beetles (Eguiarte et al. 1993).

Studies report an average of 1.6 infructescences produced per tree, with an average of 25 fruit per infructescence (Brewer and Webb, 2001). Maturation occurs mostly between late September and late October. Fruits are one-seeded nuts (technically a nuculanium) (Brewer 2001, Piñero and Sarukhán 1982). The edible endosperm is solid and white. The age of first reproduction is reported to be approximately 22 years (Mendoza et al. 1987, Piñero and Sarukhán 1982). However, the few residents of the Sierra Santa Marta that have cultivated *A. mexicanum* in their homegardens report the age of first reproduction to be approximately 6-8 years (personal communication).

Primary dispersal of seeds is through gravity. A variety of mammals are responsible for both seed dispersal and predation. Studies in Los Tuxtlas illustrated that while still attached to the tree, approximately 51% of the seeds are lost to predation by squirrels (*Sciurus auroeogaster* and *Sciurus deppei*). On the soil, seeds suffer an additional 95% predation by a diverse guild of mammals. The spiny pocket mouse (*Heteromys desmarestianus*) and the Mexican deer mouse (*Peromyscus mexicanus*) are common predators/dispersers (Brewer and Webb 2001, Sanchez-Cordero and Martinez-Gallardo 1998). Insect predation may occur even before fruit is mature and beetle infestation is common in fruit on the ground (Brewer and Webb, 2001).

Studies in Los Tuxtlas have shown that both growth and reproduction of *A. mexicanum* are light-limited (e.g. Martinez-Ramos and Alvarez-Buylla 1995, Piñero et al. 1982). To my knowledge, growth, and reproductive output of *A. mexicanum* populations subject to harvest and in the context of managed environments have not been evaluated.

Assessing growth of A. mexicanum in different forest settings:

In order to compare growth rates of *A. mexicanum* seedlings in different forest settings and their associated light environments, I established plots following settings: closed-canopy primary forest, “managed”/partially cleared-canopy primary forest, and in homegardens. Closed-canopy primary forest was defined as forest patches that have not been deforested or burned within the last 100 years, and with approximately 80-90% canopy cover. Partially cleared or “managed” primary forest was defined as forest patches that had not been deforested or burned, but that have had partial clearing of the canopy in order to increase irradiation for other understory crops. This may include

removal of a few canopy trees as well as clearing of underbrush. These sites had approximately 70-80% canopy cover. Homegarden sites consisted of cultivated individuals of chocho and were found near homes and with less than 70% canopy cover.

I established replicate plots, located in different forest patches, for each forest type. Based on availability, I located 5 replicate plots in closed-canopy forest, and 3 replicate plots each for managed forests and homegardens. Closed-canopy and managed plots measured 10 x 10 meters and were standardized on the horizontal by adjusting for slope. Homegarden plots were limited to the existing size and shape of the gardens, but all were smaller than the 10 x 10 meter forest plots. Forest sites with similar palm density, soil type and hydrology were selected in order to minimize other environmental differences among sites. I asked landowners about the specific land-use history of each plot, including past tree removal or understory crops.

I measured the percent canopy cover for each plot using a convex densiometer. I quantified light transmittance by measuring Photosynthetic Photon Flux Density (PPFD) at ground level. I used a LI-COR LI-190 point quantum sensor and a LI-COR[®] LI-1400 data logger (LI-COR Environmental, 4647 Superior Street, P.O. Box 4425, Lincoln, Nebraska USA). Readings were taken in 5 locations within each plot: one meter in from each corner and in the center. The average of the readings was logged every thirty seconds for a period of 3 minutes in each location. In order to calculate the percent of total light transmittance in the plots, light readings were taken simultaneously in an open area, such as a cow pasture using the combination point sensor and data logger: HOBO[®] Pendant Temp/Light Data Logger (part # UA-002-08, Onset, P.O. Box 3450, Pocasset, MA). I initially calibrated the Li-cor and HOBO sensors in open areas. Light readings

were taken during dry season on March 26th, 27th, 30th, 2006, and during the wet season on July 4th, 17th, and Aug. 5th 2006. All light readings were taken between 9 o'clock in the morning and 12 noon. The variation in light transmittance as described by the variation in percent canopy cover of the different plots was assessed using least-squares regression (Sokal & Rohlf 1995).

To assess differences in growth among the different sites, I used two different classes of seedlings: seedlings with one leaf, and seedlings with 3-5 leaves. These two classes were selected based on availability, as abundance of middle size-classes was low (see Chapter 2). I randomly selected ten individuals from each class in each plot, and each was tagged, numbered and mapped. For each individual I recorded height, the number of leaves and the length of longest leaf. The youngest leaves were marked with non-toxic, non-water soluble paint in order to observe the production of new leaves. Initial and final measurements were made in October 2005 and July 2006, respectively. Due to the lack of existing cultivated *A. mexicanum* individuals, I was unable to locate any seedlings with fewer than 5 leaves in homegardens. These individuals were of a larger size-class than those available in the forest sites, with an average of 6-10 leaves.

To assess differences in the relative growth rate (RGR) among the different environments, I used seedlings produced by the germination experiment. Relative growth indicates growth relative to mass, which is typically measured as dry mass. We randomly selected fifteen seedlings for the initial dry mass measurements. To assess biomass allocation, (root/shoot mass fraction or RMF and SMF), I separated the roots and shoots and dried them in an oven at a minimum of 70 degrees Celsius for 72 hours before dry mass determination (Nakahashi et al. 2005). I randomly selected an additional 45

seedlings to be out-planted in the three forest settings. I planted five seedlings into each of 3 replicate plots per forest type, for a total of 15 seedlings per forest type. Seedlings were out-planted in August 2006, and were harvested for dry mass determination in April 2007. I calculated the relative growth rate (of the whole plant) using the equation: $RGR = \ln(\text{mass}_2 / \text{mass}_1) / (t_2 - t_1)$.

I analyzed growth, in terms of the number of new leaves produced, using Poisson regression analysis. Poisson regression models are generalized linear models with the logarithm as the (canonical) link function and the Poisson distribution. The Poisson distribution is typically skewed, with discrete, non-negative values. It is therefore often appropriate for analyzing count data. The Poisson model assumes the variance is equal to the mean of the distribution (Kutner et al. 2005). I performed the Poisson regression analysis with SAS[®] Enterprise Guide[®] 9.2.1 (1994) software using the Generalized Linear Model (PROC GENMOD):

$$\log(y) = \beta_1x + \beta_2a + \beta_3b + \beta_4c + \epsilon.$$

y = count of new leaves produced

x = the original number of leaves on the seedling

a = the effect of the closed-canopy forest site

b = the effect of the managed-canopy forest site

c = the effect of the homegarden site

Due to overdispersion in the distribution of new leaves produced, I scaled the deviance to fit to 1. Contrasts were made between each of the different forest types. A scatterplot was made of the original number of leaves versus the number of new leaves produced for each forest setting.

The relationship between light transmittance and growth (leaf production) was described using least-squares regression, and regression equations were derived. I used ANOVA to analyze the relative growth rate (RGR) of out-planted seedlings, as well as the increases in dry mass of the whole plant, and of the shoots alone. I used the nonparametric Mann Whitney Test with Bonferroni adjustments to analyze the increase in root dry mass. The root to shoot ratios and root mass fractions (RMF), were compared using ANOVA on log-transformed data (Sokal and Rohlf 1995).

Assessing productivity in different forest environments:

To assess the effects of forest type on productivity, I monitored inflorescence emergence and fate within the permanent forest plots established for the growth experiment. Only two homegarden sites contained reproductive adults for comparison with the forest sites. I tagged, numbered and mapped all *A. mexicanum* individuals of 1 meter in height or greater (this is the smallest height noted for reproductive individuals in Mendoza et al. 1987). I recorded the height and number of leaves of each.

Between November 2005 and June 2006 plots were monitored every two weeks by my field assistant for the emergence of inflorescences. We recorded flower fate, including fruit production and loss due to predation or harvest, each inflorescence. Predation of inflorescences was easily distinguished from harvest.

I compared the mean percent of inflorescences produced per adult in the different sites using a Chi-square Goodness of Fit Test. The mean number of inflorescences produced per reproductive individual was compared among groups using ANOVA (Sokal and Rolf 1995).

