

2001

Palm community development and influence on seedling establishment in a tropical moist forest, Panama

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PALM COMMUNITY DEVELOPMENT AND INFLUENCE ON SEEDLING
ESTABLISHMENT IN A TROPICAL MOIST FOREST, PANAMA

A Thesis

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Master of Science

in

The Department of Biological Sciences

by
Krista Farris Lopez
B.S., Oregon State University, 1995
December 2001

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DEDICATION

This thesis is dedicated to my father, Jerry Farris, my son, Lucas Lopez Farris, and my husband, Omar Lopez. I dedicate this thesis to my father because he gave me his spirit and passion for the natural world. Because of him, I learned to love and respect many forms of life; from hellgrammites, skinks, and rattlesnakes to coyotes, mountain lions, and eagles. Because of him, I grew up camping and trekking down endless streams in search of trout. My father taught me important life lessons; you can be anything you want to be, and any trout big enough to hook is big enough to eat. I want to thank my father for his endless support of my dream to be a tropical biologist and for his visits with me to the jungles of Belize and Panama.

I dedicate this thesis to my son, Lucas, for giving me the inspiration to finish this research. I want to express my appreciation for his endurance during the first seven months of gestation, during which he was bounced around in Brazil and Panama while I was doing field work. I also want to thank Lucas for putting up with the craziness of daycare while I was writing my manuscripts.

Finally, I dedicate this thesis to my husband, Omar, because I could not have done this without him. Omar has helped me with this research from the day it started to the day it finished by providing technical and logistical support, endless discussions on research design and ecological theory, and valuable feedback throughout the development of the thesis.

ACKNOWLEDGEMENTS

I am grateful to Heather Passmore for field assistance and Julie Denslow for chairing my committee and providing invaluable guidance throughout the thesis preparation. I would like to thank my other committee members, Barry Moser for his statistical input and help in writing several statistical programs and Bill Platt for his encouragement and helpful comments on the manuscripts. I am also grateful to Saara DeWalt for her critical input on early drafts. I would like to thank Jens Svenning for sharing his vast knowledge of palms, while I was in Panama. Finally, I would like to thank Lissy Coley and Tom Kursar for extending their lab to me at the University of Utah and for their input at various stages of the thesis preparation. This research has been supported by the National Science Foundation, A. Mellon Foundation, and the Smithsonian Tropical Research Institute.

ABSTRACT

Plants often modify microsite conditions important for seedling establishment. Palms may reduce light levels and produce deep leaf litter; both may suppress seedlings, affecting the local abundance, distribution, and species composition of tree seedlings. The abundance and composition of palms were examined along a tropical forest chronosequence at the Barro Colorado Nature Monument, Panama. Palms were sampled along transects in secondary (20, 40, 70, and 100 y in fallow) and old-growth forests. Palm abundance and basal area significantly increased with forest age. Palm distribution was driven by the most abundant palm, *Oenocarpus mapora*, which accounted for 60% of the total stems.

I examined the effects of *O. mapora*, on seedling distributions on Barro Colorado Island, Panama. I asked: a) what are the effects of *O. mapora* on light availability and leaf litter accumulation; b) how does *O. mapora* affect abundances of seedlings; c) does seed size of established seedlings differ between palm and non-palm sites? Seedling composition, light availability, leaf litter and palm presence were measured in 1-m² contiguous plots along transects in one late second growth and two old growth forest stands. I conducted a seedling transplant experiment to determine the effect of *O. mapora* and its leaf litter on growth and mortality rates of *Gustavia superba* seedlings. Leaf litter depth was higher and light availability was lower in plots where palms were present. There was a lower probability of seedling presence where large palms were present. The probability of seedling presence increased with light availability. Seed size was greater for seedlings in palm plots relative to non-palm plots. Seedling survival was significantly lower for palm and litter treatments relative to controls. I conclude that *O. mapora* creates poor establishment conditions for seedlings which may affect the local abundance, distribution, and species composition of the seedling pool.

INTRODUCTION

Palms are a unique and isolated group within the monocotyledons (Uhl & Dransfield 1987, Duvall et al. 1993). Most palms are restricted to the Tropics, and approximately one third of the species in the palm family (Arecaceae) are native to the Western Hemisphere (Henderson 1995). Palms are an important component of neotropical rainforests ecosystems where they exhibit a variety of growth forms, from acaulescent understory plants to large canopy trees (Balslev et al. 1987, Faber-Langendoen & Gentry 1991, Kahn & de Granville 1992, Peres 1994, Borchsenius et al. 1998). Palms often are common in the understory of neotropical forests (Kahn et al. 1988, Martinez-Ramos et al. 1988), where they can represent as much as 70% of the total understory cover (Kahn & de Granville 1992). Because of their abundance in many forests, palms may interfere with seedling establishment through resource competition and environmental modification (Aide 1987, Denslow et al. 1991, Svenning 2001). Recent data from a chronosequence study by Denslow & Guzman (2000) suggests that the expansion of palm populations may contribute to the low seedling establishment in a moist tropical forest of Panama. Higher densities of palms in older forest stands corresponded to lower seedling densities (Denslow & Guzman 2000), suggesting that the distribution of palms may affect the abundance and distribution of the seedling pool. The main questions of this thesis are 1) what are the patterns of palm community development during forest succession? 2) Do palms lower seedling abundance below their canopies? 3) Do palms influence diversity or species composition of seedlings? And 4) through what mechanisms do palms influence seedling establishment?

The focus of my thesis is the development of the palm community along a chronosequence of forest stands and the impacts of a common palm on woody seedling establishment. In the first chapter, I examine the abundance, distribution and size structure of species in the palm community in forests stands aged 20 to 100 years since last human disturbance and in old growth stands. In the second chapter, I examine the impacts of a common palm, *Oenocarpus mapora*, on patterns of establishment of woody seedlings. In this chapter, I looked at how this palm affects microsite conditions that may be important for seedling establishment. Then, I examined the effects of altered microsite conditions on seedling density and composition. Finally, I conducted a transplant experiment to examine the effects of *O. mapora* on seedling survivorship and growth.

Patterns of seedling establishment

A common source of seedling mortality is unsuitable environmental conditions at the time of germination. Tree seedling germination and establishment have been shown to be sensitive to light availability (Augspurger 1983, 1984) and quality (Vazquez-Yanes et al. 1990), soil moisture (Garwood 1983), nutrient supply (Burslem 1996), and quantity and quality of leaf litter (Molofsky & Augspurger 1992, Facelli & Facelli 1993, Facelli 1994). Biotic factors such as pathogens (Augspurger 1983, 1984, Augspurger & Kelly 1984, Kitajima & Augspurger 1989), insects (Coley 1983, Brown 1990), and competition from other plants (Denslow et al. 1991, George & Bazzaz 1999) alone or by their interaction with abiotic factors, may affect seedling survivorship as well. Some or even

all of these factors may interact in complex ways to influence patterns of seedling establishment.

Light availability

Photosynthetically active radiation (PAR) plays a major role in growth, survival and establishment of tropical seedlings. Mature tropical rain forests are dynamic communities with a high frequency of tree and limb falls which open gaps in the canopy resulting in a heterogeneous light environment on the forest floor. Small treefall gaps are a common canopy disturbance where light availability on the forest floor typically reaches 8-10% full sun. Larger multiple treefall gaps also occur although are less common and light availability is typically 20-35% full sun in these gaps (Denslow et al. 1990). Tropical tree species vary greatly in their light requirements, falling along a continuum from gap-requiring to deep shade tolerant (Augsburger 1984, Kitajima 1994, Kobe 1999).

Light availability in the tropical forest understory is typically between 1-2% full sun (Chazdon and Fetcher 1984). However, understory light levels are not uniform, but punctuated by short-duration sun flecks which account for 30-80% of the irradiance used by plants growing in this environment (Chazdon and Pearcy 1991, Chazdon 1988, 1992, Chazdon et al. 1996). Photosynthetic response of seedlings to sunflecks depend on their duration and frequency but in general plant growth approximates a linear function of available light for levels less than 20% full sun (Chazdon 1988), suggesting that even small increases in total incident light will have a strong positive effect on C fixation in the understory.

Seedlings of even the most shade tolerant tree species often live at or near their compensation points in the understory and require a light-gap at some stage to reach the canopy (Hartshorn 1978, Brokaw 1980, Augspurger 1983, Denslow et al. 1990, Saverimuttu & Westoby 1996). Augspurger (1984) studied the light requirements of seedlings from 18 tropical tree species in Panama. She found that 17 species germinated in both light gaps and deep shade, but that mortality rates were higher and seedling growth was slower among seedlings growing in deep shade. These findings suggest that many seedling species benefit from higher light availability in treefall gaps. However, there are shade-tolerant species that can persist in the deep shade of the understory for many years (Kitajima & Augspurger 1989, Kitajima 1994). Canopy tree seeds that germinate in the forest understory can establish as suppressed seedlings and saplings until a tree fall gap or other disturbance releases valuable resources (Clark & Clark 1987, Denslow et al. 1990, Augspurger 1994). Suppressed seedlings in the forest understory, referred to as "advance regeneration" are thought to make a major contribution to the future stand composition (Brokaw 1985, Uhl et al. 1988, Ashton 1992).

Effects of leaf litter

Leaf litter may affect microsite conditions important for seedling establishment. Litter has been reported to alter levels of light and humidity (Vazquez-Yanez et al. 1990, Facelli & Pickett 1991), surface soil temperature (Molofsky & Augspurger 1992), soil nutrients (Vitousek 1984, McClaugherty et al. 1985, Facelli & Pickett 1991), allelopathic interactions (Rice 1984) as well as act as a physical barrier to seedling establishment

(Molofsky & Augspurger 1992). Leaf litter may also play a role in protecting seeds and seedlings from detection by herbivores (Cintra 1997).

Litter production depends primarily on the productivity of the plant community at a site (Facelli & Pickett 1991). The amount of litter accumulated at a given site is influenced by the balance of litter production and litter decomposition by physical and biotic agents (Sure & Philips 1987, Facelli & Pickett 1991). Leaf litter distribution varies spatially as affected by both overstory and understory vegetation (Facelli & Pickett 1991, Kohyama & Grubb 1994, Cintra 1997), but can be spatially unpredictable at scales as small as 1m (Molofsky & Augspurger 1992). Leaf litter distribution varies seasonally as well (Cintra 1997) with peak litter accumulation in Panama occurring at the end of the dry season (Golley et al. 1975, Garwood 1983).

The impact of leaf litter cover on seedling establishment varies by species, habitat type, and timing of germination suggesting a complex interaction (Molofsky & Augspurger 1992). For example, the presence of litter decreased emergence and survival for shade-intolerant species (Guzman-Grajales & Walker 1991, Molofsky & Augspurger 1992), but differed in the magnitude of its effect and the stage (germination, emergence, postemergence survival) at which it became influential (Molofsky & Augspurger 1992). Survival of large seeded seedlings is often either positively affected or unaffected by deep litter whereas survival of small seeded species is often negatively affected (Molofsky & Augspurger 1992, Cintra 1997, Svenning 2001). The type of leaf litter is also important for seedling establishment. A study by Facelli and Pickett (1991) found that litter from a hardwood tree, *Quercus alba*, intercepted more light and reduced the density of two dominant grasses when compared to litter from other species. Leaf litter may increase soil moisture and decrease soil temperature (Molofsky & Augspurger 1992), which may be beneficial for seedling establishment in seasonally dry forests.

