Thrips as Primary Pollinators of Sympatric Species of *Chamaedorea* (Arecaceae) in Belize

by

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Abstract

Thrips as Primary Pollinators of Sympatric Species of *Chamaedorea* (Arecaceae) in Belize

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Adviser: Dr. Andrew J. Henderson

Chamaedorea is the largest genus among the New World palms. These dioecious palms often represent a dominant component of the forest understory, where they play an important role in the ecosystem by providing a source of fruit for frugivores when other food resources are unavailable. In addition, *Chamaedorea* palms play an important economic role in Mexico and Guatemala, where leaves of several species are harvested from the wild as Non-Timber Forest Products for use as greenery in the floral industry. Although many species possess characteristics typically associated with both wind and insect modes of pollination, the majority of *Chamaedorea* are believed to be entomophilous.

This thesis involves an investigation into the reproductive biology of four sympatric palm species, *Chamaedorea ernesti-augustii*, *C. oblongata*, *C. neurochlamys*, and *C. tepejilote*, in Belize. The main questions addressed are: (1) What is the flowering phenology for each of the study species? (2) What is the primary pollination vector for each of the study species? (3) What differences exist between the study species with respect to floral morphology, insect visitation and behavior, and floral activity during anthesis?

Fieldwork was conducted at the Las Cuevas Research Station, Belize, Central America. A series of study plots were established in June 2002 and adult *Chamaedorea* individual were identified to species, measured, and mapped. Phenological data was collected on a monthly basis for 24 months. Field observations, bagging experiments, and laboratory tests were implemented to identify the mode of pollination and pollen vectors for each study species. Insect specimens were collected and the general sequence of floral events including insect visitation and behavior was documented for each of the species under study.

The main conclusions are as follows: study species are pollinated by single species of thrips, these thrips are engaged in a dependant mutualism with the palms, and this mutualism is supported by the flowering phenology of the *Chamaedorea* community.

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Chapter 1

Introduction

1.1. Background

Palms (Arecaceae) are one of the most well known and important plant families worldwide (Balick & Cox, 1996). Not only are they highly abundant and of great ecological significance to forest ecosystems in tropical and subtropical regions where they occur, they also are among the most frequently used plants (Henderson et al., 1995). A variety of products can be obtained from palms including food, building and thatch materials, fiber, oils, waxes, alcohol, medicines, and ornamentals to name a few (Uhl & Dransfield, 1987). There are also a number of major palm commercial crops such as coconuts, peach palms, oil palms, and palm hearts (Henderson, 1988). Additionally, numerous palms are utilized for religious or ritualistic purposes and therefore have great cultural significance (Balick & Beck, 1990).

Despite their importance in so many realms of life, research on the reproduction of palms historically has been scarce. Over the past few decades however, there has been steady increase in the literature on palm pollination ecology, with several papers published each year (Henderson, 2002). Initially, the majority of studies involved cultivated or heavily utilized taxa such as date palm (Uhl & Dransfield, 1987). However, recent investigations have focused on a wide variety of palms. Therefore it is surprising that little is known about the reproductive ecology of *Chamaedorea* Willd. species. Along with their high economic value as ornamental palms, members of the genus *Chamaedorea* are of particular interest for a number of reasons. The genus often represents a dominant component of the forest understory throughout its range, forming dense, natural stands (Hodel, 1992a). In fact, two taxa have been described as keystone species in Central America (Hess, 1994), where they ensure the year-round availability of food resources for frugivore populations (Ataroff & Schwarzkopf, 1992). In addition, several species of *Chamaedorea* play an important economic role in Central America, where leaves of several species are extracted from the wild as Non-Timber Forest products (NTFP) (Reining et al., 1992). The leaves are utilized in the international floral industry as greenery in floral bouquets. As the majority of leaves have been collected from the wild for decades, problems with over-harvesting and reduced reproductive capacity of *Chamaedorea* populations are well recorded (Bridgewater et al., 2006).

My interest in *Chamaedorea* reproduction stems from its use as an NTFP, and the concomitant decline in wild *Chamaedorea* populations. The research described in this thesis was motivated by the lack of reliable information regarding the reproductive ecology of this genus. With the recent implementation of several programs to establish plantations of the most valuable species, the knowledge of reproductive strategies, and the components that support effective pollination is crucial. Therefore, the goal of this thesis was to provide data detailing the pollination systems of four *Chamaedorea* species: *C. oblongata* Mart, *C. ernesti-augustii* Wendl., *C. neurochlamys* Burret, and *C. tepejilote* Liebm. Both field observations and experiments were used to determine the flowering patterns, identify the mode of pollination, and document the complete sequence of floral morphology and insect visitation over the floral life cycle. Not only will this data improve knowledge of reproductive ecology within this genus, it may also be used to inform management and conservation decisions within heavily harvested areas.

Additionally, this project is the first to investigate the pollination systems of several sympatric *Chamaedorea* species and thereby provides an opportunity to shed light on how closely related tropical species co-exist in the same habitat.

1.2. Chapter Summaries

In chapter 2, I describe the current state of knowledge for the genus *Chamaedorea*. Details of the taxonomic history, morphology, distribution, and habitat of the genus are reported, and the literature regarding *Chamaedorea* demography, ecology, and economic botany is discussed. In addition, a detailed description of the morphology, habitat, and usage for each of the four study species is provided. In this chapter, I also supply descriptions of both the study site and the study plots. Finally, data collected on mortality and spatial distributions are presented, because these factors, which affect the community composition, will in turn affect the diversity, abundance, and behavior of floral visitors (Proctor et al., 1996).

In chapter 3, I address the flowering phenology of the sympatric *Chamaedorea* species included in this research. The main questions are: What is the annual flowering pattern for each of the study species? Are flowering patterns seasonal or aseasonal? Does flowering phenology vary among these sympatric species in terms of regularity, duration, and synchrony? These data are the result of monthly surveys over a two-year period.

Chapter 4 explores the pollination systems of the four study species in detail. The questions addressed are: What is the pollination system for each of the study species? What differences exist between species with respect to floral character, morphology, and floral activity during anthesis? Are there differences in the identity, diversity, abundance, and behavior of floral visitors between species? The results of several experimental treatments, along with floral and visitor observations, are assessed in the context of Baker and Hurd's (1968) criteria for pollinators. The most likely pollination vectors are identified for each of the study species and several components of the pollination systems are explored.

In the final chapter, I integrate the results of the previous chapters in order to provide a broader understanding of the components that comprise these pollination systems. The contribution of each component to *Chamaedorea* reproduction as a whole is discussed and the nature of *Chamaedorea*-pollinator mutualisms is explored.

Chapter 2

Background

2.1. Taxonomy

The use of such diverse features as leaf morphology, habit, size, and floral characters by taxonomists has played a part in the history of this genus. The generic name *Chamaedorea* was established by Willdenow (1806), and is derived from the Greek *chamai*, which translates as low to the ground, and *dorea*, meaning gift (Hodel 1992a). Therefore, these palms are characterized as a gift from the ground, perhaps in reference to their understory habit. As exploration into unfamiliar areas accelerated and previously unknown palms were discovered, such botanists as Liebmann (1846), Martius (1849) and Oersted (1859) named several new species in the mid-19th century. Subgenera or sections of the genus were described by Martius (1849) and included *Collinia*, *Euchamaedorea*, and *Stachyophorbe*. As more palms with potential for inclusion in the *Chamaedorea* "group" were encountered in the late 19th century, several new generic names were proposed to account for the extensive variety, especially the diversity in floral morphology (Cook, 1943a). These included *Anothea*, *Docanthe*, *Edanthe*, *Mauranthe*, *Morenia*, *Neanthe*, *Omanthe*, *Paranthe*, and *Stephanostachys* (Liebmann, 1846; Martius, 1849; Oersted, 1859; Cook, 1943a, 1943b). Nonetheless, by the mid-20th century, all of the above named taxa were placed in the genus *Chamaedorea* (Hodel, 1992a).

In Genera Palmarum (Uhl & Dransfield, 1987), the genus is classified in the subfamily *Ceroxyloideae*, tribe *Hyophorbeae*. It is closely related to the South American genera *Wendlandiella*, *Synechanthus*, from Central and South America, and *Hyophorbe* native to the Mascarene Islands (Henderson et al., 1995). While the above represents the accepted classification, a forthcoming edition of Genera Palmarum, which relies heavily on molecular data, classifies the genus in subfamily *Arecoideae*, tribe *Chamaedoreeae* (Asmussen et al., 2006; Dransfield, per. comm.).

Hodel (1992a), in his monograph of the genus and subsequent publications (Hodel, 1992b, 1995, 1996, 1997), described 96 species of *Chamaedorea*, as well as 12 hybrids. Although hybrids have been documented by a number of researchers (Dammer, 1904; Marque, 1923; Barry, 1957; Young, 1974; Douglas, 1987), they have been found to occur only between species within subgenera. Hodel (1999) notes that his monograph was intended to serve as a means for identification of species in this widespread and diverse genus, rather than a tool for interpreting phylogenic relationships. It accomplishes this goal by providing an excellent foundation upon which further investigations into the taxonomy and classification of this complex genus will be based.

Hodel (1992a) delineated eight subgenera based primarily on staminate petal characteristics and secondarily on the arrangement of flowers/inflorescences: *Collinia*, *Eleutheropetalum*, *Morenia*, *Chamaedorea*, *Chamaedoropsis*, *Moreniella*, *Moreniopsis*, and *Stephanostachys*. Since his monograph was published, Hodel (1999) has identified several areas of study that require further analysis. He states that at least two of the subgenera are poorly defined and admittedly artificial. He also notes that the boundaries between both subgenera and species are inadequate, and it is possible that several species may be misplaced within his subgeneric classification scheme (Hodel (1999). Hodel (1999) explains that his broad approach to *C. pinnatifrons* reflects the problems that exist in interpreting the taxonomic significance of variation within this widespread and incredibly variable species.