The effects of experimental treatment of seeds on germination:

I collected two hundred mature seeds from multiple populations (approximately 50 seeds per population). Seeds were collected while still attached to the tree for 2 reasons: to avoid beetle infestation and to know the approximate age of the seed (since seeds remain on the forest for over one year). I determined the maturity of the seeds if they fell easily with a shake of the infructescence.

I randomly assigned seeds the following treatments (Marcus and Banks 1999, Pinheiro 2001, Potvin et al. 2003):

1. Control-no treatment.
2. Soaked in water for 1 week. Water was changed daily.
3. Peeled- The thick, fibrous pericarp were peeled away from the end of the seed from which the cotyledon emerges.
4. Steamed-Seeds were sealed inside a plastic bag with moist soil for one week, in a high-light location.

I planted the seeds in a “nursery” similar to those used by local people for other palm crops. The nursery consisted of two raised beds measuring 1x4 meters with a height of about 20 centimeters. A thatched roof of palm leaves was constructed. I used soil from local gardens as substrate because this is the soil that is available to local people. The nursery area was fenced in using chicken wire.

I randomly allocated seeds from all treatments to their location within the nursery and planted them 10cm apart. They were laid on their side, as this is how they germinate in the wild (personal observation) and covered with approximately 2cm of soil. Seeds were marked with numbered tags and their location was mapped. After planting, I covered nursery beds with leaf litter, again to simulate conditions in the wild.

Germination data were recorded weekly for a period of 10 months, and was defined as emergence through the soil.

The percentage of germination was compared across treatments using Chi-square tests, and the average time until germination was compared across treatments using nonparametric Kruskal-Wallis tests (Sokal and Rolf 1995).

RESULTS

Light Quantification in different forest types:

The mean light transmittance for closed-canopy plots, managed plots, and homegardens in the dry season was 0.71%, 2.65%, and 16.09%, respectively (Figure 3.1, Tables 3.1). An ANOVA of the log-transformed data was significant (DF=2, F=299.07, $p < 0.001$) and post-hoc Tukey's comparisons were significant among all treatment groups. In the wet season, the mean light transmittance in the closed-canopy plots, managed plots, and homegardens was 0.63%, 1.32 and 7.67% respectively. Mann-Whitney non-parametric pairwise comparisons among the three sample medians were all significant after Bonferroni adjustment ($p < 0.001$). The percent canopy cover in the study plots and the percent light transmittance were significantly negatively correlated in both the dry season ($r = -0.896$, $p < 0.001$) and the wet season ($r = -0.817$, $p = 0.002$). The variation in the percent canopy cover was found to explain 78% of the variation in light transmittance in the dry season ($R^2_{\text{adj}} = 78\%$, $p < 0.001$) and 63% in the wet season ($R^2_{\text{adj}} = 63\%$, $p = 0.002$). (Figure 3.2).

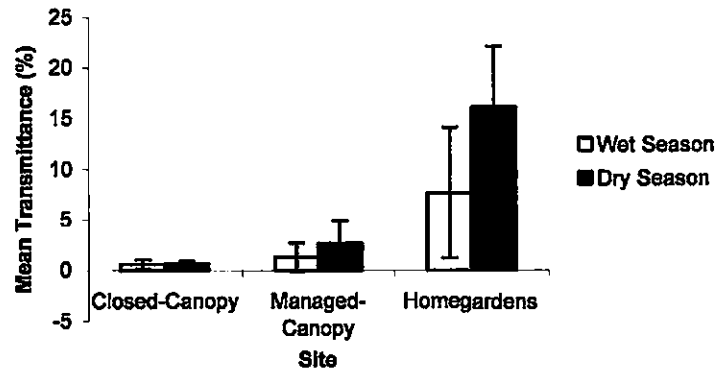
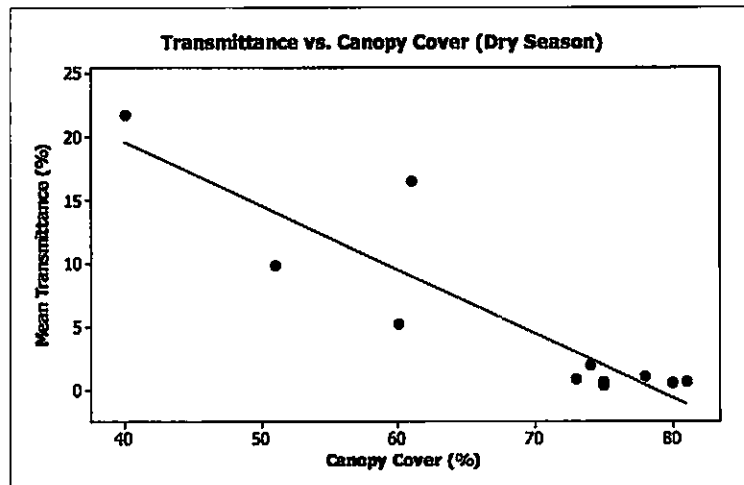


Figure 3.1. Mean light transmittance in study plots for wet and dry seasons ($p < 0.001$ both seasons). Error bars represent 1 standard deviation from the mean.

Table 3.1. Mean canopy cover and light transmittance.

(a) Dry Season	Closed-Canopy	Managed-Canopy	Homegardens	p-value
Mean Canopy Cover	77.8% ^a	69% ^a	50.7% ^b	0.002 [†]
Mean Light Transmittance	0.71% ^a	2.65% ^b	16.09% ^c	<0.001 [†]
†= ANOVA				
(b) Wet Season	Closed-Canopy	Managed-Canopy	Homegardens	p-value
Mean Canopy Cover	86.90% ^a	73.74% ^b	56.4% ^c	<0.001 [†]
Mean Light Transmittance	0.63% ^a	1.32% ^b	7.67% ^c	<0.001 [§]
†= ANOVA, §= Mann-Whitney with Bonferroni adjustments				

(a)



(b)

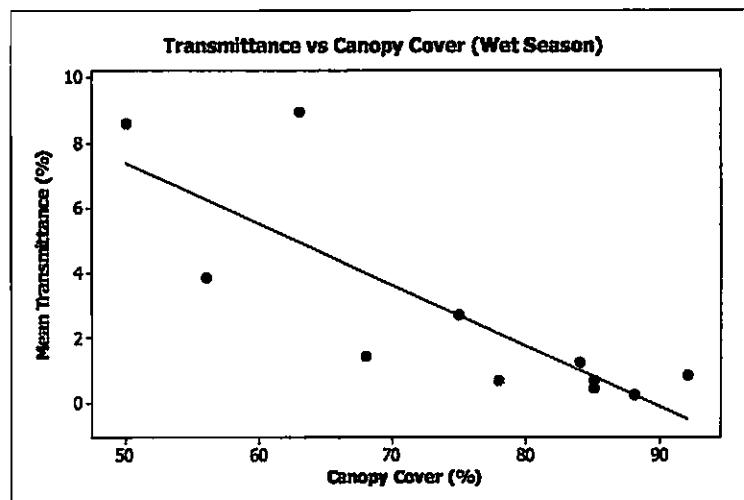


Figure 3.2. Scatterplot of mean light transmittance vs. mean canopy cover in the (a) dry season ($R^2_{adj} = 78\%$, $p < 0.001$) and (b) wet season ($R^2_{adj} = 63\%$, $p = 0.002$).

Seedling Survival and Growth:

Seedling survival was 86% in closed-canopy plots, 85% in managed plots and 99% in homegardens, but results of the Pearson's Chi-squared Goodness of Fit Test showed no significant difference among sites ($X^2=0.630$, $p=0.730$).

Seedling growth (number of new leaves produced) in the three environments was analyzed using Poisson Regression (Appendix A). Overall, the effect of forest type on the production of new leaves was significant ($p < 0.001$). The effect of the original size (number of leaves) on leaf production was not significant ($p = 0.08$). I could therefore compare seedling growth across the three environments without regard to the original size of the seedlings (Figure 3.3). Contrasts between each of the three forest settings revealed significantly greater leaf production in the homegardens when compared to both the closed-canopy and managed-canopy sites ($p < 0.001$ for both contrasts). There was no significant difference in leaf production between closed and managed canopies ($p = 0.12$).