Effects of pathogens and insects

Pathogen and insect damage can increase seedling mortality of tropical tree species. Patterns of pathogen and insect damage to seedlings result from the interaction of light availability, dispersal distance, and seedling density (Augspurger 1983, 1984, Augspurger & Kelly 1984, Sork 1987, Schupp 1988, Gilbert et al. 1994). Pathogens responsible for damping-off disease can kill large numbers of established seedlings (Augspurger 1983). However, seedlings in high light environments may be less susceptible to pathogens. Augspurger (1984) found that the major source of seedling mortality in deep shade was fungal pathogens whereas there was little evidence of mortality due to pathogens for seedlings growing in high light environments. Less favorable carbon balances in deep shade may make it harder to maintain defensive traits or recover from tissue lost to pathogen attack (Augspurger 1984, Augspurger & Kelly 1984, Kitajima 1994). Therefore, shade tolerance may be more a function of resistance to pathogens than to the physiological ability to grow in deep shade (Augspurger 1984, Kitajima 1994). Further studies suggest that mortality due to pathogens decreases with increasing dispersal distance, decreasing seedling density, and increasing light availability (Augspurger & Kelly 1984, Gilbert et al. 1994). Seed dispersal increases the distance between the seedling and a zone of high mortality near the parent plant. Seedlings under parent plants may be more likely to pick up pathogens from the parent plant and other conspecifics (Augspurger & Kelly 1984, Gilbert et al. 1994). For

example, increasing dispersal distance from conspecific trees significantly lowered disease in seedlings of common tree species such as *Platypodium* (Augspurger & Kelly 1984), *Tetragastris panamensis* (Gilbert & De Stevens 1995), and *Ocotea whitei* (Gilbert et al. 1994). Density of conspecific seedlings also decreases with distance from the parent plant, lowering the rate of secondary infection through adjacent seedlings (Augspurger & Kelly 1984).

Herbivory has been shown to be an important influence on seedling establishment. The effect of herbivores on seedlings varies among sites, seasons and species. Mammalian herbivores such as agoutis and pacas significantly decreased seedling densities of the large-seeded species, *Gustavia superba*, in Panama, and the degree of seed predation varied with animal abundance at different sites (Sork 1987). Similarly, intense seed predation by mammals on Barro Colorado Island, Panama restricts the establishment of *Dipteryx panamensis* seedlings and saplings compared to other areas where mammals are less abundant (De Stevens & Putz 1984).

Insect herbivory may also influence patterns of seedling establishment. Insect herbivory tends to be sporadic with whole cohorts of seedlings lost to herbivores in one season and none lost in the next (Swaine 1996). Light availability and seedling density may also affect the rates of insect attack (Schupp 1988, Coley 1983, Clark & Clark 1985). A study in Panama, on the understory tree, *Faramea occidentalis*, found that survival of seeds and seedlings as little as 5 meters from the parent plant was significantly greater than those adjacent to the parent; survival of seeds and seedlings in treefall gaps was low due to predation by generalist vertebrates (Schupp 1988). This pattern was found for insect herbivores: Insect damage to plants by shoot-borers, defoliators, miners and sap-suckers, were higher in canopy openings (Brown 1990) than in adjacent understory, perhaps because of the large crop of young, nutrient-rich leaves (Coley 1983). Furthermore, patterns of herbivory may be influenced by the distribution of vegetation.

Competition from other plants

Co-occurring trees and shrubs may influence patterns of seedling establishment directly by resource competition or environmental modification and indirectly by increasing pathogen and herbivore attack. Light interception is affected by the density and composition of both canopy and understory species. For example, the dense foliage of *Gilbertiodendron dewevrei*, reduces incident light levels under its canopy to 50% of that in adjacent mixed canopy forests (Torti 2001). In temperate forests in New England, light transmission characteristics varied among tree species (Canham et al. 1994). The most shade-tolerant species cast the deepest shade (<2% full sun) while earlier successional species allowed greater light penetration (>5% full sun) (Canham et al. 1994). Differences in light transmission are also closely related to crown depth and architecture (Canham et al. 1994, Kabakoff & Chazdon 1996).

The understory vegetation intercepts much of the incident light in closed canopy forests reducing light availability and quality beneath their canopies (Messier et al. 1989, Denslow et al. 1991, George & Bazzaz 1999). In temperate forests, the fern understory reduces light levels below their canopies by 32% (George & Bazzaz 1999) and severely reduced red/far red ratios (Horsley 1993). Similarly, in a tropical forest understory palms and cyclanths reduced incident light availability below their canopies by 45% (Denslow

et al. 1991). Litter production of understory plants may also influence seedling distributions. Leaf litter produced by the fern understory was significantly greater than fern-free areas and decreased the emergence and survival of many tree seedlings (George & Bazzaz 1999). Understory vegetation may alter establishment sites to the extent that tree-seedling species emergence and establishment is differentially reduced (George & Bazzaz 1999).

Palms in particular may have a strong influence on seedling establishment. Denslow et al. (1991) showed that high abundance of palms in old-growth forests is significantly correlated with low seedling densities. High densities of understory palms may influence tree species recruitment and limit tree seedling and sapling abundance (Pinero et al. 1986, Denslow et al. 1991). Palms may affect seedling establishment through competition for light and through pest and litter mediated interference, however very few studies have quantified these effects. For example, where canopy palms are common, falling fronds are a major source of damage and mortality to seedlings recruiting in the understory (Aide 1987). Palm fronds tend to be tough and fibrous and do not decay as rapidly as other types of litter. The tropical palm, *O. mapora* had significantly greater quantities of leaf litter under its canopy relative to palm-free sites and is also thought to inhibit seedling establishment in those sites (Farris Lopez et al. in prep).

The extent to which a species alters environmental variables will determine the influence that particular species has on seedling establishment. My first objective was to examine the development of the palm community across a chronosequence of forest stands in Panama and determine which species are most likely to influence seedling establishment in these forests. My next objective was to quantify the impact of the most dominant palm on seedling density, diversity, and composition. My third objective was to determine the mechanisms through which palms influence patterns of seedling establishment. Specifically I asked, to what extent do palms alter light availability and leaf litter distribution? What impacts do these altered microsite conditions have on patterns of seedling density and diversity? Do palms have the same effect on all species or are some species more successful under palms than others? Finally, I asked how palms influence seedling growth and survivorship.

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CHAPTER 1

PALM COMMUNITY DEVELOPMENT ALONG A TROPICAL MOIST FOREST CHRONOSEQUENCE, PANAMA

Introduction

Palms are a characteristic component of neotropical rain forests. Palms can be so abundant in some forests that they influence the structure and composition of their communities (Sarukhan et al. 1985, Pinero et al. 1986, Svenning 2001). Palms can influence the environmental conditions on the forest floor and alter resources important for the establishment of other species (Denslow et al. 1991, Farris Lopez et al. in prep.). The most direct influences are through the modification of light availability and leaf litter distribution which in turn affect the germination and establishment success of many tree seedlings (Denslow et al. 1991, Molofsky & Augspurger 1992, George & Bazzaz 1999, Farris Lopez et al. in prep.). There is increasing evidence of a negative correlation between palm density and seedling density and diversity (Martinez-Ramos 1980, Sarukhan et al. 1985, Denslow et al. 1991, Denslow & Guzman 2000, Farris Lopez et al. in prep.). For example, Denslow et al. (1991) found that seedling density was negatively correlated with palm importance values for 10 old growth sites in Costa Rica. Recent data suggest that the palm, *Oenocarpus mapora*, reduces seedling abundance under its canopy resulting in an overall reduction in seedling diversity (Farris Lopez et al. in prep.). The impact palms have on patterns of seedling establishment may also influence the distribution of larger size classes. For example, Sarukhan et al. (1985) reported a negative correlation between crown cover of the palm, *Astrocaryum mexicanum* and the number of species of individuals among individuals > 1 cm dbh. Thus, palms may have long lasting impacts on the diversity and composition of the plant community. Therefore, it is important to understand how the distribution and abundance of palms vary across the tropical forest landscape. Tropical forests frequently are cleared for agriculture and pastureland. These areas often subsequently are abandoned and left to fallow when productivity declines. As forests regenerate after stand-destroying disturbances, changes in forest structure and resource availability take place that may influence the species distribution and densities of palms (Svenning 1998).

We examined the distribution, composition, and abundance of the palm community along a chronosequence of forest stands in central Panama. Recent studies in these stands demonstrate changes in patterns of forest structure and resource availability for forest stands 20-100 y in fallow as well as old growth stands. Canopy closure was complete in 20-y stands where canopy stature and basal area were low. Total stand basal area was greatest in 70-y stands and patch sizes of light availability at seedling height were twice as large in 70-y stands as in younger or older stands. This suggests that canopy turnover and gap size were greatest between 70-100 y, perhaps resulting from synchronous mortality of a cohort of long-lived pioneers. Mean stand height increased with stand age. Mean light availability at seedling height (75cm) declined with stand age, and older stands were characterized by lower mean light levels than the younger stands. Canopy closure, canopy structure, foliage height distribution, and treefalls all contribute to patterns of light availability in the understory (Brown & Parker 1994, Canham et al.

1994, Kabakoff & Chazdon 1996, Montgomery & Chazdon 2001). Spatial variation in the understory light environment affects growth and mortality of tree seedlings and saplings.

Palm populations are expected to vary as a function of light availability. Light requirements of canopy palms increase with increasing size due to greater stem production (de Granville 1992). Although many canopy and sub-canopy palms can germinate and establish in low light environments, growth and reproduction is dependant on the high light availability in treefall gaps (Sarukhan et al. 1985, Pinero et al. 1986, De Stevens et al. 1987, De Stevens 1989, Svenning 1999). Stilt-root palms are thought to be less gap-demanding because their unique architecture enables them to begin stem elongation before the meristem has reached its maximum diameter (Schatz et al. 1985, Svenning 1999). Many understory palms can maintain positive carbon gain and reach reproductive maturity in low light environments (<1.4% full sun) (Chazdon 1986), but most show a positive growth response to small increases in light availability such as in small gaps and along gap edges (Chazdon 1986, Svenning 2000). Differences in forest structure and resource availability may lead to differences in palm abundance, composition, and size class distribution between forests of different ages. Palm distributions may in turn influence forest structure and resource availability by modifying environmental conditions on the forest floor, important for seedling establishment.

To examine the potential influences of the palm community on forest regeneration, we assessed the patterns of palm regeneration across a chronosequence of secondary forests ranging in age from 20 to 100 y following agricultural abandonment. Specifically we asked: 1) how does palm distribution and abundance vary among stands of different ages? 2) At what stage in the regeneration process do palms become established in densities high enough to influence understory conditions? And 3) which palms are most likely to influence regeneration patterns of other species?