Henderson et al. (1995) dealt with these taxonomic issues by describing many of the problematic taxa as “species-pairs.” Members of these species pairs are sympatric taxa whose phenotypes differ by one or a few characters. For example, several species of *Chamaedorea* exhibit staminate flowers with free petals, while in others the petals are connate apically. Henderson et al. (1995) contend that these differences are insufficient for the delineation of separate taxa and instead are examples of intraspecific variation. Therefore, their key recognizes 77 species in contrast to the 95 species recognized by Hodel (1992a). Nonetheless, among New World palms, *Chamaedorea* is the largest genus, regardless of which classification is followed.

It is likely that ongoing research on the molecular phylogeny of the genus will resolve these problems. A recent study (Thomas et al., 2006), which included representatives from each of the eight subgenera, used low-copy nuclear genes to determine that *Chamaedorea* is monophyletic. Results of subgeneric classification were varied. Those with smaller numbers of species and distinct morphological differences, *Eleutheropetalum*, *Moreniella*, and *Stephanostachys*, were resolved as monophyletic. However, the two largest subgenera, *Chamaedorea* and *Chamaedoropsis*, were resolved as polyphyletic (Thomas et al., 2006). The primary morphological distinctions between these subgenera are the degree of fusion of staminate petals at anthesis, free or with a high degree of connation, respectively. Clearly, the results of this phylogenetic analysis demonstrate that the subgenera of *Chamaedorea* require revision. Additionally, further studies on biogeography, morphology, reproductive biology, and autecology were suggested to help determine the species-level relationships within subgenera (Thomas et al., 2006).

2.2. The Genus *Chamaedorea*

The available literature describing the genus *Chamaedorea* is surprisingly scarce, given the size and economic importance of the genus. In fact, Hodel's 1992 book, *Chamaedorea* Palms: The Species and Their Cultivation, remains the primary resource for botanists studying the genus. Hodel (1992a) covers the information available on numerous subjects of use in identifying and cultivating *Chamaedorea* palms including the history, distribution, ecology, hybridization, and culturing of these palms. In addition to the work by Hodel (1992a), several journals have published articles that describe various aspects of *Chamaedorea* life history (e.g. Broschat & Donselman, 1986; Douglas, 1988; Oyama & Dirzo, 1988; Ataroff & Schwarzkopf, 1994). Still, much research remains to be completed if we are to understand the intricacies of this genus.

One of the most intriguing aspects of *Chamaedorea* is the remarkable diversity that occurs among its species in each of the plant structures used in classification. Unfortunately, a common problem for many persons working with the genus is difficulty differentiating between the large number of species, specifically when in the field. For example, *C. pinnatifrons* and *C. neurochlamys* are often confused with *C. oblongata* due to their morphological similarities, such as habit, height, and leaves. This is compounded by the fact that taxa are divided into subgenus primarily on the basis of floral morphology. Even when species identification is achieved, sexing an individual typically is possible only when it reaches reproductive age, as the sexes are identical in all characters, excepting their flowers.

Chamaedorea palms exhibit a large number of variations in habit. Most species have a solitary stem; however there are a number of cespitose species (e.g., *C. costaricana*). Several clumped species, such as *C. tepejilote*, have both solitary and cespitose forms. A few species exhibit a rhizomatous (e.g., *C. brachypoda*) or stoloniferous habit (e.g., *C. stolonifera*). Although stems typically are erect, some species may appear stemless (e.g., *C. radicalis*) due to a short stem and closely spaced nodes or a stem that is subterranean or buried by leaf litter (Hodel, 1992a). Measurements of stem length may be complicated by the fact that in many species have decumbent stems (e.g., *C. pumila*) or fall to the ground at some point during the life cycle (e.g., *C. oblongata*), only to become erect at their apex. These palms often have their creeping stems covered with leaf litter to the extent that they must be uncovered to determine their true length. A single taxon, *C. elatior*, exhibits a true climbing or scandent habit (Henderson et al., 1995).

Chamaedorea are unarmed and, in most cases, stems are green and smooth, with prominent nodes. However, in a few species (e.g. *C. graminifolia*), stems are covered to some degree with dried leaf sheaths. Stem diameter is variable, with species ranging from 1 to 28 cm diameter (Hodel, 1992a). For example, individual stems of the clumping species *C. tepejilote* have been recorded as 15-28 cm in diameter in Belize. In many cases, a number of adventitious prop roots are produced at the base of the stem and along the decumbent portions of stems (e.g., *C. serpens*) (Hodel, 1992a).

The diverse nature of this genus is not limited to habit, but also is evident in leaf morphology. Although all *Chamaedorea* exhibit leaves with reduplicate folding, two main leaf forms are found (Uhl & Dransfield, 1987). The majority of *Chamaedorea* taxa have regular, pinnate leaves, while several species present bifid leaves, notched to varying degrees and often with toothed leaf margins (e.g., *C. ernesti-augustii*) (Hodel, 1992a). In a number of species (e.g., *C. adscendens*), both leaf forms may be present on a single individual. Typically, in these cases, seedlings have bifid leaves, juveniles have variously pinnate leaves, and adult plants completely and regularly pinnate leaves (Hodel, 1992a). Although the primary leaf form of the widespread and extremely variable species *C. pinnatifrons* is pinnate, populations have been found with bifid leaves (Hodel, 1992a). Leaf length varies greatly both within and among species and has been reported up to 3 meters in length (Hodel, 1992a). The number of leaves is similarly variable. Some species, such as *C. brachyclada*, have only three or four live leaves, while others, such as *C. rigida*, have up to 15 leaves (Hodel, 1992a).

There are two main types of leaf sheaths, short to long and tubular for most of their length, yet basally split where sheath is opposite petiole, or short to long and tubular, yet not split basally. The leaf sheaths of several species exhibit useful diagnostic characters. For example, in *C. pinnatifrons* and *C. neurochlamys*, the apex of the leaf sheath is distinctly white. Similarly, several species (e.g., *C. quezalteca*) have prominent ligules at the apical portion of the sheath (Hodel, 1992a). The leaf sheaths are mostly green in color and turn brown as the leaf ages.

Petioles of *Chamaedorea* range from short to long and are rounded abaxially and flat adaxially. The majority are green in color, with an abaxial band of yellow or light green that extends into the leaf sheath (Hodel, 1992a). Rachises typically are green (rarely white-spotted), and are abaxially rounded, with the adaxial portion angled (Hodel, 1992a).

Blades are various shades of green. Most are dark green adaxially and either a paler green or the same darker shade of green abaxially. One interesting case is *C. metallica*, which has an iridescent metallic sheen to its gray-green blades. The blades may also be various textures, with some (e.g., *C. oblongata*) being leathery and thick to the touch, and others (e.g., *C. pinnatifrons*) thinner and less opaque (Hodel, 1992a).

Additionally, the number of pinnae per leaf varies both between and within species, indeed even within individuals, as older leaves tend to be larger than younger ones. There might be less than 10 pinnae per side (e.g., *C. sartorii*), or up to 25 or more (e.g., *C. pochutlensis*) (Hodel, 1992a; Henderson, et al., 1995). Also, size of pinnae ranges from short (15 cm or less) to long (more than 70 cm), from narrow (less to 1 cm) to wide (greater than 15 cm), and exhibit a number of shapes including sigmoid, straight, and acuminate. Typically, the longest pinnae occur toward the middle of the frond and decrease in size toward the base. In the majority of species, with the exception of such species as *C. tenerrima*, the smallest pinnae will occur at the leaf apex. In the sole climbing species of *Chamaedorea*, *C. elatior*, the terminal pinnae have a novel form. They are strongly reflexed and form hook-like structures that enable the plant to climb into the canopy.

Typically in *Chamaedorea*, leaf blades exhibit prominent midribs, while primary and secondary nervation may be highly visible to indistinct (Hodel, 1992a). Finally, leaves are smooth, never scaly or tomentose. This characteristic, along with the papery peduncular bracts that are present on each inflorescence, aids in distinguishing *Chamaedorea* from other understory palms (Henderson, et al., 1995).

Chamaedorea is dioecious, with individuals bearing either unisexual staminate or pistillate flowers. Inflorescences may be either interfoliar or infrafoliar, and are either spicate or have one to two orders of branching (Uhl & Dransfield, 1987). The short prophylls are tubular and bifid at the apex. Peduncles are short to long, typically greenish when in flower, and orange to red when in fruit. The one to several peduncular bracts are usually tubular, and obliquely open or bifid apically (Hodel, 1992a). Although they are usually solitary, Fisher and Moore (1977) found up to eight staminate inflorescences at a single node in several species. Additionally, these authors state that in *C. alternans*, several pistillate inflorescences may occur at a node. Hodel (1992a) notes that this multiplicity of inflorescences at a node is typical of staminate individuals in the subgenera *Morenia*, *Moreniopsis*, and several taxa in subgenus *Stephanostachys*.

Rachillae are short to long, erect, and pendulous or erect with respect to the stem. Also, rachillae may be spreading or pendulous and staminate plants typically have more rachillae than pistillate plants (Hodel, 1992a). In species such as *C. tepejilote*, the branched rachillae of staminate inflorescences are pendulous or nodding, while those of pistillate individuals are stiff and erect. However, when laden with fruit, pistillate rachillae droop to some degree (Hodel, 1992a). Rachillae are medium to pale green and slender, yet during fruit development become red-orange to orange and thickened (Hodel, 1992a). Hodel (1992a) notes that few rachillae remain green when in fruit, such as *C. radicalis*.