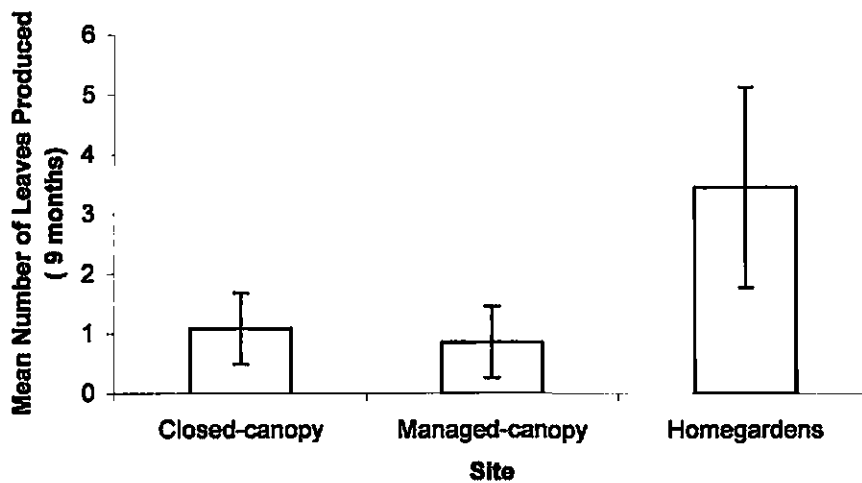
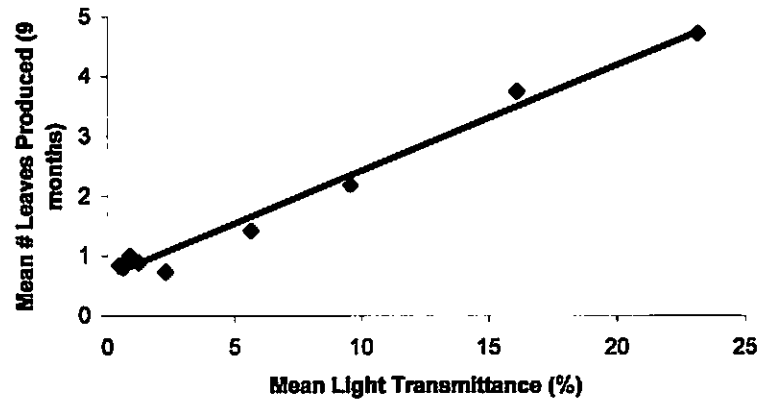


Figure 3.3. Mean leaf production in the three forest sites. Homegardens had significantly greater growth than both closed-canopy and managed-canopy sites (Poisson regression: $p < 0.001$).

The relationship between light transmittance and mean leaf production in the three environments was described using least-squares regression. The relationship was significant for both the dry season ($R^2_{\text{adj}} = 98.1\%$, $p < 0.001$) (Figure 3.4) and the wet season ($R^2_{\text{adj}} = 95.2\%$, $p < 0.001$). The regression equation for the dry season was

determined to be: new leaves = 0.663 + 0.176 (mean dry season transmittance), and for the wet season: new leaves = 0.511 + 0.417 (mean wet season transmittance).

(a)



(b)

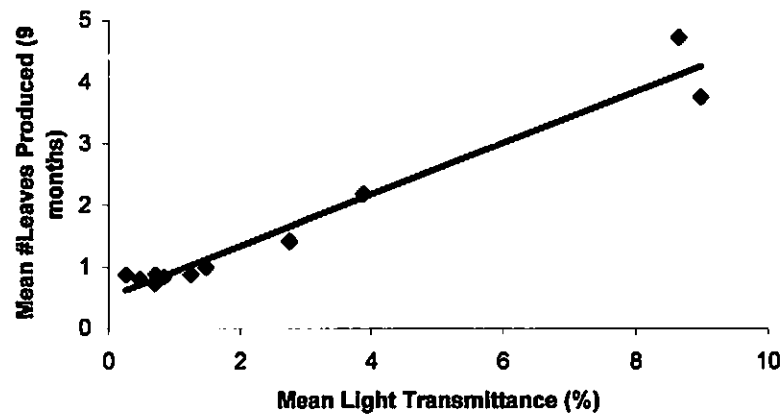


Figure 3.4. Least-square regression of leaf production as described by variation in light transmittance (a) dry season ($R^2_{adj}=98.1\%$, $p<0.001$); (b) wet season ($R^2_{adj} = 95.2\%$, $p<0.001$).

Relative Growth Rate:

The mean relative growth rate (RGR) of the out-planted seedlings was significantly greater in the homegardens than in the closed-canopy and managed-canopy plots (ANOVA: $p<0.002$, $DF=2$, $F=17.05$, post-hoc Tukey's comparisons). The RGR in

the closed-canopy was not significantly different from that of the managed-canopy plots (Figure 3.5, Table 3.3). The final weights of out-planted seedlings are listed in Appendix C.

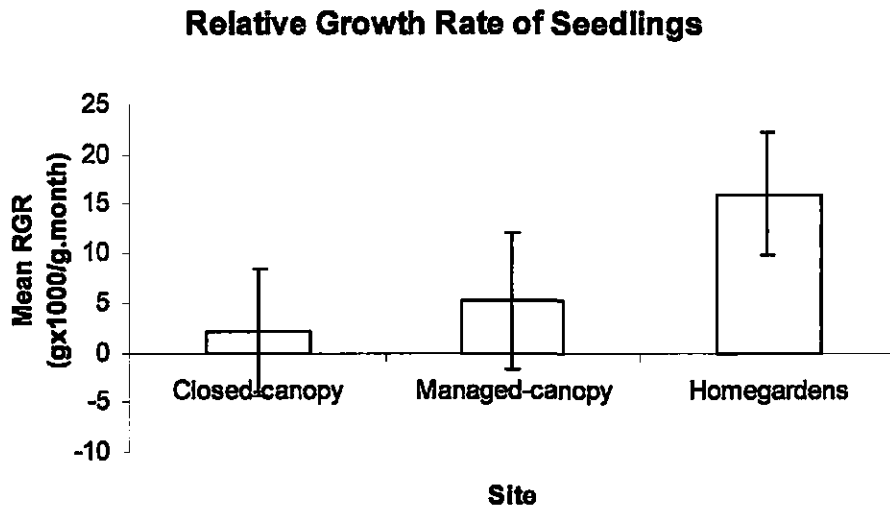


Figure 3.5. Relative growth rate of out-planted seedlings ($\times 10^3 \text{ gg}^{-1} \text{ month}^{-1}$). Homegardens had significantly greater RGR than closed-canopy and managed-canopy sites ($p < 0.02$).

Table 3.3. Growth of out-planted seedlings.

	Closed-canopy	Managed-canopy	Homegardens	p-value
RGR ($\times 10^3$ gg^{-1} month^{-1})	2.04 ^a	5.20 ^a	15.98 ^b	<0.001 [†]
Mean Whole Plant Growth -Dry Mass (g)	0.323 ^a	0.784 ^a	2.820 ^b	<0.001 [†]
Mean Shoot Growth-Dry Mass (g)	0.340	0.726	1.010	0.0750 [†]
Mean Root Growth-Dry Mass (g)	-0.030 ^a	0.060 ^a	1.720 ^b	<0.001 [§]
RMF	0.21 ^a	0.21 ^a	0.50 ^b	<0.001 [‡]

†=ANOVA, §=Mann-Whitney with Bonferroni adjustments ‡=ANOVA with log-transformed data

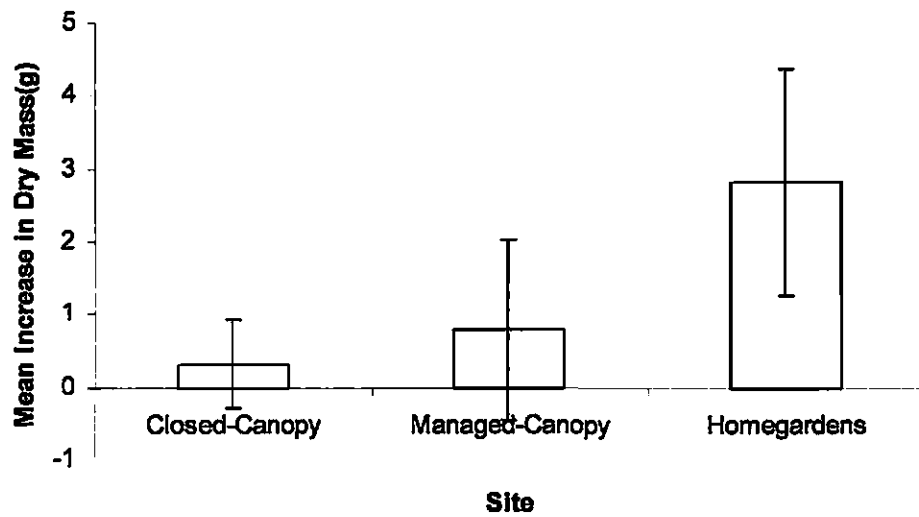


Figure 3.6. Increase in dry mass of out-planted seedlings (whole plant) over 8 months.