Methods

Study Site

Study stands were established within the Barro Colorado National Monument (BCNM), Panama (BCI, 9° 9'N; 79°51'W). BCNM encompasses both mainland and island components and houses the Smithsonian Tropical Research Institute field station. Annual rainfall at BCNM averages 2600mm, most of which occurs during the rainy season from May to December. The dry season is pronounced with less than 100 mm of rain falling during the first three months of the year (Windsor 1990) during which 18% of the forest canopy trees lose their leaves (Condit et al. 1996). The canopy of the old growth forest is composed mainly of Leguminosae and Bombacaceae. Common understory species are *Hybanthus prunifolius* and the palm, *Oenocarpus mapora* Karst. Secondary forest canopy is dominated by *Cordia alliodora* (R & P.) Oken, *Spondias mombin* L., *Annona spraguei* Saff., and *Miconia argentea* (Sw.) D.C. (Denslow & Guzman 2000). Detailed vegetation descriptions of Barro Colorado are found in Croat (1978) and Condit et al. (1996).

The land use history of BCNM is described by Leigh et al. (1996) and Denslow & Guzman (2000). The forests of BCNM reflect a long history of human disturbance along the Chagres River, mostly in the form of clearing for pastures as well as for plantation

and swidden agriculture. Barro Colorado Island was isolated from the mainland in 1914 by the damming of the Chagres River to construct the Panama Canal. Successive periods of agricultural abandonment as well as land preservation have resulted in a mosaic of secondary and old growth forests. Old growth forests occupy half of BCI and small areas at the bases of Gigante and Bohio Peninsulas. Charcoal deposits from old growth forests on BCI date back to 500 years, but these forests probably were never cleared for agriculture (Piperno 1990).

Forest stands aged c. 20, 40, 70 and 100 years in fallow (two replicates each) as well as two old growth stands were selected for a study of secondary succession in tropical moist forest (Denslow & Guzman 2000). Data on palm abundance and distribution collected as part of this study are reported here as well as more detailed information on the regeneration patterns of the most abundant species, *Oenocarpus mapora*. Study stands were at least 5 ha in size on relatively level topography. Stand ages were estimated by reference to several different sources, including early publications describing the establishment of Barro Colorado Island (Chapman 1938, Enders 1935, Kenoyer 1929, Standley 1933, Foster & Brokaw 1982), examination of aerial photographs taken between 1955 and 1983, as well as dates from known historical and local events affecting land use on the BCNM (Denslow & Guzman 2000).

Vegetative sampling

In 9 of the 10 stands, vegetation was sampled in two parallel 160-m transects composed of contiguous nested quadrats. All transects were located within 20 m of forest edges and were separated from each other by at least 20 m. Topographical constraints restricted sampling to one transect in one 20-y stand. In each stand, trees (≥ 5 cm DBH) were sampled in 32 quadrats (10-m x 10-m), treelets and saplings (>1 m tall and <5 cm DBH) were sampled in 64 quadrats (5-m x 5-m), and seedlings (<1 m tall) were sampled in 320 quadrats (1-m x 1-m). We measured the diameter at breast height for palms ≥ 5 cm dbh for each stand.

***Oenocarpus mapora* sampling**

The most abundant palm, *Oenocarpus mapora*, has a clonal growth form. To better describe the regeneration patterns in this species we subsampled individuals in six stands, aged 20 and 70 y in fallow (2 replicates each) as well as in two old-growth stands. Individuals were sampled in circular plots (10-m radius), along the two 160-m transects in each stand. Plots were established at 40-m intervals yielding 8 plots per stand. Genets were grouped into three size class categories based on the size of the largest ramet as follows: juvenile if the largest ramet was less than 1m tall, immature if the largest ramet was >1 m but <8 m tall, and adult if the largest ramet was >8 m tall. Basal diameters of *O. mapora* genets were measured at the base of each clump. Clump basal area was calculated from the diameter of the entire clump rather than for each ramet individually.

Analysis

Regression analyses were used to test whether palm density and basal area increased with stand age for second growth stands aged 20-100y. We also compared palm densities, size class distributions and basal areas in young and old forest stands. For this purpose, we contrasted the six forest stands ≤ 70 y old with the four older forest

stands using analysis of variance (ANOVA). Palm density was scaled to a hectare basis, logarithmically transformed, and regressed on logarithm of stand age to normalize residuals. Total stem basal area and clump area were also scaled to hectare. Regression analyses and analyses of variance were performed using JMP (v.4.0 SAS Institute).

Results

Species composition

We recorded a total of ten palm species from the 10 stands. Species composition, density, and size class distribution varied markedly across stand ages (Table 1.1). Some species were only present in the youngest stands, such as *Bactris barronis* and *Bactris sp.*, while other species, *Socratea exorrhiza*, were restricted to old growth stands. Five of the ten palm species occurred in more than one stand age and three species occurred in all stand ages. Mean stem densities of palms ≥ 5 cm dbh increased significantly with stand age in the secondary forests ($r^2=0.68$, $n=6$, $P<0.04$) (Figure 1.1). Stem densities of palms ≥ 5 cm dbh were also significantly greater in forests ≥ 100 y (mean \pm s.e.: 400.7 ± 42.3 stems/ha) than in forests ≤ 70 y (78.4 ± 34.5 stems/ha) ($F=35.00$, $P<0.0004$). Seedling density of all palm species did not vary significantly with stand age for secondary forests ($r^2=0.10$, $P<0.44$) nor between young and old forests ($F=0.37$, $P<0.56$). Sapling density for all palm species did not vary significantly with stand age for secondary forests ($r^2=0.09$, $P<0.47$), but densities were significantly greater in older forests (823.5 ± 130.3 stems/ha) than in younger forests (416.8 ± 106.4 stems/ha) ($F=5.8$, $P<0.04$). Mean basal area for all palm species significantly increased with stand age for all secondary forests ($r^2=0.85$, $n=6$, $P<0.01$) (Figure 1.2). However, total basal area of stems > 5 cm dbh did not differ significantly between young (0.56 ± 0.18 m²/ha) and old forests (1.10 ± 0.22 m²/ha) ($F=3.4$, $P<0.1$). Seedling densities did not vary as a function of stand age, but larger size classes appear to be more abundant in older forests. Tree stems >5 cm dbh increased linearly with stand age, whereas sapling density reached a peak abundance in middle aged stands.

Of the ten species found we had sufficient data on only three species to examine differences in size structure across the chronosequence. *Astrocaryum standleyanum* was present in all stands but reached a peak density in 100-y stands due to high abundance of seedlings in those stands (Figure 1.2a). *Attalea butyacea* was also present in all stand ages reaching peak densities in 40-y stands (Figure 1.2b). This peak in *Attalea* density also was due to a high density of seedlings in one 40-y stand. Seed rain from a remnant adult tree left standing when the area was cleared for pasture may have accounted for the high density of seedlings in this stand. Both *Attalea* and *Astrocaryum* were less abundant in old-growth stands relative to second growth stands.

The most abundant palm, *O. mapora*, accounted for 60% of all stems across all stands (44% of all stems in forests < 70 y old and over 73% of all stems in forests >100 y old). Two of the three size classes of *O. mapora* were significantly larger in older than in younger forests. Mean tree density for stems > 5 cm dbh was significantly higher in older forests (365 ± 50 stems/ha) than younger forests (48 ± 40 stems/ha) ($F=24.3$, $P<0.001$) and sapling density (stems >1 m tall, but <5 cm dbh) was also greater in older forests (769 ± 132 stems/ha) than younger forests (251 ± 1 stems/ha) ($F=9.2$, $P<0.02$).

Table 1.1. Palm abundance (all size classes pooled) for each species by stand age (mean and s.e. for replicate stands).

<i>Palm species^a</i>	<i>Growth form^b</i>	<i>20 y</i> (<i>x ± s.e.</i>)	<i>40 y</i> (<i>x ± s.e.</i>)	<i>70 y</i> (<i>x ± s.e.</i>)	<i>100 y</i> (<i>x ± s.e.</i>)	<i>Old growth</i> (<i>x ± s.e.</i>)
<i>Astrocaryum standleyanum</i> (Bailey)	S	33.8 ± 18.9	96.9 ± 84	150.1 ± 155	382.9 ± 471	23.5 ± 24
<i>Attalea butyracea</i> (Bailey)	R	141.6 ± 200	1181.3 ± 1344	511.1 ± 466	543.8 ± 124	89.1 ± 82
<i>Bactris barronis</i> (Bailey)	U	78.2 ± 111	0	0	0	0
<i>Bactris coloniata</i> (Bailey)	U	0	0	328.2 ± 464	0	0
<i>Bactris major</i> (Bailey)	U	0	78.2 ± 110.5	0	0	78.2 ± 110.2
<i>Bactris sp.</i>	U	46.9 ± 66.3	0	0	0	0
<i>Chrysophila warscewiczii</i> (H. Wendl.)	S	0	0	0	223.2 ± 316	0
<i>Geonoma deversa</i> (H.Wendl.)	U	0	9.4 ± 13	0	25 ± 35.3	0
<i>Oenocarpus mapora</i> (Bailey)	S	543.3 ± 771	847 ± 888	692 ± 979	1167 ± 336	2631 ± 110
<i>Socratea durissima</i> (Oerst.)	R	0	0	0	0	18.8 ± 17.7

^a Nomenclature follows Croat 1978

^b Growth form category U=Understory, S=Subcanopy, C=Canopy, R=Stilt-root canopy

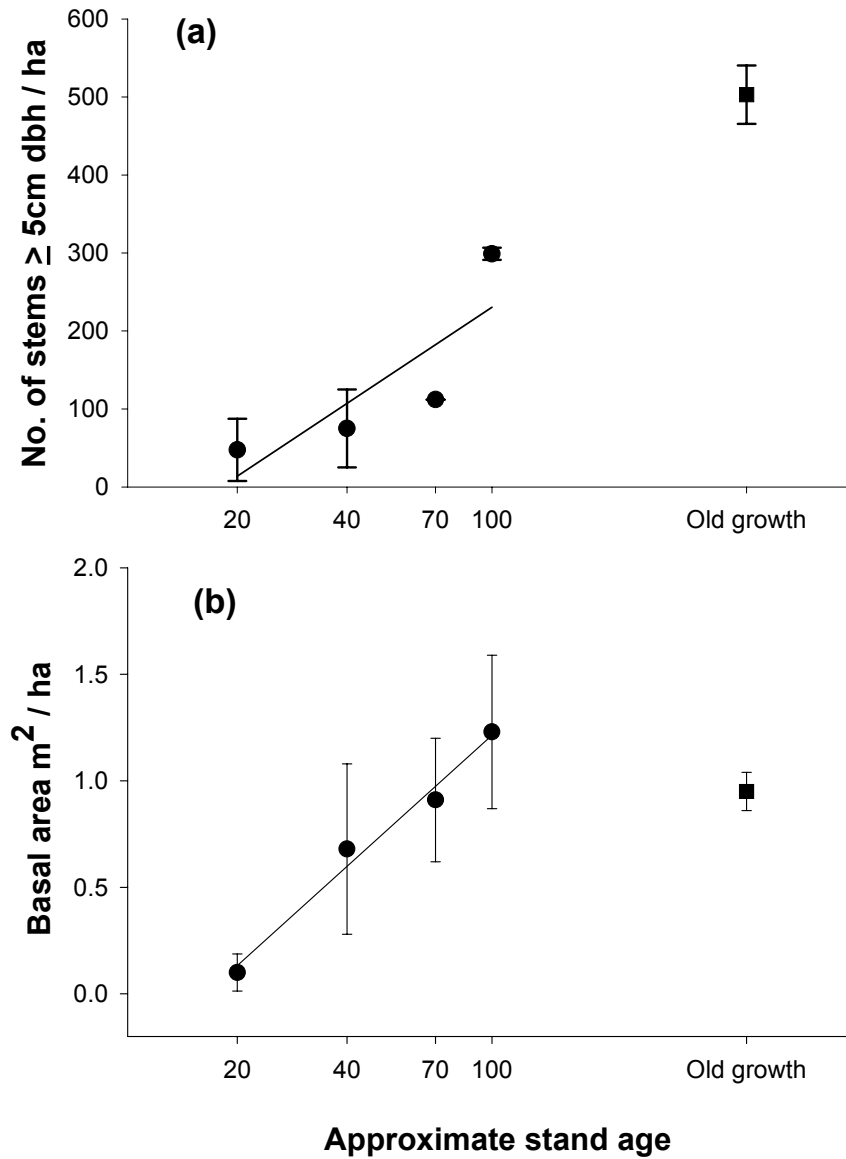


Figure 1.1. Relationship between (a) stem density for palms ≥ 5 cm dbh, and (b) basal area for palms and stand age. Each point represents the mean and s.e. for each stand age. Regression lines include only second growth stands and are significant at $P < 0.05$.