The arrangement of flowers is variable. Staminate and pistillate flowers usually are not larger than 5 mm and solitary, or rarely, in groups of two or three. They may be arranged in densely-packed to remote spirals, and are sessile or sunken into round to elliptic pits in the rachillae (Uhl & Dransfield, 1987; Hodel, 1992a). Typically, staminate flowers are more densely packed on the rachillae than pistillate flowers for a particular species (Hodel, 1992a). Flowers may have a sweet to fruity and overwhelming aroma, or no odor. Although the staminate flowers tend to have a stronger smell, the pistillate flowers of many species also may be aromatic (e.g. *C. metallica*). Uhl and Moore (1971) reported that many *Chamaedorea* flowers exhibit raphide-containing idioblasts in both stigmas and styles. Askgaard (per. comm.) also found raphides to be abundant in staminate and pistillate floral structures (e.g., petals, filaments) of several *Chamaedorea* species.

The greenish to pale calyx is usually parted or lobed to some degree. It may be ring- or cup-like, with the three sepals imbricate, distinct, or united basally (Hodel, 1992a). The corolla of pistillate flowers is greenish-yellow to yellow, or rarely orange or whitish. Petals may be thinner or fleshy, and imbricate, valvate, or connate and opening through a terminal aperture. Pistillate flowers can be divided into two main groups. First are those species (e.g. *C. glaucifolia*) that have their petals appressed to the stigma lobes and whose flowers do not open up at anthesis. Instead the stigma apices are exserted past the petals at the center of the flower. Second, other species, such as *C. pumila*, have petals that part at their apices at anthesis to reveal the pistil. This action generally creates a cup-like floral chamber into which visitors may enter to reach the stigmas. Staminodes may be absent to present and prominent. The stigmas usually are sessile and may be small to large and recurved (Hodel, 1992a).

Variety in staminate floral morphology is so prominent that Hodel (1992a) divided *Chamaedorea* into eight subgenera based primarily on characters of the staminate flowers. These floral characteristics include: odor (offensive to pleasant to no odor at all); pollen (copious, dry, powdery pollen to flowers with sticky, heavy pollen); nectar (flowers with nectar to those lacking nectar); pistillode (expanded basally to columnar or trilobed apically); color (flowers with brightly colored petals to those that are relatively inconspicuous with dull green, yellowish, or white petals); and arrangement of flowers on rachillae (flowers that are densely arranged to those that are well separated or remotely arranged). Stamens are six in number and didymous, included, or with anthers dorsifixed (Hodel, 1992a). Petals are fleshy or thin, and smooth to heavily nerved at anthesis. Finally, flowers may exhibit petals that are free and spreading, imbricate or valvate, recurved or erect apically; connate to apex and opening only by a triangular aperture; or connate basally and apically, adnate apically to the pistillode, with the corolla opening by lateral slits (Hodel, 1992a).

Fruits are one-seeded, globose to ovoid or ellipsoid, small, black to purple-black, or orange to red, and typically with a smooth epicarp (Hodel, 1992a). They contain fleshy mesocarps, thin endocarps, and the endosperms are homogenous (Uhl & Dransfield, 1987). In several species (e.g. *C. neurochlamys*), fruits are somewhat to highly curved. Fruits tend to be sparsely arranged or crowded on the rachillae (Hodel, 1992a). Seedlings exhibit adjacent germination and eophylls are bifid or pinnate (Uhl & Dransfield, 1987).

2.3. Distribution and Habitat

With more than 95 recognized species (Hodel, 1992a), *Chamaedorea* is the largest genus of New World palms, surpassing both *Bactris* and *Geonoma* (Henderson et al., 1995). *Chamaedorea* taxa inhabit forests from Mexico through Central America and extend into northern coastal Ecuador and the Amazonian portions of western Brazil, eastern Peru, and northern Bolivia (Figure 2.1). The genus is most diverse in Central America where two pockets of exceptionally high abundance occur: (1) Mexico-Guatemala, and (2) Costa Rica-Panama (Henderson et al., 1995). Mexico and Guatemala host approximately 40 species of *Chamaedorea* per country, with many shared species, such as *C. elegans* and endemics such as the Mexican species, *C. radicalis*. The Costa Rica-Panama region contains 55 species including numerous endemics, such as Panama's *C. microphylla*.

Although most species are distributed across a few countries, *C. tepejilote* and *C. pinnatifrons* are exceptionally widespread, traversing virtually the entire range of the genus (Henderson et al., 1995). Although the most widespread species occur on a variety of soil types and slopes, others are more limited. For example, *Chamaedorea castillo-montii* is found only in the wet, mid-elevation Atlantic slope forests of two districts in Guatemala. Individuals typically are found growing on limestone (Hodel, 1992a). Likewise, *C. rhizomatosa* occurs only in southern Mexico where it inhabits steep, high-elevation areas in pine-oak forests with decidedly rocky soils (Hodel, 1992a).

Chamaedorea species may be found in a variety of forest types including lowland to montane, and evergreen to seasonal deciduous forests (Wright et al., 1959; Hodel, 1992a). Most species prefer microhabitats that exhibit moderate to high degrees of shade and humidity (Castillo Mont et al., 1994). Additionally, the majority of *Chamaedorea* species occurs on well-drained, limestone-based soils and may be found in their greatest abundance on these soil types (Hodel, 1992a). The genus often represents a dominant component of the forest understory throughout its range, forming dense, natural stands. It

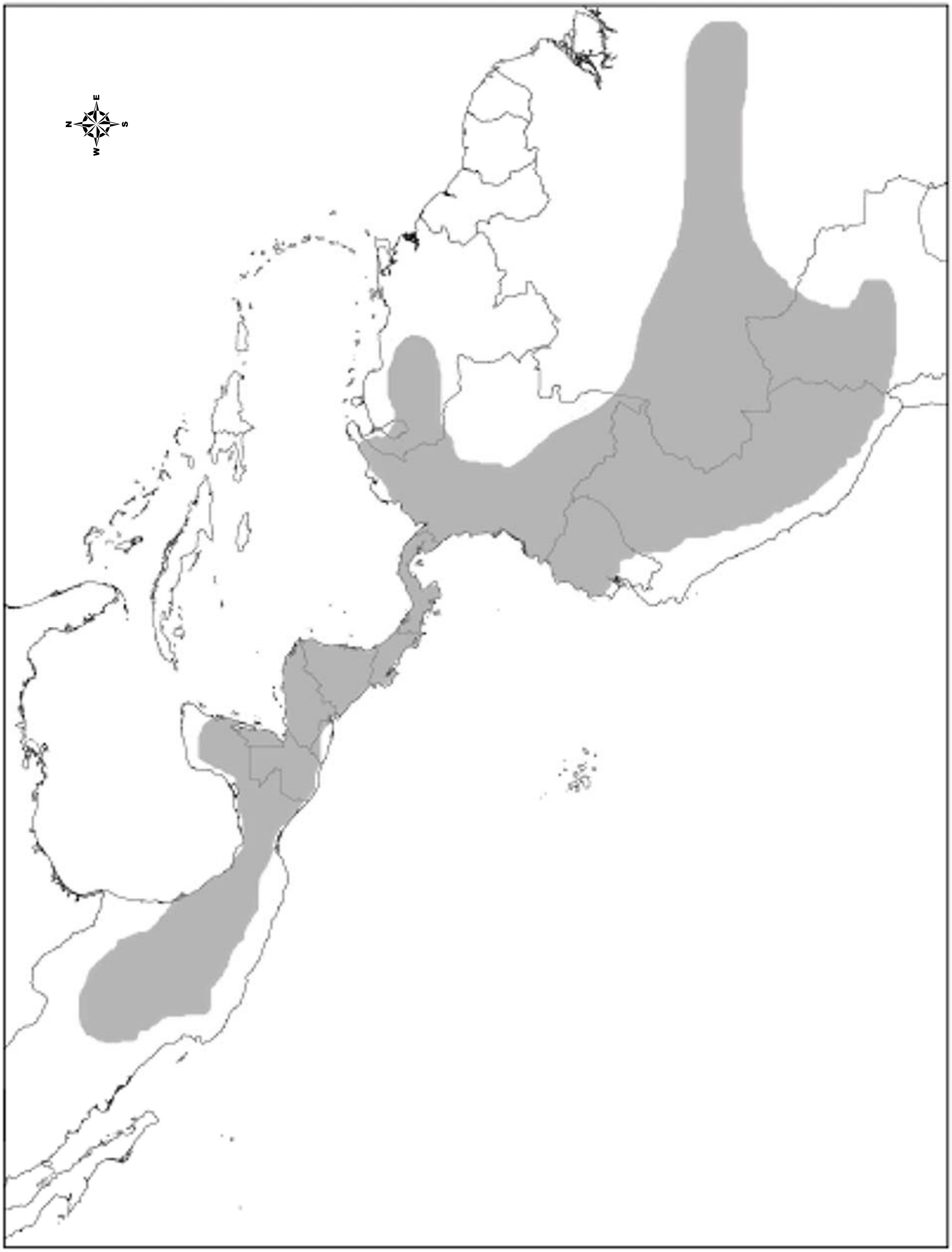


Figure 2.1
Generalalized distribution of the genus *Chamaedorea* (Arecaceae). Based on Henderson et al., 1995.

is not unusual for several taxa to grow in close proximity with one another. For example, up to eight sympatric species have been reported in Panama (Hodel, 1992a).

A few authors have written about the habitat preferences of various *Chamaedorea* species. For example, Escalera (1993) studied ecological factors related to *Chamaedorea* populations in the Petén, Guatemala. Of the two most common species, *C. elegans* was found to prefer areas below 300 m, while *C. oblongata* showed no altitudinal preference. Both species were found to prefer slightly acidic, limestone karst, well-drained soils, temperatures between 24° and 27° C, humidity levels above 80%, and less than 15% direct light.

In a similar study, Wicks (2003) conducted research in western Belize to determine how the local palm community is related to a selected set of environmental variables including edaphic, biotic, and topographic features. He also analyzed the relationships of various palms to one another. After compiling the data from all 50 plots, Wicks (2003) concluded that the most important factor in determining the presence and density of *Chamaedorea* taxa was forest type.