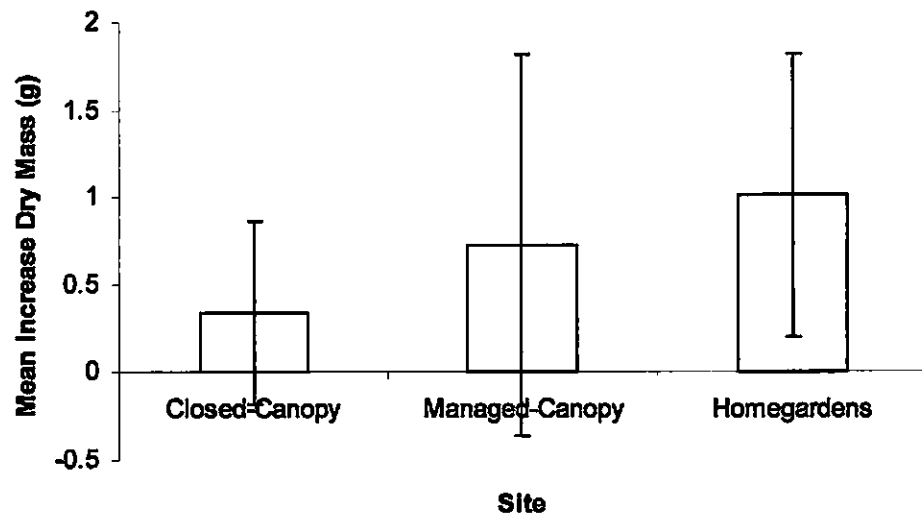


Figure 3.7. Mean increase in shoot dry mass of out-planted seedlings over 8 month growing period.

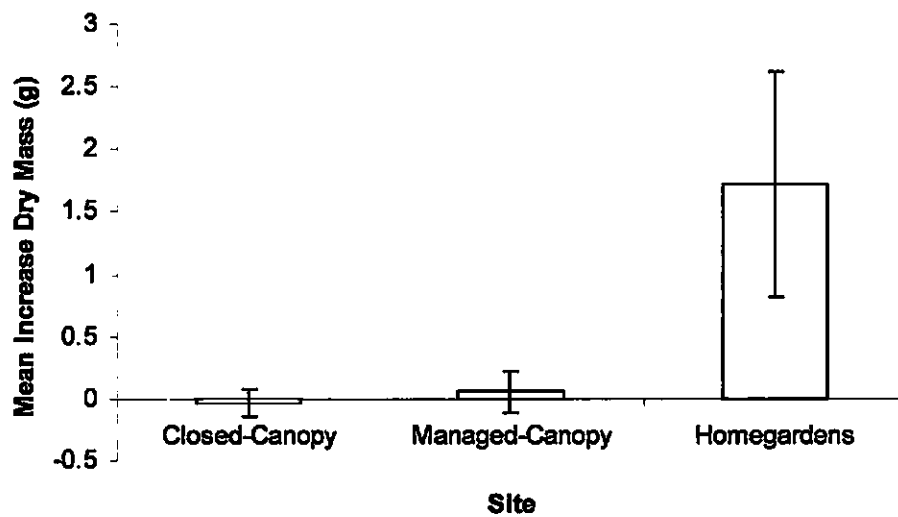


Figure 3.8. Mean increase in root dry mass of out-planted seedlings over 8 month growing period

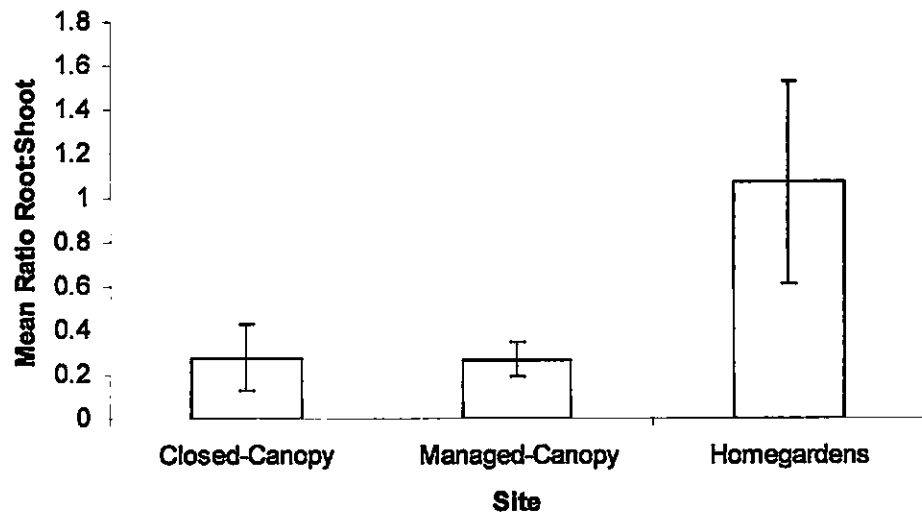


Figure 3.9. Root: Shoot ratios of out-planted seedlings over 8 month growing period.

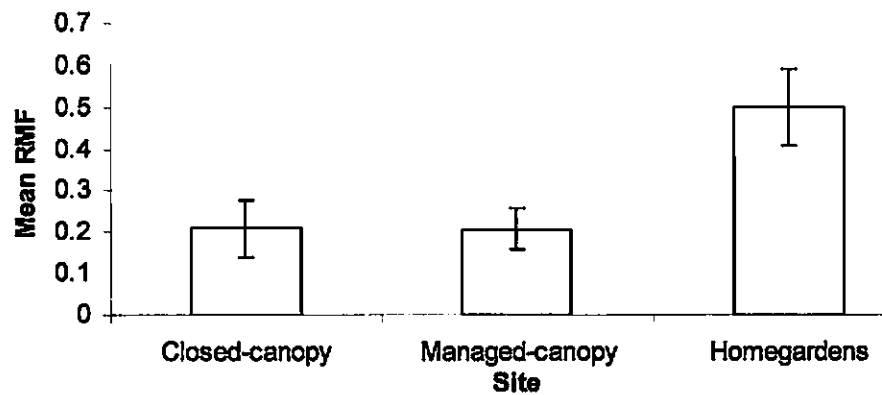


Figure 3.10. Mean Root Mass Fraction of out-planted seedlings over 8-month growing period.

Growth in terms of dry mass accumulation of the out-planted seedlings was significantly different among forest environments when I compared the growth of the entire plant. (ANOVA $F=16.81$, $DF=2$, $p<0.001$; Table 3.3, Figure 3.6). Tukey's post

hoc comparisons revealed that growth was significantly greater in homegardens than in both closed-canopy and managed plots. Whole-plant dry mass accumulation was not significant between the closed-canopy and managed forest plots.

When the specific dry mass accumulation of shoots and roots was compared, I found no significant difference in shoot growth among sites ($F=2.77$, $DF=2$, $p=0.75$; Table 3.3, Figures 3.7 and 3.8). However, differences in root growth were significant. I used non-parametric Mann-Whitney tests to make pairwise comparisons with Bonferroni adjustments. Roots grew significantly more in homegardens than in closed-canopy and managed forest plots ($p<0.001$ for both pairwise comparisons). Differences in root growth were not significant between closed-canopy and managed plots ($p=0.16$). An ANOVA comparing the root: shoot ratios on log-transformed data was significant ($F=64.38$, $DF=2$, $p<0.001$). Post hoc Tukey's comparisons revealed that root: shoot ratios were significantly higher in homegarden plots and the other two forest types, but were not significantly different between closed-canopy and managed plots (Figure 3.9). Thirty-three percent of the seedlings in the closed and managed-canopy plots had negative root growth (Appendix C).

The root mass fraction (RMF) of the out-planted seedlings was significantly greater in the homegardens than in the two forest sites. There was no difference between closed-canopy and managed canopy (ANOVA of log-transformed data with post hoc Tukey's $p<0.001$, $DF=2$, $F=59.13$; Figure 3.10, Table 3.3).