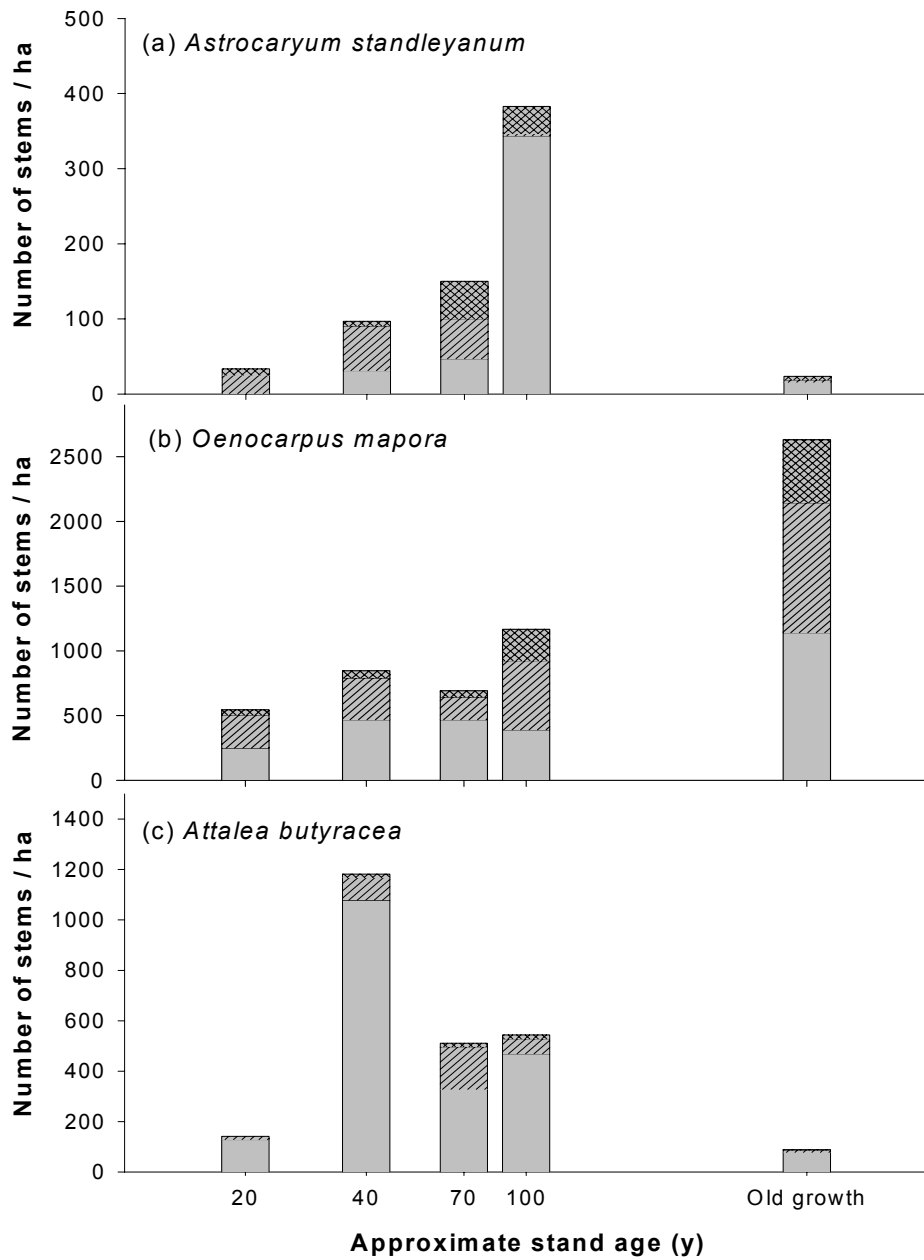


Figure 1.2. Size class distribution of the three most common palm species for second growth and old growth stands. Solid bars indicate stems < 1m tall, single hatch represents stems > 1m tall but less than 5 cm dbh, and double hatch represents stems > 5 cm. dbh. Note difference in scale for y-axis.

Mean density for stems < 1 m tall did not differ between younger (395 ± 183 stems/ha) and older forests (765 ± 225 stems/ha) ($F=1.63$, $P<0.2$). *Oenocarpus mapora* increases in relative stem density with stand age accounting for a larger portion of total palm stems in older forests than in younger forests. Stems are also of a larger size in older forests than younger forests with a greater portion of stems being in the tree and sapling classes. We also sub-sampled *O. mapora* genets. The number of adult genets of *O. mapora* was significantly greater in old growth forests than younger forests (4 ± 2.8 for 20-y and 70-y stands vs. 24 ± 3.9 for old growth stands) ($F_{1,5}=16.6$, $P<0.02$). Juvenile and immature genets did not vary significantly between stand ages. Clump area of *O. mapora* was also significantly greater in old growth stands than second growth stands ($37\text{m}^2/\text{ha} \pm 2.3$ vs. $3\text{m}^2/\text{ha} \pm 1.6$) ($F_{1,5}=146$, $P<0.0003$). *Oenocarpus mapora* has a greater number of adult genets and consequently a larger clump area in old growth stands compared to second growth stands. This suggests that the size of genets increases with forest age, but the recruitment of younger size classes does not vary between forests of different ages.

Discussion

The use of a chronosequence to study processes of forest regeneration assumes that forest stands differ only with respect to time since last disturbance. However many factors including land-use history, site conditions, and propagule availability may be confounding sources of variation. Although Denslow & Guzman (2000) found no confounding differences in soil pH, standing litter mass, or soil bulk density among stands, dispersal limitations may affect species composition of stands. Species composition of the palm community may be affected by differences in seed predator populations between BCI and mainland peninsulas as well as geographic isolation from seed sources. Populations of such seed predators as agouti, squirrels and paca are higher on BCI than on adjacent mainland sites because there are no large carnivores on the island (Emmons 1984). Although there is little evidence that seedling recruitment differs between island and mainland sites (Terborgh & Wright 1994), a recent study of seedling distributions for the palm *Attalea butyracea*, suggests that seed predation rates are higher on BCI than adjacent mainland sites (Joe Wright & Herbert Dubbert unpublished data which may explain why seedling densities of this species are lower in older stand (located on BCI) than in younger stands (located on adjacent mainland peninsulas). Differences in land-use history may also contribute to the pattern of palm distribution in young vs. old sites. For example, ranchers commonly leave large palm trees standing in pastures for shade and construction materials. Seed production from remnant trees in one of the 40-y sites may attribute to the high seedling densities of *Attalea butyracea* in this stand.

Our data suggest that the distribution of palms in older forests is more likely to influence patterns of seedling and sapling abundance than in younger forests. In general, older forests had greater palm density and total basal area than younger forests. Palm diversity did not differ among stands, but species composition and relative abundance did. Patterns of palm density, and basal area were primarily driven by the distribution of the most abundant palm, *O. mapora*. Two other palm species, *Attalea butyracea* and *Astrocaryum standleyanum* were present in stands of all ages although their distribution varied markedly from that of *O. mapora*. The high density of these two species in some stands was attributed to abundant seedlings. Sapling and adult densities of these two

species were considerably lower than those of *O. mapora* and did not contribute substantially to overall stem density or basal area. In these stands, *O. mapora* is likely the only species sufficiently abundant in large size classes to measurably influence understory conditions and patterns of seedling establishment. In Mexico, another species of *Astrocaryum*, *A. mexicanum* reaches high densities in some sites where it is thought to affect the distribution of seedling and saplings of many other species (Sarukhan et al. 1985, Pinero et al. 1986). In older forests, adult genets of *O. mapora* are relatively more abundant than juveniles. There is a corresponding increase in the average clump area that a genet occupies. Seedlings of *O. mapora* take several years to mature into juveniles where it undergoes a long phase of establishment growth until it reaches 1-m in height and then undergoes rapid stem elongation until it reaches reproductive height and becomes an adult, a process that may take up to 120 years (DeStevens 1986, 1989). New shoots or ramets are produced vegetatively beginning in the late juvenile stage and continues on throughout the adult stage where ramets begin producing new ramets when they reach the appropriate size (DeStevens 1986). This leads to the development of the large clump of varying-aged shoots that comprise a mature *O. mapora* genet. Seedling establishment and ramet production rate is somewhat dependant on light availability (De Stevens 1989). Previous demographic studies of *O. mapora* show that growth rates are higher in disturbed and secondary forests than in old growth forests resulting from greater gap formation and increased light levels in these sites (De Stevens 1989). Juvenile recruitment was higher in disturbed areas compared to secondary and old growth forests as a result of the open canopy and high light environment of the disturbed site and genet survival was very high in all forest types (De Stevens 1989). In our study, adult *O. mapora* genets were more abundant in old growth forests relative to secondary forests which is consistent with previous findings, however, we found no difference in the abundance of juvenile or immature genets among stands of different ages. This suggests that palm distribution is patchy and likely reflects small-scale changes in light availability. In the previous study, the disturbed forest is a blowdown area where many of the canopy trees were killed leaving large gaps in the canopy resulting in elevated light conditions (De Stevens 1989). The clonal growth form of *O. mapora* reduces the risk of mortality to a genet even with the death of the largest stems. The high genet survival, and high seedling and juvenile recruitment following a major canopy disturbance demonstrate mechanisms by which this palm may eventually reach and maintain high densities in older forests. A recent study of treefall gaps on BCI suggest that palms that are present during the formation of a treefall gap are likely to survive the treefall disturbance, respond by elevated growth and recruitment in the high-light environment and pre-empt this valuable resource decreasing relative diversity of other species colonizing the gap (Snitzer et al. 1999).

On Barro Colorado Island, sites with high densities of large *O. mapora* genets have lower seedling densities of other species (Denslow & Guzman 2000, Farris Lopez et al. in prep.). Light levels are lower and litter accumulation greater under adult and immature individuals of *O. mapora* than adjacent palm-free understory sites on BCI (Farris Lopez et al. in prep.). If the chronosequence of forest stands reflects regeneration patterns of the palm community with respect to time in fallow, then we can expect to see high densities of immature and adult *O. mapora* individuals between 70 and 100y. At this stage in the regeneration process, *O. mapora* may begin to modify the understory

environment to such an extent that this species may influence patterns of seedling establishment leading to changes in the structure and composition of the regenerating forest. Therefore, the implications for managing species diversity in these forests is to minimize canopy disturbance such as selective logging and thinning which would elevate light levels and potentially increase seedling recruitment and genet size of *O. mapora*.