2.4. Demography

Demographic data only are available for a small number of *Chamaedorea* taxa and *C. pinnatifrons* is one of only two species that have been the subject of a long-term studies. Ataroff & Schwarzkopf (1992) conducted research on the vegetative morphology of *Chamaedorea pinnatifrons* (as *C. bartlingiana*) in Venezuela. The authors followed 272 individuals for 3.5 years to document demographic patterns, leaf production, and reproductive dynamics. They determined that differences exist between sexes in both leaf life span and leaf production rates. Pistillate plants were found to produce fewer leaves per year, and the leaves remained on the plants for a longer period of time than did those of staminate plants. The authors posited that these differences might allow pistillate individuals to direct more of their energy to the production of flowers and fruit. The fact that pistillate plants demonstrated a higher rate of inflorescence abortion than do staminate plants also might be interpreted as the consequence of the larger amounts of energy needed for fruit production.

The above research included an investigation of vegetative morphology across the life span, from germination through adult stages (Ataroff & Schwarzkopf, 1994). Stems and leaves from pistillate and staminate plants of different ages were examined in order to study morphological changes. To examine the allocation of biomass, individuals representing the range of life stages were collected, separated, dried, and each part was weighed individually. The authors determined that individuals of this taxon survive for approximately 60-66 years and tend to be reproductive after 13 years. No morphological differences or differences in biomass were found between vegetative organs of staminate and pistillate palms. However, the importance of different organs for storage was found to change over the life span of both sexes. While roots and leaves are the primary storage organs for juveniles, adults store their biomass in roots and stems.

Oyama (1990) studied the demographics of *Chamaedorea tepejilote* in Mexico. He followed 810 palms over a period of four years to document their survivorship, vegetative growth rates, and reproduction behavior. No significant differences were found between sexes in response to leaf tissue loss and net gain in stem height. In terms of leaf production, his findings were similar to those of Ataroff and Schwarzkopf (1992).

Staminate individuals were demonstrated to produce significantly more leaves than did pistillate individuals. Additionally, staminate plants produced significantly higher numbers of inflorescences relative to pistillate plants, presumably due to their lower energetic cost of reproduction, as well as the fact that dioecious plants need to produce large quantities of pollen.

In his work on *C. tepejilote*, Oyama (1987) determined that a difference in growth rates exists as an individual progresses from seedling to adult. While individual variation can be attributed in some part to the environmental conditions affecting each individual palm, he also found differences between individuals of the same life stage that were located within the same plot (Oyama, 1987). Moreover, plants of different heights often had the same number of leaf scars. In fact, stem height was found to vary from 0-80 cm and leaf production from one to three leaves amongst comparable individuals in a single plot (Oyama, 1987). Therefore, Oyama (1987) concluded that neither counts of stem scars, nor number of leaves produced, could be used as a valid means of age estimation for *C. tepejilote*. He stated that only general correlations can be made through field observations and the age may actually be underestimated due to the amount of plasticity with which these palms respond to field conditions.

Oyama and Mendoza (1990) examined how three intensities of a single defoliation affected the population dynamics of *Chamaedorea tepejilote* in Mexico. Defoliation treatments were performed to determine their effect on growth, reproduction, and survival. After two years, all three defoliation treatments were found to increase the production of leaves, with completely defoliated palms producing three times as many leaves on average as controls, and partially defoliated palms producing approximately two times as many leaves as controls. Oyama and Mendoza (1990) suggest that the production of extra leaves is a strategy to provide more leaf area for photosynthesis in order to meet the energy requirements of developing flowers and fruit. Interestingly, although pistillate plants were found to have higher energy costs than staminate, no difference in leaf production was found for staminate versus pistillate palms. In terms of reproduction, the authors state that experimental defoliations did not negatively affect staminate or pistillate individuals. Instead, both of the partial defoliation treatments increased the probability of reproduction. While partial defoliation increased the number of inflorescences produced by staminate plants, inflorescence numbers did not increase for pistillate individuals. The authors concluded that this result is likely due to the energetic requirements of fruit production.

In addition to the demographic work conducted on *Chamaedorea tepejilote*, leaf damage and fruit predation have also been investigated. Oyama (1991) described the predation of *C. tepejilote* seeds by a curculionid beetles in Mexico. The amount of damage to seeds not yet dispersed by pistillate plants (pre-dispersal predation), as well as the damage sustained by seeds after falling to the ground around the maternal plant (post-abscission predation) was determined. Although more than 60% of the total number of seeds produced were predated by beetle larvae prior to dispersal, only 5% of the seeds that fell to the ground under the maternal plant were predated. The density of undamaged seeds (undamaged or not aborted) was found to be positively correlated to the intensity of fruit damage. The author suggested that the aggregated spatial pattern of these palms might be due to high rates of pre-dispersal seed predation and removal of seeds from the forest floor away from maternal plants. These factors suggest that the undamaged seeds, which drop to the soil near pistillate plants, are the most likely to become established, thus creating the typically clumped spatial distribution of *C. alternans*.

Oyama and Dirzo (1991) described damage to the leaves of *Chamaedorea tepejilote*) by a beetle, *Calyptocephala marginipennis* (Chrysomelidae), in Mexico. After the authors determined that herbivory occurred at extremely variable levels, they explored the possibility that this variation might be explained to some degree by inter-sexual differences. To test this premise, Oyama and Dirzo (1991) measured the selectivity of the beetle for staminate versus pistillate leaves in both field and laboratory. The authors determined that there was a slight preference for the leaves of pistillate plants. However, upon analysis, it was established that there were no significant differences between sexes in terms of either nutritional or secondary compounds in leaf tissue. Additionally, they found that not only did the beetles prefer the leaves of this palm to those of other plants at the study site, but it actually preferred the leaves of *C. tepejilote* over those of sympatric species of *Chamaedorea* at the same site. Based upon these results, the hypothesis that higher herbivory rates in pistillate leaves are due to a difference in resource allocation that is sex-related based on the need for more energy in females is not supported.

2.5. Usage

Numerous *Chamaedorea* taxa are used for a variety of purposes including horticulture, floriculture, and subsistence. Hodel (1992a) has described the popularity of *C. seifrizii* and *C. elegans*, not only as potted houseplants, but also for landscaping in appropriate climates. These species are well known among horticulturalists as ‘bamboo palm' and 'parlor palm', respectively. Vast plantations of these cultivars, primarily in Florida and Mexico, were established decades ago to provide the seeds necessary to meet worldwide demand. Additionally, large numbers of plants are cultivated in California and Florida for mass sale as potted ornamentals to chain stores (Hodel, 1992a).

Other species, including *C. metallica, C, tenella,* and *C. tuerckheimii*, have a very limited distribution and therefore are prized by palm enthusiasts. Vovoides and Bielma (1994) described the status of several endangered *Chamaedorea* taxa in the forests of Veracruz, Mexico and emphasized how removal of whole palms for sale has caused serious population declines for many species in the wild. They recommend establishing propagation and re-introduction programs for threatened taxa as future steps in *Chamaedorea* conservation and management.

Castillo Mont and his colleagues (1994) recorded the use of *Chamaedorea* flowers as a food source. They state that staminate *C. tepejilote* plants have been cultivated for centuries in the Alta Verapaz region of Guatemala. The unopened inflorescences, called *pacaya*, continue to be exploited on a small-scale today for sale in markets across the country. With the popularity of 'exotic' foods in American cuisine, today *pacaya* can be found even on grocery store shelves in Illinois (N. Garwood, per. comm.). In addition, there has been recorded usage of the intensely fragrant flowers from *C. fragrans* and *C. paciflora* as perfumes in South America (Balick & Beck. 1990; Hodel, 1992a).

Perhaps the most valuable usage of *Chamaedorea* palms as a Non-Timber Forest Product (NTFP) is the export of their fronds. Nations (1992) described how the leaves of several species, locally known as *xate*, are extracted from wild plant populations. Within

Guatemala alone, over 100 million *Chamaedorea* leaves (primarily from *C. elegans* and *C. oblongata*) are collected annually and exported to Europe and the United States for use as greenery in the floral industry. *Xate* extraction provides a source of year-round income for thousands of families and provides millions of dollars in profit for the exporting countries.

Although it is undertaken as a sustainable activity, the little-controlled and extensive collection of *Chamaedorea* leaves has led to a documented decline in population density in the Petén region of Guatemala and other areas where leaf extraction occurs (Heinzman & Reining, 1988). Studies conducted by Heinzman and Reining (1988) over a decade ago demonstrated that the density of *Chamaedorea* in protected areas (~8500 plants/ha.) was more than double that of areas subjected to regular harvesting (~3100 plants/ha.). This data, coupled with the low ratios of inflorescences and seedlings in harvested relative to protected areas, prompted the authors to state that the extraction of leaves for *xate* has adverse effects on both population size and rate of reproduction.

In addition to the research of Heinzman and Reining (1988), a large number of other studies have been conducted on *Chamaedorea* palms as NTFPs. The majority, however, focus on different facets of *xate* extraction as an industry including: the structure of the *xate* trade, economic components driving the industry, and the mechanics of extraction (Hernandez, 1988; Dugulby, 1991; Dictum & Tarifa, 1994), yet do not address the biology of these palms. In a review of literature concerning *Chamaedorea* palms over a decade ago, Oyama (1992) stressed the need for scientific research on the development, ecology, physiology, and genetics of these plants. While the bulk of this work is only in its initial stages, some research is available regarding how repeated leaf extraction has impacted *Chamaedorea* populations (Sagamuste, 1987; Solórzamo, 1992; Endress et al., 2004; Bridgewater et al., 2006).

Ceballos Solares (1996) established a series of plots to inventory the current populations and study the system of leaf harvest for three *Chamaedorea* species of high economic value: *C. elegans*, *C. ernesti-augustii*, and *C. oblongata* in Guatemala. A primary objective was to determine how defoliation has affected the abundance and spatial distribution of these taxa. The author found that *Chamaedorea oblongata* was the most abundant species per hectare; *C. elegans* was the second most abundant, and *C. ernesti-augustii* the least abundant. The leaves of study individuals were examined to determine how many met market conditions in terms of the size and quality requirements (i.e. free of blemishes and epiphylls).