Inflouescence production:

The mean percent of adults in the plots that were reproductive in the 2005-2006 flowering season in the closed-canopy plots ($n=5$), managed plots ($n=3$) and

homegardens (n=2) was 73.8% (SD 21.8%), 68.3% (SD 18.0%) and 80% (SD 1.41%), respectively (Table 3.4). Results of the Pearson's Chi-squared Goodness of Fit Test were not significant ($X^2=0.009$, $p=0.995$).

The mean number of inflorescences per reproductive adult in the closed-canopy, managed plots and homegardens was 2.3 (SD 1.3), 2.9 (SD 1.1) and 3.3 (SD 1.7), respectively (Table 3.4, Figure 3.11). An ANOVA of the square root-transformed data was significant (DF=2, F=3.93, $p=0.024$), and post hoc Tukey's comparisons revealed a significant difference between the average numbers of inflorescences produced per reproductive adult between the closed canopy and the homegardens.

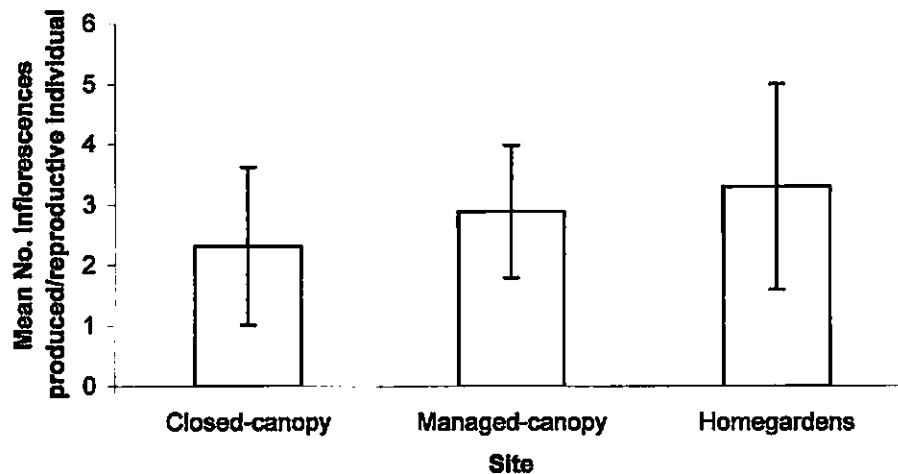


Figure 3.11. Mean inflorescence production per reproductive adult. Productivity in homegardens was significantly greater than in closed-canopy forest ($p=0.024$).

Table 3.4. Inflorescence production

	Closed-canopy	Managed-canopy	Homegardens	p-value
Mean %Adults that Reproduced	73.8%	68.3%	80.0%	0.995 §
Mean No. Inflorescences Produced	2.3 ^a	2.9 ^{ab}	3.3 ^b	0.024 [†]

§=Chi-square Test , †=ANOVA with square-root transformed data

Germination:

The percent of germinated seeds for control, water, bag and peeled treatments was 54%, 55%, 9% and 23%, respectively (Figure 3.12). Results of the Pearson's Chi-squared Goodness of Fit Test were significant ($X^2=25.05$, $p<0.001$).

The mean time until germination was not significantly different among treatments (Kruskal-Wallis $DF=3$, $H=5.87$, $p=0.118$ (Figure 3.13).

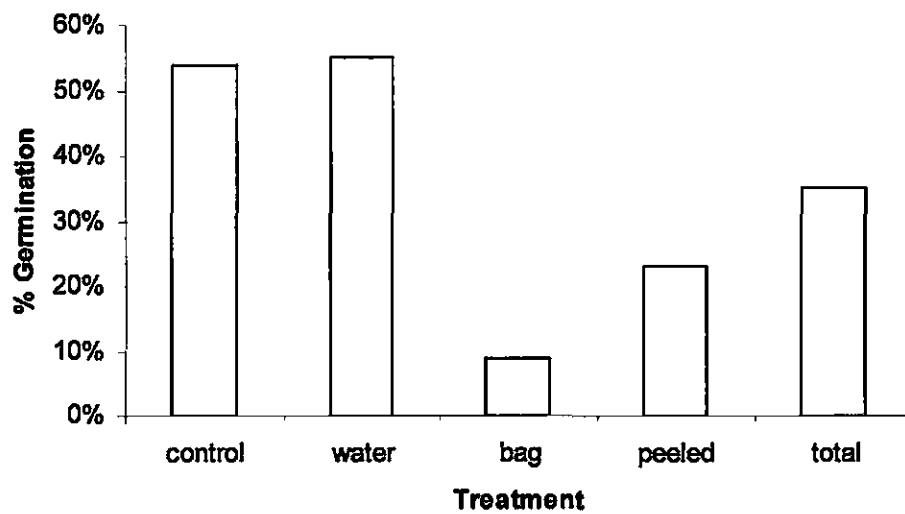


Figure 3.12. Percent germination per treatment.

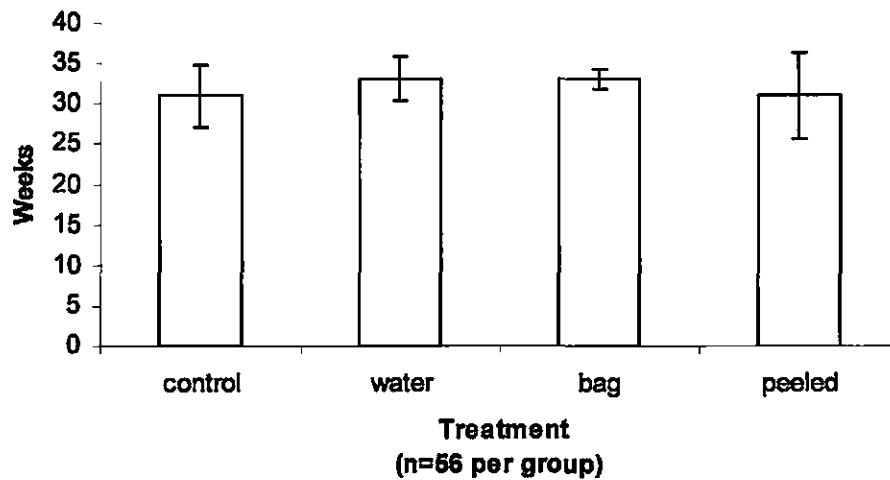


Figure 3.13. Mean time until germination per treatment.

DISCUSSION

Closed-canopy and managed-canopy forests, as well as homegardens, are all very common environments throughout the Sierra Santa Marta. In terms of canopy cover and light transmittance, they represent points along the continuum from closed-canopy conditions to forest gaps. A previous study in Los Tuxtlas Reserve observed increased growth and reproductive output of *Astrocaryum mexicanum* in forest gaps compared to closed-canopy conditions (Martinez-Ramos and Alvarez-Buylla 1995), but light levels were not documented and no information was available on the potential implications of smaller differences in light environments. Because small differences in growth can imply significant differences in income for farmers, the objective of this study was to compare light transmittance across the continuum of these three settings and evaluate their potential for the understory cultivation of *Astrocaryum mexicanum*. In addition, I wanted

to compare the effects of differences in light in the context of human-managed environments.

For all three settings, canopy cover was significantly negatively correlated to light transmittance. Canopy cover was significantly less in managed sites than in closed canopy sites, and lesser still in homegardens. Accordingly, light transmittance was significantly greater in the managed-canopy sites compared to the closed-canopy sites, and greater still in the homegardens. This information allows us to better understand and perhaps predict the performance of understory crop species in the three environments.

Although seedling survival did not differ among the three environments, seedling leaf production was significantly greater in the homegardens than in managed or closed canopy forests. While further studies are needed to isolate other potential variables (such as soil quality, interspecific competition, etc.) that may play role in these differences, these results support the earlier findings in Los Tuxtlas. The significant linear regression model describing leaf production in response to variance in light transmittance provides further evidence of the effect of light on increased seedling growth. As may be expected, the wet season model had a steeper slope, indicating light differences are most important for the season in which the most growth occurs. Although I observed increased leaf production in correspondence with increasing light transmittance, I did not evaluate the upper limits of this pattern. Future studies should investigate the light-saturated photosynthetic rate (P_{max}) of this understory species in order to further evaluate potential sites for understory cultivation.