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CHAPTER 2

INFLUENCE OF A COMMON PALM, *OENOCARPUS MAPORA* ON SEEDLING ESTABLISHMENT IN A TROPICAL MOIST FOREST, PANAMA

Introduction

Seedlings establishing in understory are often suppressed by the overstory vegetation in closed canopy forests. Seeds from many tree species germinate beneath the canopy but growth and survival of seedlings, particularly pioneer species, are often low unless a tree-fall gap or other disturbance creates more favorable light conditions (Poulson & Platt 1989, Denslow et al. 1990, Canham et al. 1994, Fraver et al. 1998, Pereira de Souza & Valio 2001). Seedlings of shade-tolerant species can survive for years in the shaded understory where they typically receive 1-2% full sunlight but grow more rapidly when a light gap occurs (Canham 1985, 1990, Kitajima & Augspurger 1989, Kitajima 1994, Poulson & Platt 1996). Suppressed seedlings and saplings previously established in the understory are a major component of the regrowth in new gaps (Brokaw 1985, Uhl et al. 1988, Ashton 1992, Morin 1994). Therefore, environmental conditions influencing the relative abundance and distribution of seedlings established in the understory prior to gap formation will also influence the seedling pool in tree-fall gaps (Hubbell & Foster 1986, Denslow 1987, Kobe et al. 1995, Pacala et al. 1996).

Species differ widely in their responses to resource availability. Studies from temperate and tropical systems have reported species differences in light-dependent growth and survival (Augspurger 1984a,b, Pompa and Bongers 1988, Clark & Clark 1992, Canham et al. 1994, Kitajima 1994, Ashton et al. 1995, Poulson & Platt 1996, Kobe 1999). Differences in light requirements are thought to correspond to influence successional status and variation in responses to canopy opening (Canham et al. 1994, Kobe 1999). However, variation in light availability alone is not a strong predictor of patterns in seedling or sapling distribution observed in the forest (Welden 1991, Denslow & Guzman 2000, Nicotra et al. 1999). In addition to light availability, tree seedling germination and establishment has been shown to be sensitive to microsite conditions such as soil moisture and nutrient supply, leaf litter distribution, as well as to such biotic factors as pathogen and herbivore pressures (Garwood 1983, Augspurger 1983, 1984a, Denslow et al. 1991, Molofsky and Augspurger 1992, Facelli 1994, Berkowitz 1995, Burslem 1996). Microsite conditions in the understory are spatially variable and this variability may be attributed in large part to the distribution of co-occurring trees and shrubs (Denslow et al. 1991, Canham et al. 1994, Kabakoff & Chazdon 1996, George & Bazzaz 1999, Torti et al. 2001). The extent to which environmental variables are altered by the overstory vegetation may determine the effect a particular species has on seedling establishment.

In tropical forests, palms, in particular, may influence microsite conditions important for seedling establishment and growth. Palms are often abundant in the canopy as well as lower strata where they can account for 60-70% of the total cover in neotropical forests (Balslev et al. 1987, Martinez Ramos et al. 1988, Kahn et al. 1988, Hodel 1992, Kahn & de Granville 1992, Peres 1994, Borchsenius et al. 1997). High

densities of palms have been suggested to reduce the abundance of seedlings and saplings of some species (Pinero et al. 1986, Denslow et al. 1991). The effects may be non-specific, affecting only seedling densities, or they may differentially influence emergence and survival of certain types of species, thereby influencing the composition and spatial structure of the seedling bank (George & Bazzaz 1999). *Oenocarpus mapora*, is a clonal, sub-canopy palm that is long-lived and forms monospecific patches. *Oenocarpus mapora* reaches high densities in old growth forests in central Panama (875 ind/ha Farris Lopez et al. in prep), and in wind-throw areas can reach densities of 1744 ind/ha (De Stevens 1986). Populations of *Oenocarpus mapora* are relatively resilient to disturbance (De Stevens 1989) and may have long lasting impacts on environmental conditions in the understory of a moist tropical forest in Panama.

In this study, we investigated the effects of an abundant palm, *Oenocarpus mapora* Bailey (Aracaceae), on microsite conditions and seedling distributions in the forest understory. Specifically, we asked whether light availability and leaf litter distribution are affected by proximity to palms and if so how these microsite conditions affect seedling density, diversity, and composition. We also conducted a transplant study to determine whether proximity to palms affects seedling survivorship and growth of a large seeded subcanopy tree, *Gustavia superba*. We predicted that forest understories containing abundant palms are more shaded and have greater accumulation of leaf litter, than palm-free areas, and therefore have lower densities of seedlings and altered species composition.

Methods

Study site

This study was located on Barro Colorado Island, Panama (BCI, 9°10'N, 79°51'W), which became isolated as an island by the formation of Gatun Lake in 1914 (McCullough 1977, Leigh et al. 1996). The forests on Barro Colorado Island are classified as a tropical moist forests receiving c. 2600mm of annual rainfall, most of which occurs between May and December (Dietrich et al. 1982, Foster & Brokaw 1982). Detailed descriptions of the vegetation on BCI are found in Croat (1978), Hubbell and Foster (1986), and Leigh et al. (1996).

We selected three study sites. We used two old-growth stands and one late second-growth stand estimated to be c.100 years old following regeneration from former pasture land (Knight 1975). These study stands were a subset of a chronosequence of forest stands described by Denslow & Guzman (2000) and were chosen for their high abundance of *O. mapora* palms. There was no significant difference in mean stand height, tree density, seedling density, basal area, or light availability among these stands (Denslow & Guzman 2000).

Microsite and vegetation sampling

In each of the three stands, microsite conditions and vegetation were sampled in two parallel 160-m transects composed of contiguous 1-m² quadrats. Each transect was established well inside the forest edge and separated from other transects by at least 20 meters (Denslow & Guzman 2000).

Palms were recorded as present for all quadrats in which *O. mapora* covered at least half the quadrat and absent for those in which *O. mapora* covered less than half of the quadrat. Palm size-class was also recorded for each genet based on the classification of the largest ramet. Palms were classified as juvenile for non-clonal acaulescent individuals, immature for clonal caulescent individuals less than 8 meters tall, and adult for clonal individuals greater than 8 meters tall. *Oenocarpus mapora* generally reproduces sexually when it reaches 8 meters tall (DeStevens 1989).

Incident light availability was measured by Denslow & Guzman (2000) at 75 cm from ground level using PAR sensors (LiCor© LI190SA) attached to Licor Plant Canopy Analysers (PCA2000). Readings were taken at 1-m intervals along each transect when the sun was obscured by continuous cloud cover or near the horizon. Above-canopy light levels were estimated concurrently with an instrument positioned outside of the forest where it had an unobscured view of the sky within 52° of zenith; percent transmittance of photosynthetically active radiation (%TPAR) was calculated as the ratio of below-canopy to above-canopy readings. Where readings within 0.5m of the sampling point were obscured by trees or fallen logs, the point was recorded as missing data. TPAR for each quadrat was estimated as the average of two measurements.

Leaf litter distribution was measured at 0.5-m intervals along each transect and the value for both leaf-litter layers and leaf-litter depth in each 1-m² plot are thus averages of two measurements. Leaf litter depth was measured on a metal probe inserted into the leaf litter to the soil surface. The number of leaf litter layers was estimated by counting the number of leaves intercepted by the inserted metal probe.

Number and species identity were recorded for all seedlings in each 1-m² plot. To sample primarily established individuals rather than new germinants, we used relatively large seedling sizes (20-100cm in height). Nomenclature follows Croat (1978) and the working list of Panamanian plants compiled by W.D'Arcy and updated by M.Correa et al. (1999). Seedlings were categorized by seed size class: 1=10-100g, 2=1-10g, 3=0.1-1g, 4=0.01-0.1g, 5= 0.1-1mg, 6=0.01-0.1mg, 7=.001-.01mg following R. Foster (1996). Total number of species was estimated using EstimateS© software developed by R. Colwell (Colwell & Coddington 1995). Because sample sizes varied between palm and non-palm plots, we used a species richness estimator rather than absolute species richness to avoid sample size bias. An incidence-based coverage estimator, ICE, was used to compare species diversity and is based on species found in less than 10 quadrats (Lee & Chao 1994, Chazdon et al. 1998). ICE is a robust estimator of species richness and is reported to be insensitive to sample size (Colwell & Coddington 1995, Chazdon et al. 1998).

Transplant experimental design

To examine the effects of *O. mapora* on seedling survival and growth, we conducted a transplant experiment. Seedlings of a common understory tree, *Gustavia superba* (Lecythidaceae) were transplanted into palm and palm litter treatments. Seedlings were grown from seed and a total of 224 one-month-old seedlings were blocked by size and planted bare-root at 8 sites in a late secondary forest on BCI. To test the importance of palm canopy on seedling growth and survival, 112 seedlings were planted under palms and another 112 seedlings were planted in adjacent palm-free understory. To test the importance of palm litter, half of the seedlings were covered by a

litter treatment. Seedlings were planted in groups of four with one plant at each corner of a quadrat measuring 25 cm on a side. Four quadrats were placed beneath each of eight adult *O. mapora* palms, and four more quadrats were placed close by but not under palms. Two of the four quadrats for each palm and non-palm site were covered by palm litter. Dead leaves from *O. mapora* fall with the rachis often still attached to the stem, so that much of the litter hangs suspended above the ground. To simulate natural leaf litter conditions, three palm fronds were suspended 30 cm above ground level laid across string tied to the corner posts of each seedling quadrat. This height was typical for suspended leaf litter of adult *O. mapora* palms. After 7 months, mortality was recorded and all surviving seedlings were harvested. Stem height, total leaf area, and above-ground dry mass were measured. Pathogen and herbivore damage was estimated as the percent leaf area missing by tracing leaves and holes in leaves on paper and calculating leaf area missing from damaged leaves using a leaf area meter. Sources of mortality were recorded as fungal pathogen, herbivory or unknown. Seedling survival was recorded for each seedling.

Statistical analyses

We analyzed the fixed effects of palm presence or absence and size class on complementary log-transformed %TPAR. Because light availability was shown to be spatially correlated in these stands (Denslow & Guzman 2000), plots that are close together may not be independent samples. To account for this spatial dependency, an ANOVA was performed using a first order autoregressive covariance structure [Sp(POW) in PROC MIXED(V.8, ©SAS Institute 1998)] which incorporates spatial dependencies into the model. Spatial dependence was estimated by $Sp = \sigma^2 \rho^{d_{ij}}$ where the variance σ^2 , is multiplied by ρ , the spatial correlation parameter where $|\rho| < 1$, and d_{ij} represents the absolute distance between plots of the i th and j th observations in the data set. Tukey's honest significant difference was used to do a posteriori multiple treatment comparisons.

We examined the effects of palm presence, leaf litter, and light availability on the probability of seedling occurrence using logistic regression analyses. Because seedling density is also spatially autocorrelated (Denslow & Guzman 2000), a first order autoregressive covariance structure [Sp(POW)] was used for all logistic regression models using PROC LOGISTIC of SAS (8.0; ©SAS Institute 1998). Importance values (IV) were calculated for seedlings present in 9 or more plots by taking the average relative abundance and frequency of each species. To test for differences in seedling seed sizes between palm and non-palm plots, we used a contingency table analyses with the Likelihood Ratio Chi-Square (G^2) test and a Kolmogorov-Smirnov two-sample test to examine differences in seed size distributions.