Ceballos Solares (1996) calculated that the proportion of saleable leaves with respect to the total number of leaves was below 12% for each of the three species. In addition, the proportion of reproductive plants with respect to the total number of pistillate plants was 13% of the total for the least commercial taxon at that point in time, *C. ernesti-augustii*. However, for *C. oblongata* and *C. elegans*, the percentage of reproductive individuals was much lower, 1% and 4% respectively. The author concluded that the low proportion of saleable leaves and the low rates of reproduction were the result of plants having a relatively low number of leaves due to over-harvesting.

Correspondingly, palm surveys by Ibarra-Manriquez (1988), and Quero (1992) in Mexico have demonstrated that the leaves of *Chamaedorea* are heavily collected for ornamental purposes. They state that many *Chamaedorea* taxa have been seriously over-harvested for both leaves and seeds, and in many cases exhibit relatively low seed set in the wild.

Further data on the effects of defoliation was produced by Anten and Ackerly (2001), who conducted a greenhouse-based study of response to defoliation by *Chamaedorea elegans*. A total of two defoliation treatments, 13 months apart, were performed. Each treatment involved the removal of approximately every other leaf from the study plants. An iterative approach was used to analyze the effects of leaf loss on growth and biomass allocation. The authors calculated that the absolute growth rate of defoliated plants was smaller than that of control plants. They concluded that compared to the control plants, the defoliated plants had a smaller mean leaf area ratio and therefore less leaf area available for light capture.

In order to provide information for use in future management plans of threatened *Chamaedorea* resources, Mendoza and Oyama (1999) collected data during a 4-year demographic study to construct Lefkovitch and elasticity matrices for populations of *C. alternans* in Mexico. Both leaves and seeds of this species are gathered for export; therefore they assessed how these practices affect *Chamaedorea* populations. The authors projected that populations of this taxon would increase if repeated removal of fronds for the floral industry did not occur. They also determined that the possibility of changes in growth or fecundity were relatively low. As the elasticity analyses demonstrated that fecundity did not contribute greatly to the population growth rate, Mendoza and Oyama (1999) conducted further research to estimate the impact of different levels of seed collection on palm populations. Based on the results of these studies, they determined that no more than 90% of seeds should be removed in order to balance regeneration with the normal rate of mortality.

It is apparent that although a number of studies concerning the genus *Chamaedorea* are available, much work remains to be done. While the existing literature provides much information on the use of *Chamaedorea* palms in floriculture and horticulture, data regarding the biology and ecology of *Chamaedorea* taxa remain relatively scarce. This dissertation addresses the demonstrated lack of information by producing quantitative data detailing the reproductive biology of four *Chamaedorea* species.

2.6. Detailed Descriptions of the Study Species

Four species of *Chamaedorea* are included in this study, representing four of the eight subgenera in the genus: *C. oblongata* Mart. (subgenus *Chamaedoropsis*), *C. ernesti-augustii* Wendl. (subgenus *Eleutheropetalum*), *C. neurochlamys* Burret (subgenus *Chamaedorea*), and *C. tepejilote* Liebm. (subgenus *Stephanostachys*).

2.6.1. *Chamaedorea ernesti-augustii*

Chamaedorea ernesti-augustii Wendl. (subgenus *Eleutheropetalum*) is a solitary-stemmed palm that grows to 3 m in height and 2 cm in diameter. It has 5-11 simple, bifid leaves and interfoliar inflorescences. Up to three staminate inflorescences (mean = 1.42 ± 0.85, n = 52) are produced during a flowering event, each bearing 23-40 pendulous rachillae (mean = 31.5 ± 6.28, n = 20) (Hodel, 1992a). At anthesis, the bright orange flowers are densely packed and slightly sunken into the rachillae. A mean of 2,180.28 ±

1,050.51 (n = 45) flowers occur on a staminate inflorescence. Staminate flowers have fleshy petals that are connate basally and free apically, where they arch over the stamens. The clear to whitish pistillodes equal or exceed petal height and has noticeable apical lobes. Pollen is moist and sticky and flowers are highly aromatic (Douglas, 1987).

The spicate (rarely branched to one order with 2-4 rachillae) pistillate inflorescences are thick and erect. From one to four inflorescences have been reported on reproductive individuals (mean = 1.53 ± 0.84, n = 72). They bear 16-65 aromatic flowers (mean = 44.44 ± 11.34, n = 72) in prominent depressions with fleshy petals. At anthesis the corolla is cup-shaped and bright, almost fluorescent orange in color, with small, yet visible staminodes situated just outside of the pistil. Flowers may develop into ellipsoid, 8-18 mm black fruits on red-orange rachillae (Hodel, 1992a). In the study described here, the mean number of mature fruit produced per inflorescence was 19.46 ± 12.48 (n = 41), with a mean fruit set of 43%.

Chamaedorea ernesti-augustii has been documented as occurring in dense or wet rain forests along the Atlantic slope of Mexico, in northern Guatemala, across western Belize, and down into north-eastern Honduras (Figure 2.2A) (Hodel, 1992a; Henderson et al., 1995). Note, however, that this documented range could be expanded, as is the case with all the study species, as collections and locality data are subject to ease of collection and many areas remain uncollected. Typically, this species is established on limestone soils, and may be found growing on steep slopes (Hodel, 1992a). *Chamaedorea ernesti-augustii* can be found at a variety of elevations, from 100-1000 m, although Hodel (1992a) notes that it is most abundant at lower altitudes.

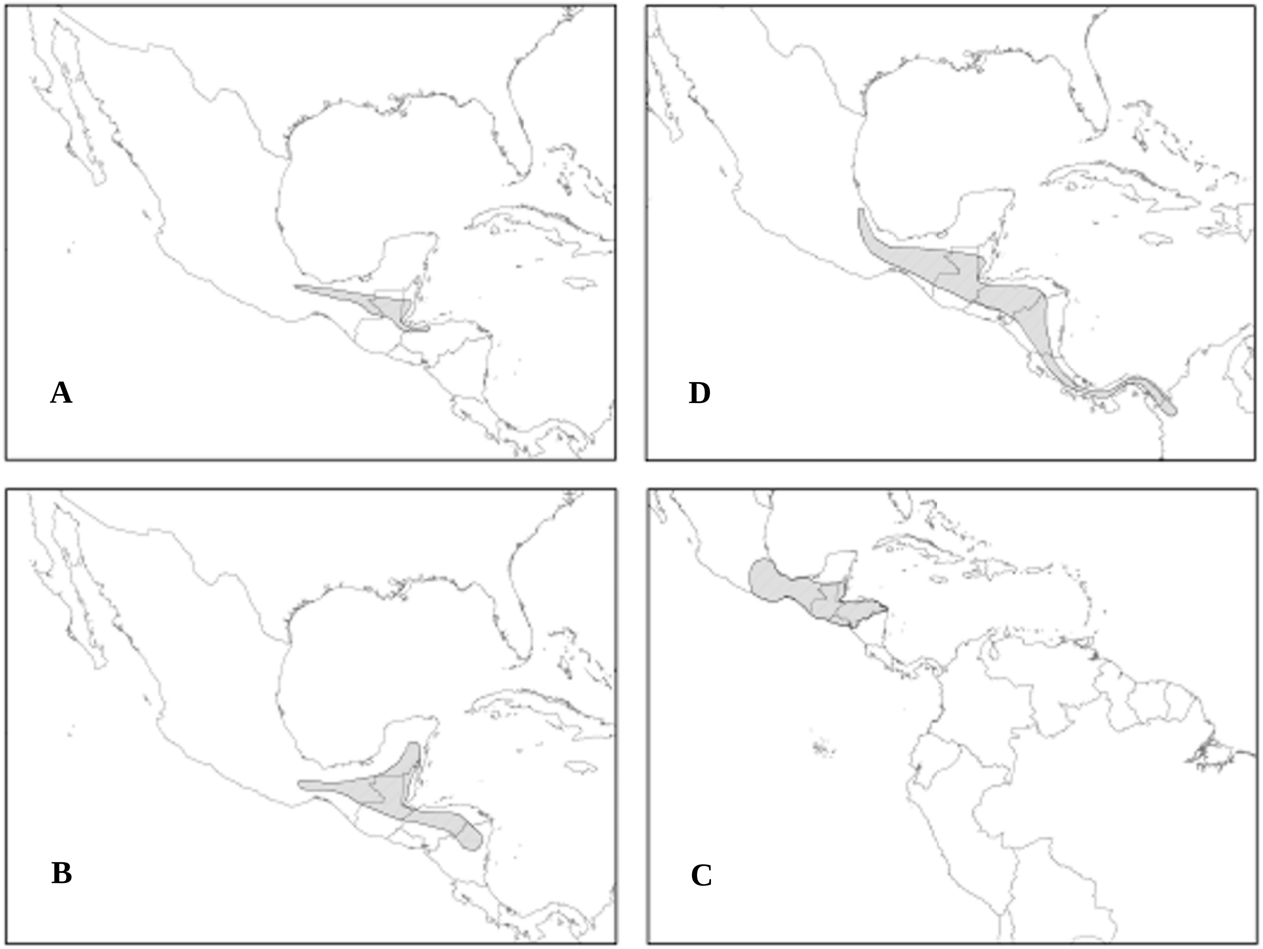


Figure 2.2 Generalized distribution of the four study species of *Chamaedorea*. Based on Henderson et al., 1995. **A.** *C. ernesti-augustii* **B.** *C. oblongata* **C.** *C. neurochlamys* **D.** *C. tepejilote*

As with other species in the genus, *C. ernesti-augustii* tends to occur in fairly dense patches. In fact, the mean number of individuals over 20 cm in height of this species was recorded as 216 ± 171 (n = 62) in a series of 20 m x 20 m plot at the study site, individuals over 20 cm in height of this species were recorded (Porter-Morgan et al., 2004). In western Belize, extensive fieldwork has determined that between zero and 2100 individuals occur in a square hectare (Wicks, 2003). The density of *C. ernesti-augustii* is noted as inversely proportional to canopy cover, such that as the canopy becomes thicker and less light reaches the understory, fewer individuals of the taxon will be present (Wicks, 2003). Wicks (2003) also determined that the presence of *C. ernesti-augustii* corresponds with the presence of two other understory palms, *Bactris* spp. and *Desmoncus* spp.