The relative growth rate of the out-planted seedlings was also significantly greater in the homegardens than in the two forest sites, and there was no difference between the

two forest sites. My analyses of specific root and shoot growth reveal that the difference growth rate results from the significantly lower root growth in the two forest environments. In fact approximately half of the seedlings planted in the closed and managed-canopy sites had negative root growth. It is possible that these seedlings were essentially cannibalizing themselves in these environments with fewer resources. There was no negative root growth observed in the homegardens. I noted that seed stores were removed prior to out-planting; thus, seedlings could not rely on these reserves to promote initial growth of roots and shoots.

It is important to note that our growth studies involving both existing and out-planted seedlings showed no significant difference in growth between closed-canopy and managed-canopy sites. The current practice of clearing forest canopy does not appear to provide any benefit for farmers in terms of enhanced growth of seedlings.

The average number of inflorescences produced per reproductive tree was significantly greater in the homegardens than in the closed-canopy plots. This supports the findings of studies on the protected populations of *A. mexicanum* of the Los Tuxtlas Biosphere Reserve, where researchers reported fecundity in forest gaps to be two-fold compared to that under closed canopy, as both the probability of reproduction, and the reproductive output were greatly enhanced (Martinez-Ramos and Alvarez-Buylla 1995, Martinez-Ramos, et al. 1988). However, I found no differences in reproductive output between closed-canopy and managed forests, again suggesting the ineffectiveness of the current practice of canopy clearing.

In contrast to the Los Tuxtlas findings, I did not observe a significant difference in the probability of reproduction across the different light environments. However, a

range of 68-80% of mature adults produced inflorescences during our study season. This is considerably greater than the 41% probability of reproduction observed in Los Tuxtlas. Furthermore, the mean numbers of inflorescences observed per reproductive adult (reproductive this season) for all three environments in our study were greater than the average of 1.13- 2.09 reported in Los Tuxtlas (Pifíero and Sarukhán 1982). These differences may be due to environmental differences between the sites or over time. Alternatively they may be due to positive effects of harvest on inflorescence production. Such “compensatory reproduction” was observed in two *Melampyrum* species that, in response to flower and fruit removal, increased seed production later in the season (Lehtila and Syrjanen 1995). The authors concluded that compensation was a result of changes in the abortion regimes of reproductive structures, rather than through re-growth. Future investigations of *A. mexicanum* are needed to compare the probability of reproduction as well as the rate of inflorescence production between individuals in protected and human-managed systems while also isolating additional environmental variables that were not evaluated in this study. I also recommend studies that address the impact of heavy immature inflorescence harvest on the rate of cross-breeding.

The overall germination rate of 35% in my study was lower than expected. Previous studies reported low germination as a result of predation, but a high degree of seed viability. Martínez-Ramos and Alvarez- Buylla (1995) reported 2.5% of produced seeds germinated and transitioned to the seedling stage, but that seeds surviving predation had a viability of close to 99%. Germination time in our study averaged 31-32 weeks, and there was no significant difference among treatments, suggesting that seed manipulation has no effect of the rate of germination. Studies of germination time in the

wild vary, but reports suggest a period of 6 months to 1 year (Brewer and Webb 2001, Martinez Ramos and Alvarez-Buylla, 1995).

At the same I conducted my germination study, local residents also planted *A. mexicanum* seeds in their own nurseries. They observed greater percentages of germination. Seeds planted by the local residents were collected from the ground, while ours were collected directly from the tree in effort to reduce the probability of collecting insect-infested seeds and seeds of the previous year. As a result, the seeds used in my experiment may not have been completely mature. Immature seeds do not have a thoroughly hardened endocarp, the part of the seed responsible for protecting the embryo once the fibrous pericarp has disintegrated. As a result, experimental treatment such as peeling the pericarp could have detrimental effects if the endocarp is not fully formed.

Experimental manipulation of the seeds prior to planting did not have a positive effect on the likelihood, or the rate of germination. Based on these results, pre-treatment of seeds does not appear to be worthwhile for cultivators. However it appears imperative that harvesters ascertain the maturity of seeds, which may mean collecting only seeds that have already fallen from the parent tree.

CONCLUSION

The prevalence of secondary forests throughout the Sierra Santa Marta, in varying stages of succession provide for a variety of light environments. It is likely that many of these environments will provide the light conditions that induce understory species such as *Astrocaryum mexicanum* to grow and produce at improved rates. I highly recommend these areas be targeted for understory cultivation. Furthermore, our growth and productivity studies revealed no significant difference between closed and managed-

canopy sites. This information has implications for conservation of canopy species, as it could encourage farmers to clear a greater percentage of canopy trees to further increase light levels. As an alternative to planting in old-growth forests and manipulating the forest canopy, understory cultivation of *A. mexicanum* should be promoted in secondary forests where many of the canopy species are non-native. Future studies will need to address additional variables in secondary forest that were not evaluated in this study including: soil characterization, interspecific interactions, and predation.

Of obvious concern for farmers is the length of time until the first reproduction. Until now, the age of the reproductive individuals in the forests was unknown. However, as a result of the recent plantings in the communities, it will be possible to monitor the age of their first reproduction. It is recommended that this be monitored in a variety of environments such as homegardens, managed-canopy forests in order to assess potential environmental effects.

LITERATURE CITED

- Anderson, A.B. 1990. Alternatives to Deforestation: Steps Toward Sustainable Use of the Amazon Rainforest. Columbia University Press, New York.
- Brewer, S.W. and M.A.H. Webb. 2001. Ignorant seed predators and factors affecting the seed survival of a tropical palm. *Oikos* 93: 32-41.
- Cunningham, A.B. 1993. African medicinal plants: Setting priorities at the interface between conservation and primary healthcare. People and Plants Working Paper I. UNESCO, Paris, France.
- Durand, L. and E. Lazos. 2004. Colonization and tropical deforestation in the Sierra Santa Marta, Southern Mexico. *Environmental Conservation* 31(1): 11-21.
- Eguiarte, L.E., A. Burquez, J. Rodriguez and M. Martinez. 1993. Direct and indirect estimates of neighborhood and effective population size in a tropical palm, *Astrocaryum mexicanum*. *Evolution* 47(1): 75-87.
- Elevitch, C.R. 2004. The Overstory Book: Cultivating Connections With Trees. 2nd Edition. Permanent Agriculture Resources. Holualoa, Hawaii, USA.
- Endress, B.A., et al. 2004. Non-timber forest product extraction: effects of harvest and browsing on an understory palm. *Ecological Applications* 14(4): 1139-1153.
- FAO 1995. Non-wood forest products for rural income and sustainable forestry. FAO technical papers, Non-Wood Forest Products Series. FAO, Rome, Italy
- Gliessman, S.R. 2000. Field and Laboratory Investigations in Agroecology. Lewis Publishers, Boca Raton, FL.
- Guevara-Sada, S., J. Laborde-Dovali and G. Sanchez-Rios. 2000. La Reserva Biosfera Los Tuxtlas. Documentos de Trabajo, Programa de Cooperación Sur-Sur Sobre Desarrollo Socioeconómico Ambientalmente Adecuado en los Trópicos Húmedos. UNESCO, Paris, France.
- Kutner, M.H., C.J. Nachtsheim, J. Neter and W. Li. 2005. Applied Linear Statistical Models 5th Edition, McGraw-Hill International Edition. New York, NY.
- Lehtila, K. and K. Syrjanen. 1995. Compensatory responses of two *Melampyrum* species after damage. *Functional Ecology* 9(3): 511-517.
- Marcus, J. and K. Banks. 1999. A practical guide to germinating palm seeds. *Palms* (formerly *Principes*) 43(2).
- Martinez-Ramos, M. and E.R. Alvarez-Buylla. 1995. Seed dispersal and patch dynamics in tropical rain forests: A demographic approach. *Ecoscience* 2 (3): 223-229.
- Martinez-Ramos, M., M.J. Sarukhán and D. Piñero. 1988. The demography of tropical trees in the context of forest gap dynamics: the case of *Astrocaryum mexicanum* at Los Tuxtlas tropical rainforest. In: Plant Population Ecology (D.J. Davy, M.J. Hutchings & A.R. Watkinson, eds.) Blackwell, Oxford, England.
- Mendoza, A., D. Piñero, and J. Sarukhán, 1987. Effects of experimental defoliation on growth, reproduction and survival of *Astrocaryum mexicanum*. *Journal of Ecology* 75: 545-554.
- Nakahashi, C.D., K. Frole and L. Sack. 2005. Bacterial leaf nodule symbiosis in *Ardisia* (Myrsinaceae): Does it contribute to seedling growth capacity? *Plant Biology* 7: 495-500.