Seedling growth parameters were analyzed using split-plot ANOVA with Site and Plot factors as covariates. The model used for the split plot analyses is:

$$Y_{ijkl} = P_i + B_j + \sigma_{ij} + L_k + P_i L_k + \sigma_{ijk} + \sigma_{ijkl}$$

where P= palm canopy treatment, B= block (8 reps), σ_{ij} is the variance used to test the effect of the main treatment P. L=palm litter treatment, $P_i L_k$ = palm and litter treatment interaction, and σ_{ijk} = the error term used to test for the effects of litter treatment and Palm*Litter interaction. Stem length and herbivory were log transformed whereas the square roots of leaf area and dry mass were used to normalize residuals. To test the

effects of palm canopy and palm litter treatments on seedling survival GlimMix (SAS V. 8.2 SAS Institute) was used with a binomial error and logit link function.

Results

Microhabitat characteristics

Oenocarpus mapora modifies the environment of the forest floor in several ways. Mean light availability was low in the forest understory ranging from 0.9 to 1.2 %TPAR for the three sites. The presence of *O. mapora* reduced light availability to seedlings by 27% of non-palm sites ($0.80 \text{ \%TPAR} \pm 0.3$ vs. $1.07 \pm 0.03 \text{ \%TPAR}$ (mean \pm s.e.) for palm and non-palm sites respectively; $F=4.66$, df 1, 808, $P<0.03$). Light availability also decreased as a function of palm size class. Juvenile palms reduced light availability by 13%, immature palms by 21%, and adults palms by 28% of palm-free understory (Figure 2.1). Both number of leaf litter layers and leaf litter depth were greater near palms. Number of leaf layers and depth of leaves were significantly, but not strongly, correlated ($r^2=0.30$, $P<0.0001$). The effect of leaf number on seedling abundance was similar to leaf litter depth, so only data on leaf-litter depth will be presented. Leaf-litter depth was greater in plots under palms of all size classes than in plots not under palms ($F=163.95$, $df=3,956$, $P<0.0001$). Less than 5% of the plots measured had no leaf litter and, of those plots, only two were under palms. Mean leaf-litter depth increased from 3.15 cm for non-palm plots to 12.15 cm, 16.19 cm, and 25.48 cm for juvenile, immature, and adult palms respectively (Figure 2.2). Variation in leaf-litter depth was higher among plots under palms than among non-palm plots.

Oenocarpus mapora creates microsite conditions unfavorable for the establishment of many seedlings. There was a greater probability of seedling presence with greater light availability regardless of palm presence (Figure 2.3). The probability of seedling presence was also significantly lower under palms relative to non-palm sites ($F=8.45$, $df=1$, 956, $p<0.0037$). Juvenile palms did not affect seedling presence significantly, whereas the presence of immature and adult palms reduced the probability of seedling occurrence by 33% relative to non-palm sites (Figure 2.3). There was a lower probability of seedling presence as leaf-litter depth increased (Figure 2.4). Mean seedling densities were generally low (0.9-1.65 seedlings/m²). Seedling densities under palms were significantly lower than in non-palm plots ($F=3.75$, $df=3,956$, $P<0.01$).

The number of species of seedlings was lower under palms relative to non-palms. Estimated numbers of species values (ICE) for seedlings under palms (mean \pm s.e.) are 55.76 ± 12.5 (ranging 31-72 species) compared to 92.93 ± 8.35 (ranging 83 -110 species) for non-palms (Chi square=3.67 $df=4$, $P<0.055$). Species richness estimators (i.e. ICE) estimate the number of potential species that would be present if the entire area was sampled. Total observed number of species for seedlings under palms (mean \pm s.e.) was 29.6 ± 8.36 species versus 57.6 ± 3.5 species for non-palms which is lower than ICE estimates as we anticipated. Observed and estimated numbers of species are listed for each site in Table 2.1.

The most abundant species among the seedlings differed between palm and non-palm plots. Under non-palm canopies, *Tetragastris occidentalis* (Burseraceae) was the most abundant seedling, whereas the most abundant seedling under palm canopies was *Beilschmiedia pendula* (Lauraceae). Of the most common seedlings (present in at least 9

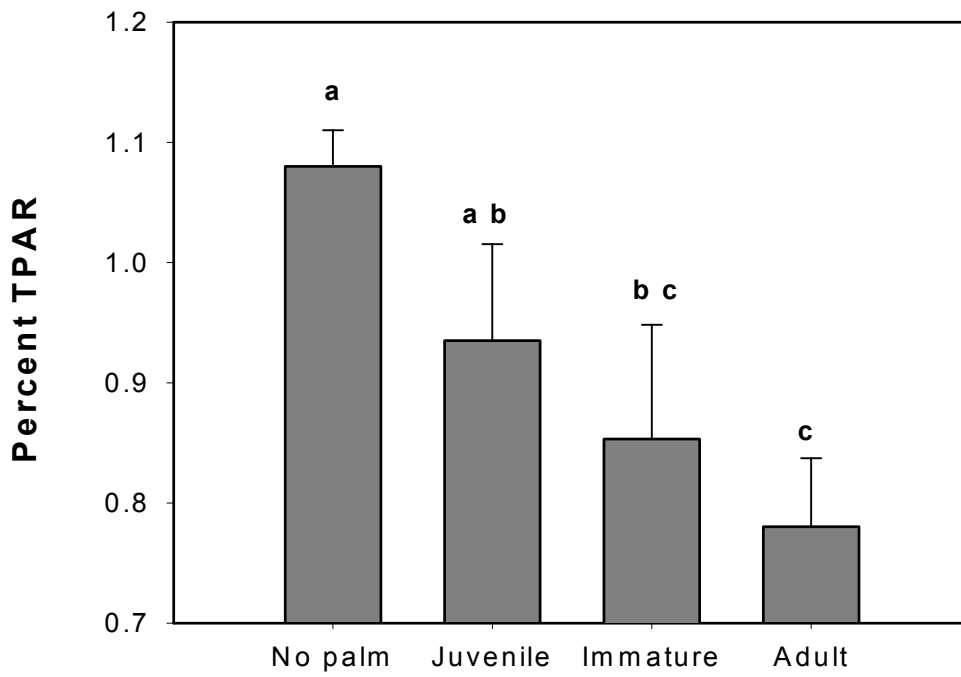


Figure 2.1. Light availability (mean s.e.) in plots with no palms and with palms in 3 size classes. Shared letters indicate that means are not significantly different at $P < 0.05$.

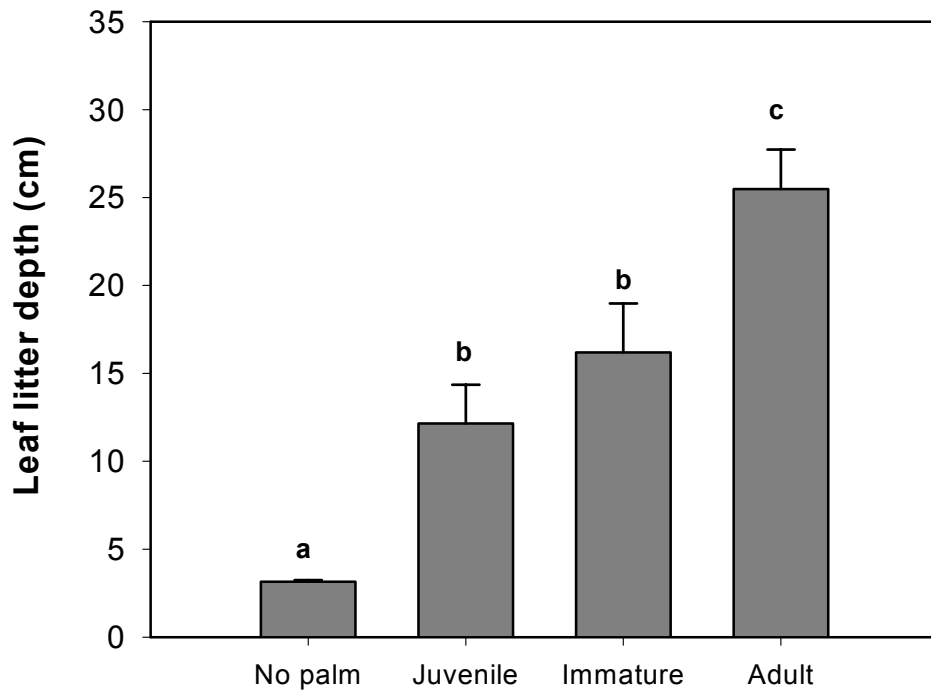


Figure 2.2. Leaf litter depth (mean \pm s.e.) in plots with no palms and with palms in 3 size classes. Shared letters indicate that means are not significantly different at $P < 0.05$.

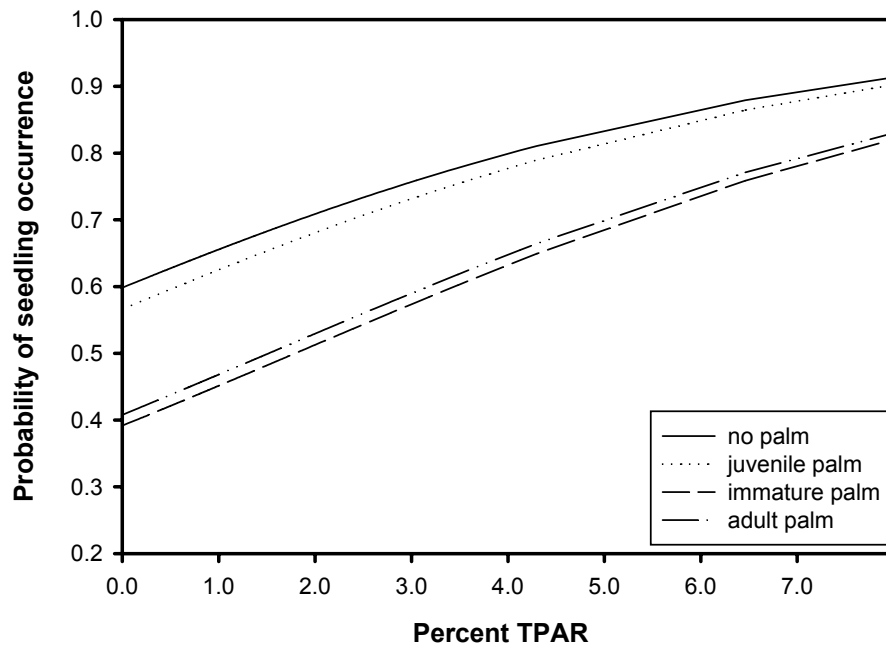


Figure 2.3. Logistic regression of the probability of seedling occurrence as a function of light availability (%TPAR) for plots with no palms and palms in 3 size classes.