The species is known primarily by two common names, "fishtail" or "cola de pescado" in Belize and Guatemala, and "guaya" in Mexico (Henderson et al., 1995, Bridgewater et al., 2006). *Chamaedorea ernesti-augustii* is well known in both Belize and Guatemala, as it is one of the most valuable and therefore highly sought sources of fronds exported for use as greenery in the floricultural industry. This is likely due to the fact that the forms occurring in Guatemala and Belize are noted for having particularly large leaves (Hodel, 1992a). For approximately eight years, leaf collectors have harvested heavily from western Belize, illegally crossing over the border from Guatemala to extract large numbers of fronds primarily from protected areas. In this short period of time, the majority of *C. ernesti-augustii* individuals in western Belize have been seriously overexploited and their long-term future threatened. Declines in leaf production, as well as reproduction, are well known to leaf collectors, yet not common knowledge among consumers of this resource (Porter-Morgan, et al., 2004). No other uses for *C. ernesti-augustii* have been recorded.

2.6.2. *Chamaedorea oblongata*

Chamaedorea oblongata Mart. (subgenus *Chamaedoropsis*) is a solitary-stemmed species that grows to over 3 m in height, 2.5 cm in diameter, and may be erect or creeping in habit. Individuals bear 3-8 pinnate leaves with 3-9 lanceolate to oblong leaflets on each side (Hodel, 1992a). Pinnae are thick, leathery, and distinctly glossy adaxially.

Staminate individuals produce up to four erect, infrafoliar inflorescences (mean = 1.25 ± 0.74, n = 130). The pendulous staminate inflorescences bear 12-36 (mean = 22.42 ± 6.93, n = 28) slightly angled then drooping rachillae, which exhibit slightly sunken flowers with corollas that are free and spreading nearly to the base where they are briefly connate. A greenish pistillode, which is apically lobed and basally flared, is quite prominent in all flowers at anthesis. The mean number of flowers per staminate rachillae is 2,141.41 ± 879.95 (n = 41). The aromatic flowers are greenish-yellow to yellow in color, turning dark green and then black as they age and release their dry, light pollen (Hodel, 1992a).

Pistillate individuals develop up to three inflorescences per flowering event (mean = 0.98 ± 0.78, n = 136) and exhibit 16-32 stiff, spreading rachillae (mean = 24.25 ± 5.7, n = 32). A mean of 493.65 ± 312.12 (n = 46) pistillate flowers are produced on each inflorescence. At anthesis, stigmas of the greenish-yellow flowers are fragrant, and glisten with stigmatic exudate. The three staminodes are distinctly triangular in shape, much smaller than the stigmas, yet obvious nonetheless. Flowers may develop into 8-14 mm ellipsoid, black fruit on reddish-orange rachillae (Hodel, 1992a). Mean number of mature fruit produced per inflorescence was measured at 236 ± 252 (n = 40), with a mean fruit set of 47%.

The species, *Chamaedorea oblongata*, is known to occur from the Atlantic slopes of Mexico, in northern and central Guatemala, along the western border of Belize, and through the middle of Honduras and Nicaragua (Figure 2.2B) (Hodel, 1992a). Although Hodel (1992a) states that this species occurs in forests at elevations of up to 400 m and occurs in a variety of soil types, including limestone-based soils. It is widespread across Central America, and tends to be found growing alongside other *Chamaedorea* taxa.

In his study of the palm community of western Belize, Wicks (2003) found that *C. oblongata* was the most abundant palm overall with a mean of 1109 ± 916 (n = 50) individuals per hectare. Concurrently, the abundance of *C. oblongata* was found to be twice as high in deciduous semi-evergreen forest versus that found in deciduous seasonal forest. This difference was attributed to the fact that *C. oblongata* densities are closely related to canopy cover, and the taxon thrives in forest where the canopy cover is adequate, yet not high (Wicks, 2003). He also states that this species exhibits an antagonistic relationships with other understory palms, such that where *C. oblongata* is present, it tends to be the dominant palm at the exclusion of other palms.

This species is primarily known by the common name “xate macho” in Mexico, Guatemala, and Belize. However, additional names, such as “tepejilote”, “pacayita”, “palmilla”, “brillosa”, “chate”, and “caquib” have been reportedly used in Mexico, Guatemala, and Nicaragua (Hodel, 1992a; Henderson et al., 1995). In their 1990 study of non-timber forest products in the Petén, Guatemala, Reining et al. (1992) found that *Chamaedorea oblongata* was one of the two species that had been heavily harvested from the wild for the floral industry for over 50 years (Reining et al., 1992). Several trade names are used to denote regional species varieties (e.g. "jade", "emerald", "teepee"), yet many of the terms are used interchangeably such that all leaves of *Chamaedorea* cut for the floricultural trade can be grouped under the super-categories of "camedor" and "xate" (CEC, 2002). The collection of leaves as non-timber forest products is its main use, although it is also a popular ornamental palm (Hodel, 1992a). However, leaf harvesting has resulted in the decline of populations of this species across Guatemala, and a number of plantations and community concessions have been established to meet the steady demand for leaves by overseas floral markets (Bridgewater et al., 2006).

2.6.3. *Chamaedorea neurochlamys*

Chamaedorea neurochlamys Burret (subgenus *Chamaedorea*) has a solitary habit and grows up to 4.5 m tall and 2.5 cm in diameter. This species has 3-8 pinnate leaves, each with 12-16 rhombic-sigmoid, relatively thin pinnae. The leaf sheath is distinctly white at the apex, with prominent green longitudinal nerves, a primary identifying characteristic. Inflorescences are either inter- or infrafoliar (Hodel, 1992a). Staminate individuals exhibit up to three inflorescences (mean = 1.58 ± 0.99, n = 26), with 10-22 pendulous rachillae (mean = 17.8 ± 4.76, n = 20) on which the aromatic, light green staminate flowers may be slightly sunken (Hodel, 1992a). The mean number of staminate flowers per inflorescence is 3,813.69 ± 919.82 (n = 26). Petals are connate basally and apically, where they are adnate to the apically tri-angled pistillode. Therefore, at anthesis the corolla opens only by lateral slits (Hodel, 1992a).

Pistillate individuals have up to two inflorescences each (mean = 1.07 ± 0.64, n = 30) with between 10-19 erect rachillae (mean = 13.8 ± 3.42, n = 20) with greenish-yellow flowers sunken in depressions. The mean number of pistillate flowers per inflorescence is 443.93 ± 173.74 (n = 30). Petals are connate basally and imbricate nearly to the apex. No staminodes are present. The clear-colored stigma lobes are short and recurved, and the flowers remain fragrant throughout anthesis. Developing fruits range from yellow to orange, to orange-red in color. At maturity, the orange or red brown fruits, typically sub-reniform, or less likely sickle-shaped or bilobed (mean = ± 65, n = 18, mean fruit set = 23%), are borne on red-orange rachillae and measure up to 20 mm long (Hodel, 1992a). As they age, the color changes to a deep brown when ripe. The intense orange and red colors of developing fruit, as well as the white apex, help botanists to distinguish this species from other morphologically similar taxa, such as *C. pinnatifrons*.

Although the species *C. neurochlamys* is placed under *C. pinnatifrons* as a synonym by Henderson et al. (1995), the molecular analysis by Thomas et al. (2006) confirms that it is a separate species. Based on samples collected from and in the vicinity of the study site, the species included in the research described here is *C. neurochlamys*.

Chamaedorea neurochlamys can be found in southern Mexico, central and northern Guatemala, southern Belize, as well as along the central and southern western portion of Belize, and across Honduras (Figure 2.2C) (Hodel, 1992a). Hodel (1992a) notes the species occurs in wet lowland forests from 0-400 m in elevation. The species grows on a variety of soil types, including limestone-based soils. In western Belize, this species is documented as growing sympatrically with *C. oblongata* and *C. ernesti-augustii*, although it occurs in relatively small numbers, scattered in small clumps (77 ± 200 ha^{-1}) (Wicks, 2003). One reason that the populations are low relative to similar species, such as *C. oblongata*, may be the fact that *C. neurochlamys* develops no more than two pistillate inflorescences annually, while other taxa might produce up to four inflorescences. Additionally, while *C. oblongata* often undergoes more than one flowering event per year, *C. neurochlamys* is restricted to a single flowering event.

This species exhibits similar habitat requirement to *C. oblongata*. In his 2003 study, Wicks determined that the abundance of *C. neurochlamys* is almost three times as high in deciduous seasonal forest, where the canopy cover occurs to some degree, yet does not completely obscure sunlight. Conversely, *C. neurochlamys* occurs in lower numbers in semi-evergreen deciduous forest, where the canopy cover is relatively thick (Wicks, 2003). Likely due to this habitat preference this species typically does not occur near *C. tepejilote* or *C. elegans*, at least in western Belize.