- Pare L. and E. Velasquez. 1997. In: L. Pare and E. Velasquez, Editors, Gestion de recursos naturales y opciones agroecologicos para la Sierra de Santa Marta, Institución de Investigaciones Sociales y UNAM, Mexico.
- Piñero, D. and J. Sarukhán. 1982. Reproductive behavior and its individual variability in a tropical palm, *Astrocaryum mexicanum*. *Journal of Ecology* 70: 461-472.
- Piñero, D., J. Sarukhán, and E. González. 1977. Estudios demográficos en plantas-*Astrocaryum mexicanum* estructura de las poblaciones. *Boletín de la Sociedad Botánica de México* 37: 69-118.
- Plotkin and Famolare, 1992. Plotkin, M., Famolare, L. (Eds.), 1992. Sustainable Harvest and Marketing of Rain Forest Products. Island Press, Washington, DC.
- Popma J. and F. Bongers. 1991. Acclimation of seedlings of three Mexican tropical forest tree species to a change in light availability. *Journal of Tropical Ecology* 72: 777-795.
- Potvin, C., R. Cansari, J. Hutton, I. Caisamo and B. Pacheco. 2003. Preparation for propagation: understanding germination of giwa (*Astrocaryum standleyanum*), wagara (*Sabal mauritiiformis*), and eba (*Socratea exorrhiza*) for future cultivation. *Biodiversity and Conservation* 12: 2161-2171.
- Sanchez-Cordero, V. and R. Martinez-Gallardo. 1998. Post dispersal fruit and seed removal by forest dwelling rodents in a lowland rainforest in Mexico. *Journal of Tropical Ecology* 14(2): 139-151.
- Sarukhán, J. 1978. Studies on the demography of tropical trees. In: Tropical Trees as Living Systems (P.B. Tomlinson, P.B. & M.H. Zimmermann, eds.), pp. 163-184. Cambridge University Press, London.
- Sarukhán, J. 1980. Demographic problems in tropical systems. In *Demography and Evolution in Plant Populations* (O. Solbrig, ed.) Blackwell Scientific Publications, Oxford: 161-188.
- Sokal, R.R. and F.J. Rohlf. 1995. *Biometry : the principles and practice of statistics in biological research*. 3rd edition. W.H. Freeman, New York.
- Svenning, J.C. 2002. Crown illumination limits the population growth rate of a neotropical understorey palm (*Geonoma macrostachys*, Arecaceae). *Plant Ecology* 159:185-199.
- Ticktin, T. and P. Nantel. 2004. Dynamics of harvested populations of the tropical understorey herb *Aechmea magdalenae* in old-growth versus secondary forests. *Biological Conservation* 120: 461-470.
- Ticktin, T., T. Johns, and V. Chapol-Xoca. 2003. Patterns of growth in *Aechmea magdalenae* (Bromeliaceae) and its potential as a forest crop and conservation strategy *Agriculture, Ecosystems and Environment* 94: 123-139.
- Vantomme, P. 1997. Non-wood forest products for rural income and sustainable forestry. In Nair, M.N.B, et al. 1998. *Sustainable Management of Non-Wood Forest Products*. University Putra Malaysia Press. Serdang.
- Vasquez, R. and A.H. Gentry. 1989. Use and misuse of forest-harvested fruits in the Inquitos area. *Conservation Biology* 3(4): 350-361.

CHAPTER IV

Conclusions

The effects of human management on NTFP species and their environments:

The results of this study suggest that the harvest of *Astrocaryum mexicanum* inflorescences in the Sierra Santa Marta is affecting wild populations. I observed significantly lower densities and differences in population structures in the harvested populations compared to the protected populations. The limitation of this study was the distinct geographic locations used to compare harvested and unharvested populations, and the inability to consider all environmental differences between the two locations that may influence population structure. Further studies should evaluate potential environmental differences.

However, environmental differences and harvest practices are not the only two aspects that should be considered. As evidenced in this study, there are abiotic and biotic variables associated with human-managed landscapes that can affect the ecology of the resource. The human-managed forests of the Sierra Santa Marta where chocho is harvested are likely affected by human activities such as the trampling of seedlings, the selective clearing or sparing of other species, the cultivation of other understory crops, hunting, the manipulation of the canopy and understory, and logging.

Through the monitoring of current inflorescence harvest and interviews with local harvesters, we found harvest intensity to be very high. As a result, I encourage the enrichment planting/understory cultivation, that has already begun in a few communities and recommend it be extended to additional communities.

Growth and productivity in different forest sites and implications for understory cultivation:

There are different biotic and abiotic variables associated human-managed landscapes. For this reason, I assessed growth and productivity of *A. mexicanum* in the very same forests where it is harvested. Many studies carried out in protected, research stations etc., may not necessarily translate to communities where the resource is harvested. Closed-canopy, partially-cleared canopy “managed” forests and homegardens are very common throughout the Sierra Santa Marta, though differences among these environments had not previously been assessed. Homegardens and managed forest sites represent points along the continuum of light conditions between closed-canopy forest and forest gaps. It is important to assess differences in growth and productivity of potential understory crops along this continuum as even small differences in growth and productivity can mean significant differences in yield for farmers.

In this study, I observed significantly enhanced growth and inflorescence production in homegardens, though no difference between the closed and managed-canopy sites. The upper limits of this pattern (P_{max}) remain to be tested. The prevalence of secondary forests throughout the Sierra Santa Marta, in varying stages of succession provide for a variety of light environments, many of which will provide conditions that induce *A. mexicanum* to grow and reproduce at improved rates. I recommend these areas be targeted for understory cultivation. Furthermore, growth and productivity studies revealed no significant difference between closed and managed-canopy sites. This information has implications for conservation of canopy species, as it could incite

farmers to clear greater amounts of canopy trees in order to further increase light levels. As an alternative to planting in old-growth forests and manipulating the forest canopy, understory cultivation of *A. mexicanum* should be promoted in secondary forests. Future studies need to address additional variables associated with secondary forests that were not evaluated in this study including: soil characterization, interspecific interactions, etc.

Of obvious concern for farmers is the length of time until the first reproduction. Until now, the age of the reproductive individuals in the forests was unknown. However, as a result of the recent plantings in the communities, it will be possible to monitor the age of their first reproduction. It is recommended that this be monitored in a variety of environments such as homegardens, managed-canopy forests in order to assess the potential environmental effects. Further studies should likewise address the potential for “compensatory reproduction” in response to harvest. Inflorescence production in this study was observed to be greater than in previous studies at the Los Tuxtlas Research station, though I could not discern whether this is an effect of harvest or environment.

Implications for forest conservation and economic development:

In order to succeed as a conservation strategy, economic incentive must outweigh the demands associated with cultivation. There is a history in the Sierra Santa Marta of failed economic endeavors and residents wary of further futile efforts. Cultivation can result in higher, more reliable yields; however consumer demand must be great enough such that income outweighs the investment of land, labor and time. I observed significant demand based on information gathered by interviews and by assessing harvest intensity. However, socio-economic studies should be performed to evaluate market potential in surrounding areas. I found that many people in nearby cities were not familiar with this

resource and the researchers at the UNAM Research Station in Los Tuxtlas were unaware of its exploitation. Additionally, future studies should address the nutritional content of the inflorescences as well as shelf life. Local farmers will likely need assistance in accessing potential markets and in the development of commercialization strategies.

There is potential for the cultivation of *A. mexicanum* to positively affect the livelihoods of local farmers. The average wage for day laborers' arduous and often dangerous work is approximately 120 pesos per day. The harvesters I interviewed reported selling inflorescences for approximately 12 pesos each. Therefore, residents, including women and children have the potential to earn the equivalent of a day laborer by selling only 10 inflorescences.

The implications of cultivation of *A. mexicanum* for conservation are two-fold: cultivation may assuage the current harvest pressures on wild populations and it may also provide an alternative to further clearing of both primary and secondary forests for cattle. In addition to the favorable light conditions associated with secondary forests, I recommend understory cultivation concentrate on secondary forest in an effort to avoid further clearing of primary forest canopy trees. Understory cultivation of *A. mexicanum* may provide the opportunity to compliment reforestation efforts with a native species. Current reforestation projects in the region often plant fast-growing, non-native tree species. Native palms may be a viable alternative for understory restoration efforts as they are presumably better adapted to local environmental conditions.