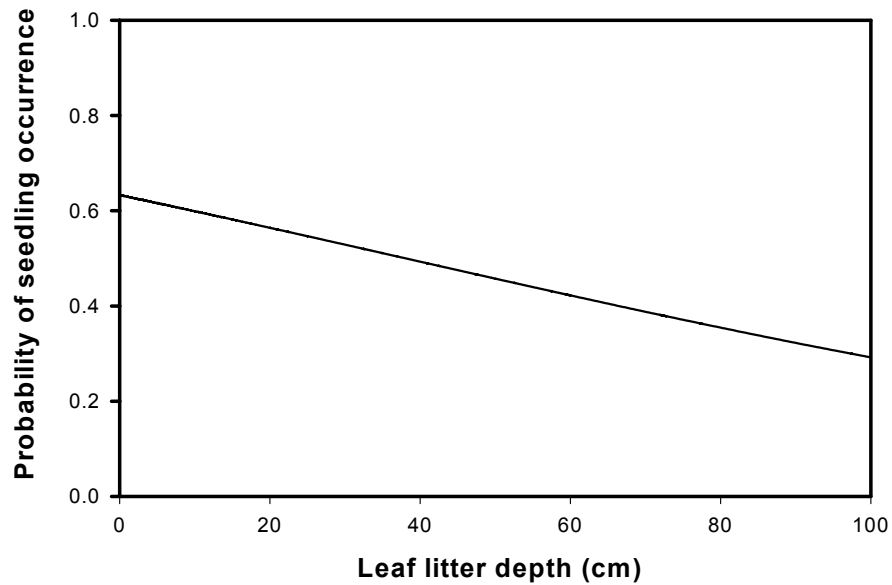


Figure 2.4. Logistic regression of the probability of seedling occurrence as a function of leaf litter depth.

Table 2.1. Number of quadrats in which at least one seedling was present under palm and non-palm canopies. Total number of seedlings and observed number of species as well as estimated total number of species (ICE) are presented for each site.

	No. of quadrats	No. of seedlings	Observed no. species	ICE species estimates
- Palms				
Armour	192	245	61	110
Zetek	190	337	54	88
Barbour	258	326	58	83
+ Palm				
Armour	128	199	35	63
Zetek	130	127	34	73
Barbour	62	38	20	31

plots) only four species had greater IV values in palm plots (Table 2.2). Of those four species, *B. pendula*, a shade-tolerant, large-seeded, disease-resistant species, had an IV that is markedly greater in palm plots than non-palm plots. Seedlings established under palms came from significantly larger seeds than seedlings established in non-palm plots ($G^2=33.5$, $df=6,680$, $P<0.0001$). Relative frequencies for each seed size category for palm and non-palm plots are shown in Figure 2.5. The distribution of seed size was also significantly different for seedlings established in palm and non-palm sites as determined by the Kolmogorov-Smirnov two-sample test ($D=0.18$, $P<0.0004$).

Transplant results

Growth and survival of *Gustavia superba* seedlings were significantly reduced by palm-canopy and palm-litter treatments. Survival of *G. superba*, was significantly lower for seedlings planted in palm-canopy (53 survived) vs. non-palm canopy treatments (85 survived) ($F=6.88$, $df=1,7$, $P<0.03$). Seedling survival was also reduced under palm-litter treatments (49 survived) compared to non-litter treatments (89 survived) ($F=11.83$, $df=1,14$, $P<0.004$). Seedling growth rates were slow and stem height was often reduced as a result of stem loss from pathogens and herbivory. Palm canopy significantly reduced stem length, but not leaf area or dry mass (Table 2.3 & 2.4). The presence of suspended litter significantly increased total % herbivory but had no effect on growth (Table 2.3). Palm canopy and litter may have had more marked effects on seedling growth if the experiment was carried out over a longer duration. Mean leaf area and dry mass had lower values under palm canopy and litter treatments relative to controls but reductions were not significant at $P<0.05$ level (Table 2.4). It is likely that these reductions in growth would have continued over time.

Table 2.2. Importance values (IV) calculated as the average relative frequency and abundance for species found in 9 or more quadrats. Each species is categorized into a seed size class: 1=100-10g, 2=10-1g, 3=1-0.1g, 4=0.1-.01g, 5=1-0.1mg, 6=0.1-.01mg.

<i>Species (Family)</i>	+ Palm IV	- Palm IV	Seed size
<i>Beilschmiedia pendula</i> (Lauraceae)	37	2	2
<i>Tetragastris panamensis</i> (Burseraceae)	27	24	3
<i>Faramea occidentalis</i> (Rubiaceae)	19	21	3
<i>Mouriri myrtilloides</i> (Melestomataceae)	12	19	4
<i>Pouteria reticulata</i> (Sapotaceae)	11	8	3
<i>Capparis frondosa</i> (Capparidaceae)	6	8	3
<i>Swartzia simplex var grandiflora</i> (Fabeaceae)	6	3	3
<i>Hybanthus prunifolius</i> (Violaceae)	4	4	4
<i>Alseis blackiana</i> (Rubiaceae)	4	6	6
<i>Cupania sylvatica</i> (Sapindaceae)	4	6	3
<i>Garcinia intermedia</i> (Guttiferae)	3	4	?
<i>Swartzia simplex var ochracea</i> (Fabeaceae)	3	3	3
<i>Ouratea lucens</i> (Ochnaceae)	3	4	4
<i>Desmopsis panamensis</i> (Annonaceae)	3	3	3
<i>Gustavia superba</i> (Lecythidaceae)	2	2	2
<i>Rinorea sylvatica</i> (Violaceae)	2	11	4
<i>Coussarea curvigemma</i> (Rubiaceae)	1	4	5
<i>Psychotria horizontalis</i> (Rubiaceae)	1	5	5
<i>Psychotria deflexa</i> (Rubiaceae)	1	3	5
<i>Psychotria marginata</i> (Rubiaceae)	1	4	5
<i>Simarouba amara</i> (Simaroubaceae)	1	2	4
<i>Stylogyne standleyi</i> (Myrsinaceae)	0	4	4

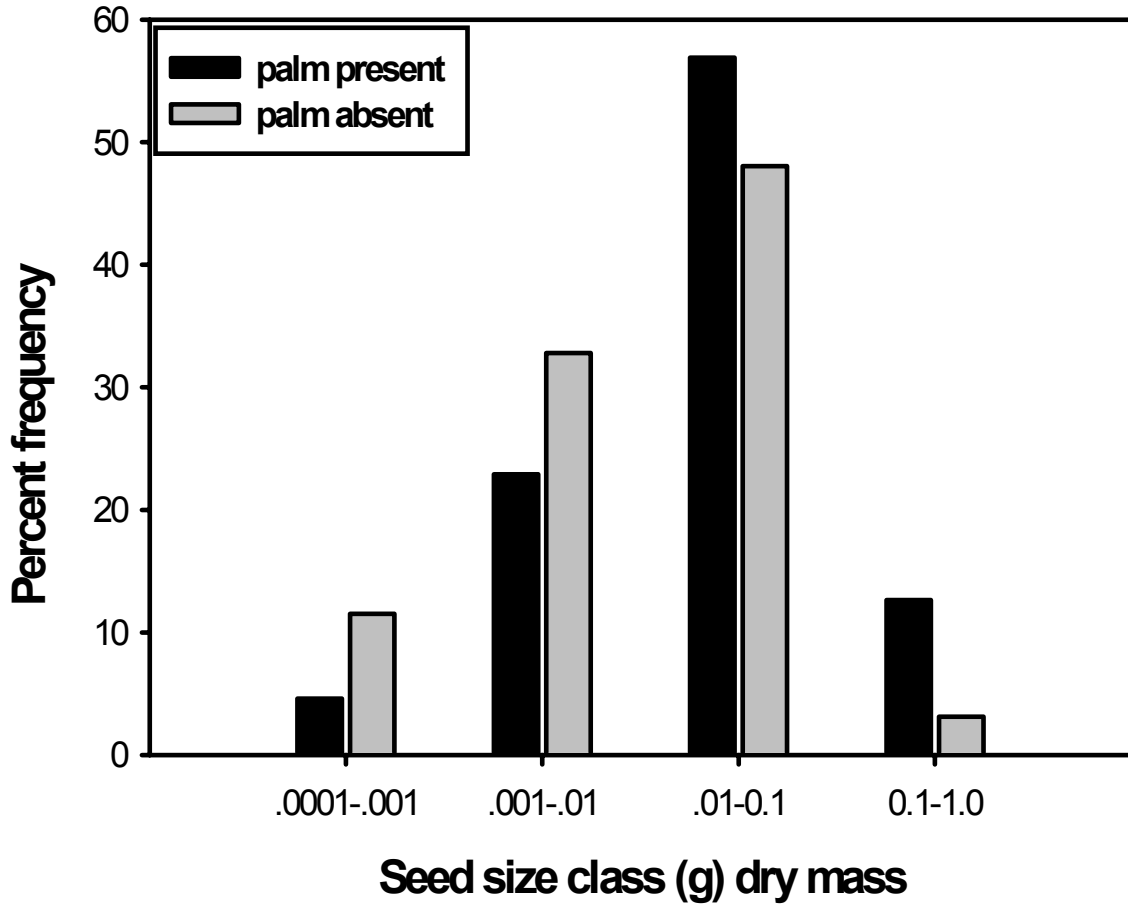


Figure 2.5. The percent frequency of seed sizes among seedlings established under palm and non-palm canopies ($G^2=33.5$, $df=6,680$, $P<0.0001$).

Table 2.3. The effects of *O. mapora* palm canopy and leaf litter treatments on *Gustavia. superba* seedling growth and survival. Split-plot ANOVA source table.

Source of Variation	d.f.	F value	P<	Effect
Survival				
Palm	1	6.88	0.03	**Reduced
Litter	1	11.83	0.004	**Reduced
Palm * Litter	1	.66	0.42	
N	256			
Dry Mass (g)				
Palm	1	1.77	0.22	
Litter	1	2.36	0.12	
Palm*Litter	1	0.01	0.91	
N	134			
Leaf Area (cm²)				
Palm	1	4.09	0.09	
Litter	1	0.58	0.47	
Palm*Litter	1	0.01	0.91	
N	133			
Stem length (cm)				
Palm	1	5.32	0.02	**Reduced
Litter	1	3.28	0.07	
Palm*Litter	1	2.56	0.11	
N	139			
Herbivory				
Palm	1	0.84	0.37	
Litter	1	5.64	0.02	**Increased
Palm*Litter	1	1.87	0.18	
N	85			

Table 2.4. LS means (s.e.) for growth parameters of *Gustavia superba* seedlings planted in palm canopy and palm litter treatments.

	Palm		Litter	
	+	-	+	-
Stem length (cm)	13.6(1.04)	14.9(1.03)	13.72(1.04)	14.8(1.03)
Dry mass (g)	0.62(0.002)	0.72(0.001)	0.63(0.002)	0.72(0.001)
Leaf area (cm ²)	87.4(0.39)	119(0.27)	98.7(0.30)	106.9(0.19)
Herbivory (%total area)	8.8(1.4)	6.5(1.3)	11.2(1.4)	5.1(1.2)

Discussion

Light availability appears to be a primary factor limiting growth and survival for many tree seedlings (Augspurger 1984b, Saverimuttu & Westoby 1996). Increasing light levels from <1% to 20% full sun, has been shown to decrease mortality rates for species with a variety of life histories (Kobe 1999). The lower density of seedlings found in palm sites relative to non-palm sites suggests that light availability in the former is below the compensation points for many shade-tolerant tree species (Augspurger 1983, 1984b, Clark & Clark 1987, Denslow et al. 1990). In a survey of growth responses among other species at BCI, Kitajima (1994) found that relative growth rates of seedlings were higher for sun-grown plants than for shade-grown plants for both pioneer and shade-tolerant tree species. However, survival in the shade may be more strongly related to how well a seedling is defended against physical damage and biotic agents rather than the maximization of net carbon gain and growth in low light environments (Kitajima 1994). A major source of seedling mortality in deep shade of the understory is pathogens and insects (Augspurger 1984 a,b, Augspurger & Kelly 1984, Kitajima & Augspurger 1989, Augspurger & Kitajima 1994). Thus, species which allocate resources to defense against herbivores, and pathogens should have higher survival in the understory. Shade-tolerant species often allocate more to defense at the expense of growth (Kitajima 1995).