Common names for *C. neurochlamys* include: “pacaya”, “pacayo”, “chilac”, and “monkey-tail” (Hodel, 1992a). Although this species is not cited in the primary literature on the *Chamaedorea* leaf trade, it is known to be collected. Numerous leaf-collectors in Guatemala stated that when populations of similar, yet more valuable species (e.g., *C. oblongata*) are low, or when leaves are not available in the populations found, the fronds from *C. neurochlamys* are substituted (per. comm.). They explained that it was simple to distinguish between the different taxa in the field, as *C. oblongata* exhibits thick, leathery leaves, while the leaves of *C. neurochlamys* are relatively thin and therefore will not remain commercially viable for as many days. In fact, when visiting a *Chamaedorea* processing plant in the Petén, Guatemala, several sorted bundles of this species were encountered. Although the practice is understandable when standing supplies of more popular species are low, the collection of leaves from *C. neurochlamys* may have a larger impact on its demographics due to it low abundance, than does leaf harvesting of most abundant species. This is due to the fact that repeated defoliation adversely affects the reproduction (both in terms of developing inflorescences and in the number of flowers produced (Porter-Morgan et al., 2004). Therefore, any program on the use of *Chamaedorea* fronds as non-timber forest products should address this effect.

2.6.4. *Chamaedorea tepejilote*

Chamaedorea tepejilote Liebm. (subgenus *Stephanostachys*) is a rarely cespitose palm with stems that grow to 8 m or taller, are up to 30 cm in diameter, and may form clumps (Hodel, 1992a). The 3-7 pinnate leaves have 12-25 lanceolate leaflets on each side of the rachis. There may be from one to 15 stems on a single individual (per. obs.). Individuals exhibit infrafoliar inflorescences, one to six per stem, which on staminate plants contain 16-26 spreading to pendulous rachillae (mean = 20.6 ± 3.847, n = 20). Along the rachillae, aromatic staminate flowers with dry pollen are borne contiguously. The mean number of staminate flowers per inflorescence is 5,165.4 ± 1,469.71 (n = 20). The petals of these greenish-yellow flowers are valvate and distinct, yet they appear basally connate due to the dense arrangement. The pistillode is prominent and lobed apically (Hodel, 1992a).

Pistillate inflorescences have 13-24 spreading rachillae (mean = 18.22 ± 4.32, n = 20). The mean number of pistillate flowers per inflorescence totals 1,099.3 ± 309.92 (n =

20), and up to six inflorescences have been found on a single stem. The aromatic flowers are slightly sunken into the rachillae and vary in color from greenish-yellow to white (Hodel, 1992a). Petals are somewhat fleshy and imbricate to the rounded apex. They remain pressed against the stigma lobes during anthesis and may exhibit 0-6 small staminodes. Pistillate flowers may develop into 7-8 mm ellipsoid to globose, black fruits on reddish rachillae (Hodel, 1992a). The mean number of mature fruit produced per inflorescence in this species was 369 ± 128 (n = 14), with a mean fruit set of 30%.

Chamaedorea tepejilote is among the most widespread of the *Chamaedorea* species. It occurs throughout the greater part of the generic range, from southern Mexico, throughout Central America, and into northern South America (Figure 2.2D) (Hodel, 1992a). It can be found at elevations of 0-1600 m and often occurs on limestone soils. The species tends not to occur in forests with a high amount of canopy cover, yet requires some degree of shade when fully mature. Wicks (2003) found that 93 ± 291.2 individuals per square hectare and noted that this species preferred similar microhabitats as *C. pinnatifrons*. It also was found to be highly correlated with several species of the palm *Bactris*, which also occupy the same microhabitats (Wicks, 2003). Of the four species studied, *C. tepejilote* was the most likely to be found growing on gentle to moderate slopes.

There are an overwhelming number of common names associated with this particular species including: “pacaya”, “pacaya grande”, ‘”tepejilote”, “guaya”, “chem-chem”, “palmito dulce”, “boda”, and “cana verde” (Hodel, 1992a; Henderson et al., 1995). *Chamaedorea tepejilote* has been cultivated for centuries in central Guatemala, for its edible male inflorescences (Castillo Mont et al., 1994). The inflorescences, which resemble ears of corn, are harvested when not yet mature, and are locally known as “pacaya.” A cottage industry employing a large number of individuals has been established, and the product has even been spotted for sale in groceries of several states including Indiana and New York (Cook & Doyle, 1939; Hodel, 1992a; Castillo Mont et al., 1994; Garwood, per. comm.). After stripping off the green bracts, inflorescences are chopped and added to scrambled eggs, stews, and other dishes (Hodel, 1992a).

It is important to note that several articles on various ecological aspects of this species are available in peer-reviewed journals (Oyama & Dirzo, 1988; Oyama & Mendoza, 1990; Oyama, 1991, Oyama, 1993), yet the taxonomic status of *C. tepejilote* in relation to *C. alternans* has been unclear. Some authors recognize the two species as synonymous due to their morphological similarity (e.g., Oyama & Dirzo, 1988; Oyama & Mendoza, 1990), while others designate them as separate species (e.g., Otero-Arnaiz & Oyama, 2001). However, recently, a phylogenetic study by Bacon and Bailey (2006) has demonstrated that *C. alternans* and *C. tepejilote* are indeed two distinct species.

2.7. Study Site

The research presented in this thesis was conducted in the vicinity of the Las Cuevas Research Station (LCRS), which is located in the southwestern portion of the Cayo District, Belize (16° 44´N, 88° 59´W) (Fig. 2.3). The station is situated close to the center of the Chiquibul National Park and Forest Reserve in western Belize, near Guatemala’s eastern border. The Chiquibul Forest Reserve was created in 1956 in order to conserve forest that occurs from the Maya Mountains west of the main divide to the international border with Guatemala (Johnson & Chaffey, 1974).

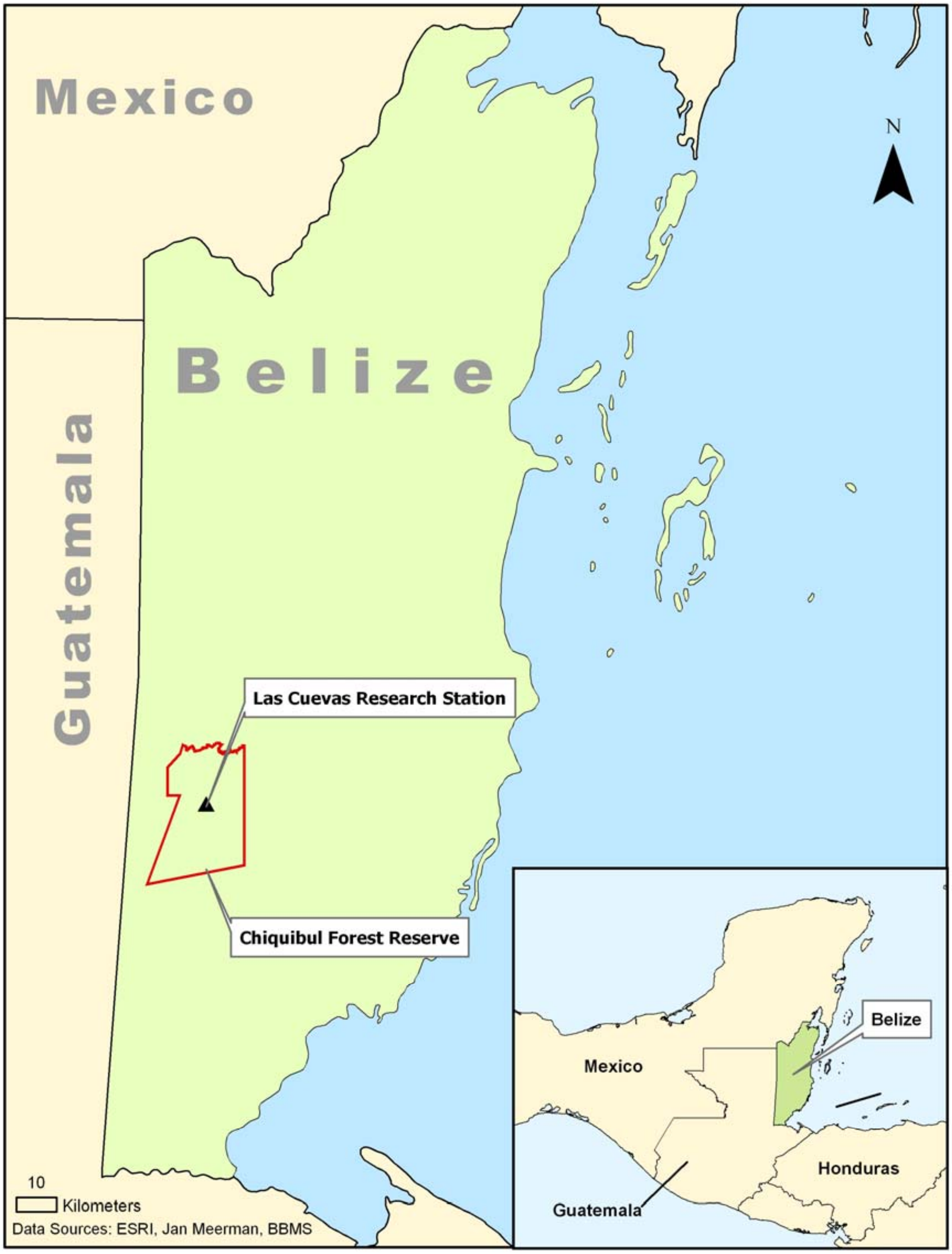


Figure 2.3
Map of Belize with the Las Cuevas Research Station and the Chiquibul Forest Reserve indicated. The inset map locates Belize within Central America.

The only permanently settled portion of the Reserve is the research station, although small settlements of Guatemalan nationals have been found periodically near the border. In contrast, until approximately 900 AD, the area was under intensive cultivation by Mayan groups, the impact of which is reflected in the composition of the present vegetation. In the centuries since widespread Mayan use, portions of the Chiquibul forest have been subjected to small-scale agriculture. After 1920, the area has experienced numerous cycles of selective logging, primarily for mahogany (*Swietenia macrophylla* King) and cedar (*Cedrela odorata* L.). Additionally, much of the Chiquibul forest has been affected by natural disturbances including hurricanes (e.g., Hurricane Hattie in 1961) and fires (e.g., significant fire damage occurred in 1964) (Bird, 1994). Since 2000, the reserve has been seriously impacted by the incursion of illegal *xateros* (*Chamaedorea* leaf harvesters) from Guatemala.