As a strategy for both forest conservation as well as economic development, I encourage the understory cultivation of *A. mexicanum* that has recently been initiated in a

few of the communities of the Sierra Santa Marta and recommend further planting in the secondary forests that are common throughout the region.

APPENDIX A

Poisson Regression Table for Chapter III

Forest type 1 =closed-canopy
 Forest type 2 =managed-canopy
 Forest type 3 =homegarden
 Orig = original # of leaves
 New = # of new leaves

The GENMOD Procedure-The SAS System

Analysis of Parameter Estimates

Parameter	DF	Standard Estimate	Wald Error	95% Confidence Limits		Chi-Square	Pr > ChiSq
Intercept	1	0.8967	0.2052	0.4945	1.2989	19.09	<.0001
foresttype 1	1	-1.1759	0.1623	-1.4941	-0.8577	52.47	<.0001
foresttype 2	1	-0.9562	0.1679	-1.2853	-0.6271	32.43	<.0001
foresttype 3	0	0.0000	0.0000	0.0000	0.0000	.	.
orig	1	0.0531	0.0300	-0.0056	0.1119	3.15	0.0761
Scale	0	0.7511	0.0000	0.7511	0.7511		

NOTE: The scale parameter was estimated by the square root of DEVIANCE/DOF.

LR Statistics For Type 3 Analysis

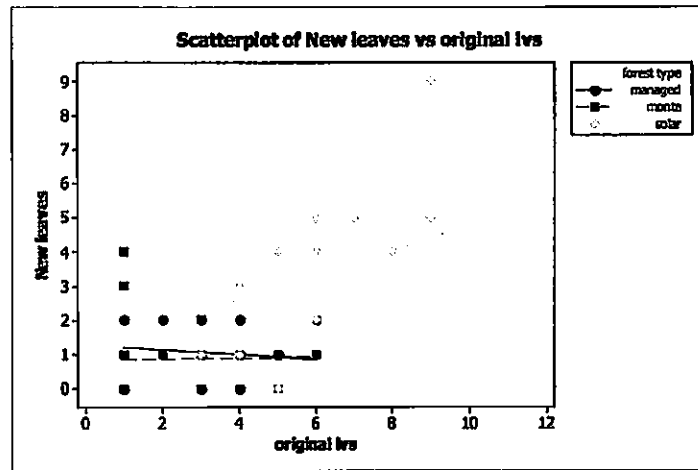
Source	Num DF	Den DF	F Value	Pr > F	Chi-Square	Pr > ChiSq
foresttype	2	165	27.10	<.0001	54.19	<.0001
orig	1	165	3.12	0.0792	3.12	0.0773

Contrast Results

Contrast	Num DF	Den DF	F Value	Pr > F	Chi-Square	Pr > ChiSq	Type
monte vs. managed	1	165	2.47	0.1179	2.47	0.1160	LR
monte vs. solar	1	165	53.17	<.0001	53.17	<.0001	LR
managed vs. solar	1	165	33.60	<.0001	33.60	<.0001	LR

APPENDIX B

The relationship of the original number of leaves and new leaves produced



APPENDIX C

Final weights of out-planted seedlings

<u>Tag</u>	<u>Forest Type</u>	<u>Final Shoot Mass (g)</u>	<u>Final Root Mass (g)</u>	<u>Final Total Mass (g)</u>	<u>Shoot Growth (g)</u>	<u>Root Growth (g)</u>	<u>Total Growth (g)</u>	<u>Root Mass Fraction</u>	<u>Shoot Mass Fraction</u>	<u>Root-Shoot Ratio</u>
SM09	Closed-canopy	0.80	0.20	1.00	-0.26	-0.17	-0.43	0.20	0.80	0.25
SM08	Closed-canopy	1.60	0.40	2.00	0.54	0.03	0.57	0.20	0.80	0.25
SM17	Closed-canopy	1.90	0.40	2.30	0.84	0.03	0.87	0.17	0.83	0.21
SM16	Closed-canopy	0.40	0.30	0.70	-0.66	-0.07	-0.73	0.43	0.57	0.75
SM18	Closed-canopy	1.20	0.40	1.60	0.14	0.03	0.17	0.25	0.75	0.33
SM10	Closed-canopy	1.50	0.50	2.00	0.44	0.13	0.57	0.25	0.75	0.33
SM20	Closed-canopy	1.70	0.30	2.00	0.84	-0.07	0.57	0.15	0.85	0.18
SM06	Closed-canopy	1.60	0.30	1.90	0.54	-0.07	0.47	0.16	0.84	0.19
SM07	Closed-canopy	1.00	0.30	1.30	-0.06	-0.07	-0.13	0.23	0.77	0.30
SM29	Closed-canopy	1.30	0.20	1.50	0.24	-0.17	0.07	0.13	0.87	0.15
SM30	Closed-canopy	1.70	0.30	2.00	0.64	-0.07	0.57	0.15	0.85	0.18
SM26	Closed-canopy	2.10	0.40	2.50	1.04	0.03	1.07	0.16	0.84	0.19
SM28	Closed-canopy	0.70	0.20	0.90	-0.36	-0.17	-0.53	0.22	0.78	0.29
SM27	Closed-canopy	2.10	0.60	2.70	1.04	0.23	1.27	0.22	0.78	0.29
SA23	Managed-canopy	2.00	0.60	2.60	0.94	0.23	1.17	0.23	0.77	0.30
SA21	Managed-canopy	1.40	0.30	1.70	0.34	-0.07	0.27	0.18	0.82	0.21
SA25	Managed-canopy	1.50	0.40	1.90	0.44	0.03	0.47	0.21	0.79	0.27
SA22	Managed-canopy	1.00	0.30	1.30	-0.06	-0.07	-0.13	0.23	0.77	0.30
SA05	Managed-canopy	1.80	0.30	2.10	0.74	-0.07	0.67	0.14	0.86	0.17
SA01	Managed-canopy	0.80	0.30	1.20	-0.16	-0.07	-0.23	0.26	0.76	0.33
SA03	Managed-canopy	1.20	0.50	1.70	0.14	0.13	0.27	0.29	0.71	0.42
SA04	Managed-canopy	1.40	0.30	1.70	0.34	-0.07	0.27	0.18	0.82	0.21
SA02	Managed-canopy	1.20	0.40	1.60	0.14	0.03	0.17	0.26	0.75	0.33
SA24	Managed-canopy	3.00	0.50	3.50	1.94	0.13	2.07	0.14	0.86	0.17
SA11	Managed-canopy	0.80	0.30	1.10	-0.26	-0.07	-0.33	0.27	0.73	0.38
SA12	Managed-canopy	1.70	0.40	2.10	0.64	0.03	0.67	0.19	0.81	0.24
SA14	Managed-canopy	5.00	0.90	5.90	3.94	0.53	4.47	0.15	0.85	0.18
SA15	Managed-canopy	2.10	0.50	2.60	1.04	0.13	1.17	0.19	0.81	0.24
MG317	Homegarden	0.50	1.12	1.62	-0.56	0.75	0.19	0.69	0.31	2.24
MG293	Homegarden	2.60	2.10	4.70	1.54	1.73	3.27	0.45	0.55	0.81
MG291	Homegarden	1.40	1.60	3.00	0.34	1.23	1.57	0.53	0.47	1.14
MG326	Homegarden	2.50	2.00	4.50	1.44	1.63	3.07	0.44	0.56	0.80
MG324	Homegarden	2.40	2.20	4.60	1.34	1.83	3.17	0.48	0.52	0.92
MG315	Homegarden	1.10	1.70	2.80	0.04	1.33	1.37	0.61	0.39	1.55
MG289	Homegarden	3.20	4.70	7.90	2.14	4.33	6.47	0.59	0.41	1.47
MG320	Homegarden	2.40	1.60	4.00	1.34	1.23	2.57	0.40	0.60	0.67
MG301	Homegarden	3.20	1.90	5.10	2.14	1.53	3.67	0.37	0.63	0.59
MG328	Homegarden	2.70	2.30	5.00	1.64	1.93	3.57	0.46	0.54	0.85
MG329	Homegarden	2.10	1.70	3.80	1.04	1.33	2.37	0.45	0.55	0.81
MG288	Homegarden	2.50	2.80	5.30	1.44	2.43	3.87	0.53	0.47	1.12
MG302	Homegarden	1.50	1.40	2.90	0.44	1.03	1.47	0.48	0.52	0.93