Leaf litter distribution may also influence patterns of seedling establishment. Leaf litter from *O. mapora* accumulates during the dry season so that at the beginning of the rainy season when the majority of seedlings germinate (Garwood 1983) this litter may present a physical barrier for newly germinating seedlings to establish their roots into the soil or to emerge from below the litter. Leaf litter also can affect seedling establishment by influencing light conditions, microclimate, nutrient cycling, and allopathic interactions, in addition to producing mechanical damage (Facelli & Pickett 1991, 1993, Molofsky & Augspurger 1992, Aide 1996, Metcalf & Grubb 1997, Torti et al. 2001). The impact of leaf litter cover on seedling establishment varies by species, habitat type, and timing of germination, suggesting a complex interaction (Molofsky & Augspurger 1992). For example, seedling survival of the large seeded species, *Gustavia superba* was greater when seeds were buried under thick litter in high-light environments than when seeds were placed on top of litter. For this species, litter depth had no effect on seedling survival in the deep shade, regardless of seed position (Molofsky & Augspurger 1992). Leaf litter may also increase soil moisture levels, which may be beneficial for seedling establishment in seasonally dry forests (Molofsky & Augspurger 1992). However, high humidity caused by leaf litter may also increase the probability of pathogen attack on seedlings thereby lowering their chance of survival.

We found evidence that large seeds may be able to establish seedlings more frequently under palms than can small-seeded species. Seedlings established under palm canopies were from species with significantly larger seed sizes than those in palm-free sites. Differences in seed size below palm and non-palm canopy may be attributed in part to differences in seed rain. Larger seeds may have a higher probability of penetrating the multi-layered canopy of *O. mapora* than do smaller seeds. However, these palms are roosting sites for frugivorous bats which may disperse small seeds to palm sites. Seed traps placed below *O. mapora* canopy and adjacent palm free sites would be necessary to test for potential differences in seed rain.

Large seed size has been correlated with seedling longevity in shaded environments (Leishman & Westoby 1994, Saverimuttu & Westoby 1996). Seed size also may affect a species response to leaf litter accumulation. Survival of small-seeded seedlings often is affected negatively by deep litter whereas survival of large-seeded species is either positively affected or unaffected by deep litter (Molofsky & Augspurger 1992, Cintra 1997, Svenning 2001). Large seeds tend to produce large seedlings producing an initial size advantage (Fenner 1987, Westoby et al. 1992). Large initial seedling height promotes emergence through leaf litter (Molofsky & Augspurger 1992) and most likely provides resistance to physical disturbance of falling leaf litter (Aide 1987) and an ability to resprout after damage by falling litter. Large-seeded seedlings are likely to resprout after damage from falling litter, herbivores, and pathogens (Harms & Dalling 1997, Dalling & Harms 1999).

The dampening effect of *O. mapora* on seedling growth and survivorship of the large-seeded tree *Gustavia superba*, suggests that even some large seeded species may be inhibited by palms. Although *Gustavia superba* has a large seed and a strong capacity for resprouting after repeated mechanical damage (Dalling & Harms 1999) seedling mortality was high under palms. The major source of mortality and decreased stem length for seedlings was apparently pathogen attack and herbivory. Similar observations of insect damage were reported for *Inga* seedlings planted in close proximity to understory palms (Denslow et al. 1991). Low light levels and high humidity under palms may influence the distribution of pathogens. The significant increase in herbivory for seedlings with leaf litter treatment are consistent with previous findings in which oak litter increased invertebrate damage to seedling cotyledons of the herb, *Ailanthus altissima* (Facelli 1994). Microsite differences in light, humidity, temperature, and air movement likely affect not only the dispersion of pathogens and insects but also the vulnerability of seedlings to pathogen and herbivore pressure (Coley 1983, Augspurger 1984, Augspurger & Kelly 1984, Kitajima 1995).

The species recruiting under *O. mapora* were a subset of the species recruiting in adjacent palm-free canopies. It is apparent that both seedling density and diversity are lower under *O. mapora* canopy. *Oenocarpus mapora* likely affects particularly small-seeded and shade-intolerant species. Of all the seedlings recorded, only one species, *Beilschmiedia pendula*, a large-seeded (dry mass category=10-1g.), canopy tree was much more common under palms than non-palms. In addition to having a large seed, *B. pendula* is resistant to disease which is reported to cause high mortality in other common canopy tree seedlings (Gilbert et al. 1994). A potential explanation for the low abundance of *B. pendula* in non-palm sites is a higher risk of seed predation. Leaf litter under *O. mapora* may protect large seeds from predation by making them harder for seed predators to find (Cintra 1997).

The degree to which *O. mapora* may reduce the size and diversity of the seedling bank will depend on the extent of the palm populations. Populations of *O. mapora* can be high in both old growth and late second-growth forests, where it forms large dense clones on Barro Colorado Island (Farris Lopez et al. in prep.). Denslow & Guzman (2000) examined patterns in seedling densities across a chronosequence of forest stands and suggested that lower seedling abundance in those stands may be attributed to high densities of *O. mapora*. The results of our study provide evidence that both seedling density and diversity are reduced under *O. mapora* canopy and suggest factors

contributing to this pattern. Thus, where *O. mapora* is dense and widespread, we suggest that it is likely to influence seedling establishment and forest dynamics at a community level.

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SUMMARY AND CONCLUSIONS

The palm community in BCNM varies in abundance and composition across the forest chronosequence. Of the 10 species of palms sampled, only one species, *Oenocarpus mapora*, was abundant enough to warrant investigation into the potential influence on seedling establishment. *Oenocarpus mapora* reached its highest density and clump area in older forests stands (100 y to Old growth) where a greater proportion of genets were of adult size. Based on this distribution, *O. mapora* should have a greater impact on the seedling community in these older forests than in younger forests.

The influence of *O. mapora* on patterns of seedling establishment was substantial. There were fewer seedlings under *O. mapora* canopy and also fewer species of seedlings compared to understory plots that were not covered by palm canopy. One of the mechanisms by which *O. mapora* inhibits seedling establishment is through its alteration of incident light availability reaching the forest floor. Light is a limited resource in the understory of closed canopy forests. Although many forest species are shade-tolerant and their seeds can germinate in the understory, survival and growth of seedlings increases with light availability. *Oenocarpus mapora* has a multi-layered canopy that intercepts much of remaining radiation that penetrates through the forest overstory. Light levels under *O. mapora* canopy were 27% lower than adjacent palm-free understory sites. In the deep shade under palm canopies, seedlings may persist until they exhaust their carbon reserves and no longer have resources available for growth. A negative carbon budget also increases the risk of mortality by fungal pathogens and insects because there are less resources available for investment in structural and chemical defense or regeneration after mechanical damage. Large seed size is advantageous in such low light environments because seedlings can maintain a negative carbon balance longer than seedlings with small seed reserves. High light interception by *O. mapora* canopy significantly reduces the light available to seedlings growing below its canopy, resulting in a decreased probability of seedling presence relative to the adjacent palm-free understory. Seedlings planted under palm canopies had lower survival, and reduced leaf area and stem height compared to seedlings planted in the adjacent palm-free understory.

Another mechanism by which *O. mapora* influences seedling establishment is through its production of leaf litter. Leaf litter can facilitate or inhibit seedling establishment depending on the quantity of litter and the species of seedling. Leaf litter accumulation is significantly greater under *O. mapora* canopies relative to the adjacent understory. In general, when small seeds are buried under large quantities of leaf litter, the litter layer acts as a physical barrier preventing the germinating seedlings from penetrating through its depth. Similarly, seeds that fall on top of a thick layer of leaf litter may not be able to penetrate their roots through the litter to reach the soil. Therefore, large accumulations of leaf litter inhibit seedling establishment for many small seeded species.

The probability of seedling presence decreased as leaf litter depth increased. Leaf litter of *O. mapora* was often suspended above the forest because the rachis was still attached to the parent stem. This suspended leaf litter further reduces light availability to seedlings on the forest floor in addition to creating a physical barrier to growth. Large-seeded species have an advantage over small-seeded species in high litter environments. Larger seeds tend to produce larger seedlings which are better able to penetrate thick

litter layers. Larger seeds also have a greater capacity to resprout after mechanical damage by falling fronds.

The impacts of *O. mapora* on seedling survival and growth varied among canopy and litter treatments. *Oenocarpus mapora* canopy significantly reduced seedling survival and stem height of *Gustavia superba*. Palm canopy has a lesser effect on dry mass and leaf area. Leaf litter treatments also reduced seedling survival relative to controls and to a greater extent than did the palm canopy. Leaf litter also increased total seedling herbivory. Seedlings planted under litter treatments showed higher total herbivory than seedlings in non-litter treatments. Leaf litter may produce this effect by further reducing light availability to seedlings resulting in a decrease in available resources allocated for defense, or by providing microsites that are conducive for insect herbivores.

There is some evidence that at least one species may benefit from *O. mapora* microsites. *Beilsschmiedia pendula* (Lauraceae) was the only species markedly more abundant under palm canopy than adjacent non-palm sites. *Beilsschmiedia pendula* is a large-seeded, shade-tolerant, disease-resistant species. Many species of Lauraceae have oil-rich seeds that are sought after by a variety of vertebrates, and predation rates can be quite high. The deep litter present under *O. mapora* canopy may reduce the visibility of seeds and seedlings thereby protecting them from predation. The transplant experiment showed that *Oenocarpus mapora* canopy and leaf litter may inhibit seedling establishment even for the large-seeded species, *Gustavia superba*. Therefore, *Oenocarpus mapora* microsites may only be advantageous for species that are extremely shade-tolerant and disease resistant, in addition to having large seeds that are highly sought after by seed predators.

In general, *O. mapora* creates microsite conditions that are unconducive for seedling establishment by decreasing light availability and increasing leaf litter depth. *Oenocarpus mapora* decreases overall seedling density and diversity below its canopy. Therefore, if *O. mapora* has such effects locally, then in forests where it is abundant, it may influence patterns of seedling establishment on a community level.

VITA

Krista Farris Lopez was born on September 1, 1971, in Phoenix, Arizona. She grew up in Southern California, attending public schools in the Los Angeles Unified School District. Krista went to the University of California at Santa Cruz upon finishing high school in 1989 where she studied biology and environmental science. In 1991, Krista moved to Oregon and transferred to Oregon State University where she graduated with a Bachelor of Science in Botany and Zoology, in 1995. Krista then worked for the USDA Forest Service in Sweethome, Oregon, as a botanist and wildlife technician where she monitored endangered plant and animal populations before coming to Louisiana State University in 1998.