The Chiquibul Forest Reserve covers approximately 170,000 ha and has an altitudinal range of 100-700 meters (Mallory & Brokaw, 1996). The forest in this area corresponds to a transition between the subtropical lower montane moist and the subtropical moist life zones as designated by the Holdridge System (Hartshorn et. al., 1984). Primary vegetation types found within the reserve are deciduous seasonal and semi-evergreen forest (Wright, et al, 1959). The majority of soils are calcareous clays with underlying Cretaceous limestone (Mallory & Brokaw, 1996). Climate conditions at the study location are distinctly seasonal, with a dry season that typically runs from (January) February through May (June), and a wet season that typically begins in mid-June, and continues through December (January). The area has an average annual precipitation of approximately 2,000 mm, and an average annual temperature of 24°C to 32°C (Johnson & Chaffey, 1974).

2.7.1. Study Plots

Seven 20m x 20m study plots were established in the vicinity of LCRS in June 2002. *Chamaedorea* is among the most abundant palm generum in the study area, and dominates the understory in the two study areas used. The plots were placed in the two main forest types that occur in the reserve, deciduous seasonal forest and semi-evergreen forest. Those study plots designated as 1, 2, and 3 were laid out in the deciduous seasonal forest. In addition to *Chamaedorea* spp., the major tree species found in this forest type are *Manilkara chicle* (Pittier) Gilly and *Pseudomedia spuria* (Sw.) Griseb., with abundant *Brosimum alicastrum* Sw., *Drypetes brownii* Standl., *Manilkara zapota* (L.) P. Royen, *Protium copal* (Schltdl. & Cham.) Engl., *Cedrela odorata* L. and *Vitex gaumeri* Greenm. (Mallory & Brokaw, 1996). The canopy in deciduous seasonal forest reaches from approximately 21 to 30 meters in height, and the altitude is between 540 and 560 meters. Soils tend to be rocky and shallow, while the slopes tend to be steep (Bird, 1994; Mallory & Brokaw, 1996).

The plots designated as 4, 5, 6, and 7 were located in semi-evergreen forest, which is dominated by *Brosimum alicastrum* Sw. and *Manilkara chicle* (L.) P. Royen, as well as *Chamaedorea* spp. This forest type also includes large numbers of *Drypetes brownii* Standl., *Swietenia macrophylla* King, *Dialium guianense* (Aubl.) Sandwith, *Coccoloba belizensis* Standl. and *Sabal maritiiformis* (H. Karst.) Griseb. & H. Wendl. (Mallory & Brokaw, 1996). The majority of soils are clays, with moderate drainage and numerous small, rolling hills. Finally, canopy height and elevation differ little from those reported for deciduous seasonal forest (Bird, 1994; Mallory & Brokaw, 1996).

In each of the first three plots, a total of three *Chamaedorea* species were found: *C. oblongata*, *C. ernesti-augustii*, and *C. neurochlamys*. In plots 4 through 7, four *Chamaedorea* species were present: *C. ernesti-augustii*, *C. oblongata*, *C. neurochlamys*, and *C. tepejilote*. In sum, 361 *Chamaedorea* individuals were located within the study plots: 216 *C. oblongata*, 85 *C. ernesti-augustii*, 40 *C. neurochlamys*, and 20 *C. tepejilote*. Vouchers representing each of the species are deposited at the Forestry Herbarium in Belmopan, Belize and The New York Botanical Garden. For an inventory of the *Chamaedorea* individuals in each plot, refer to Table 2.1. Two additional *Chamaedorea* taxa occur in the vicinity of LCRS, *C. elegans* and *C. graminifolia*. However, both taxa occur in low numbers, have limited or specialized distributions, and were not present in the study plots.

Table 2.1 Number of *Chamaedorea* individuals with evidence of previous reproductive activity located in each of the 20 x 20 m study plots. Abbreviations: ER = *C. ernesti-augustii*; OB = *C. oblongata*; NE = *C. neurochlamys*; TP = *C. tepejilote*.

	ER	**OB**	**NE**	**TP**	**Number of study individuals in plot**
Plot 1	9	16	1	0	26
Plot 2	6	23	6	0	35
Plot 3	10	29	3	0	42
Plot 4	16	46	2	4	68
Plot 5	12	41	4	3	60
Plot 6	14	25	8	5	52
Plot 7	18	36	16	8	78

It is important to note that the placement of study plots was not random. Instead placement was constrained to some degree by the presence of *Chamaedorea* leaf collectors (*xateros*) in the immediate area. *Xateros* made it difficult to locate areas where no leaf removal had occurred and because of them, some places were considered unsafe for researchers by station staff. At the time study plots were established, the majority of *xateros* were giving the research station wide berth, although many areas had been harvested in the past. However, by 2004 confrontations between station personnel, researchers, and *xateros* were occurring on a regular basis. Also, due to declining supplies, leaves were removed from palms located within 1 km of the research station, including plants in close proximity to the study plots. Therefore, all study plots were established within 0.5 kilometers of the station, near access trails patrolled by station personnel, and in areas where *Chamaedorea* leaves had not been collected. Only the leaves of *C. ernesti-augustii* were removed from study individuals during the study period, and a total of eight of the 85 individuals of this species within the study plots were damaged.

In each of the study plots, all adult *Chamaedorea* individuals of reproductive age were identified to species, labeled with aluminum tags, and mapped (Cartesian coordinates) (Figure 2.4, Figure 2.5). Palms were classified as adults if they showed evidence of previous reproductive events such as old inflorescences. Other measurements recorded for each study individual included the number of leaves and stem length. When possible, sex was determined based on characters such as rachillae orientation (e.g. pendulous versus erect) and floral anatomy. Individuals that died during the study period were not included in phenological calculations. Additionally,

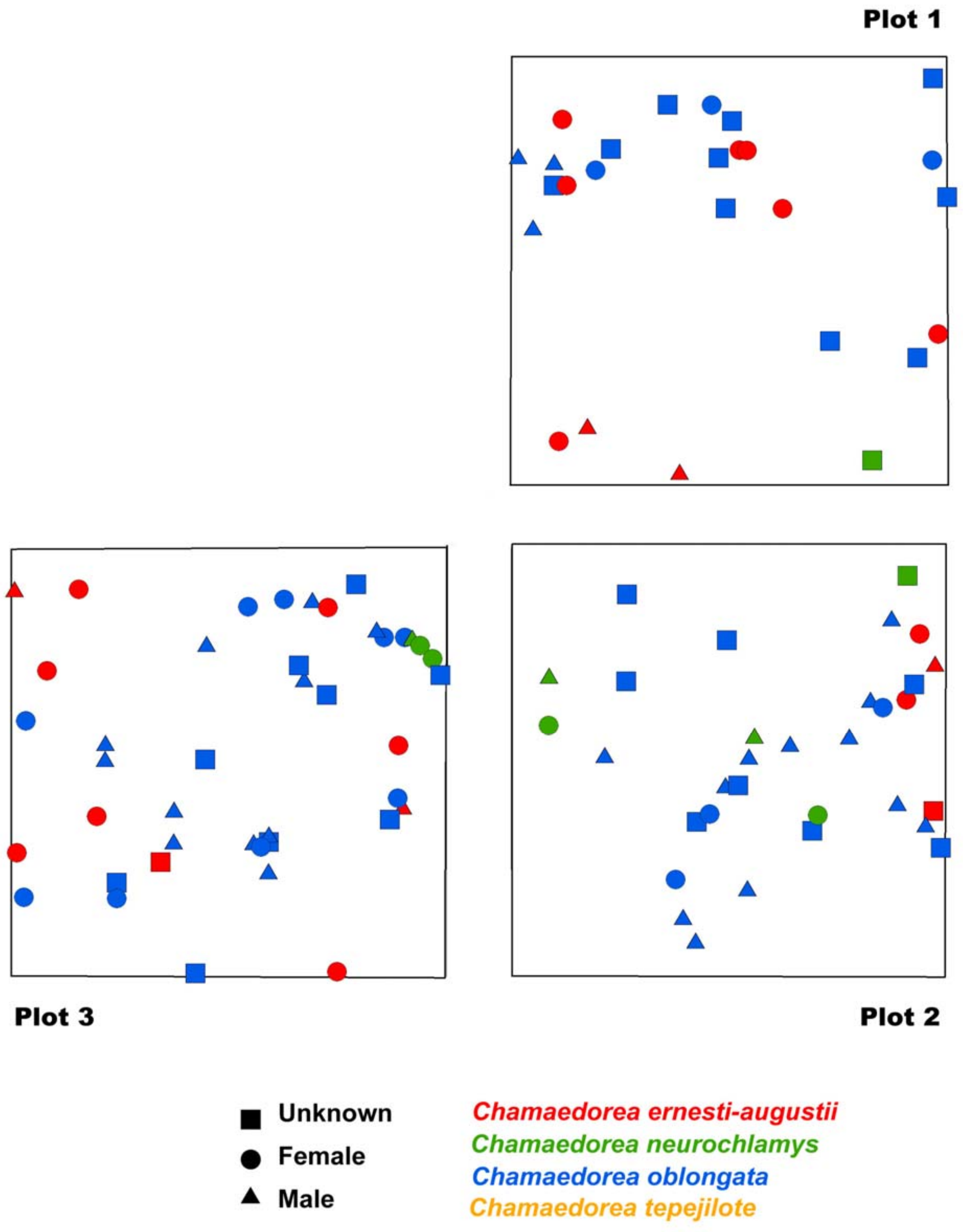


Figure 2.4
Plots 1-3, located in deciduous seasonal forest. Each of the four study species is represented by a different color and the sex is indicated by one of three symbols. Note that the points represent where the stem enters the ground and not the crown of the palm, because the crown position can change over time due to such factors as bending toward sunlight and treefall.

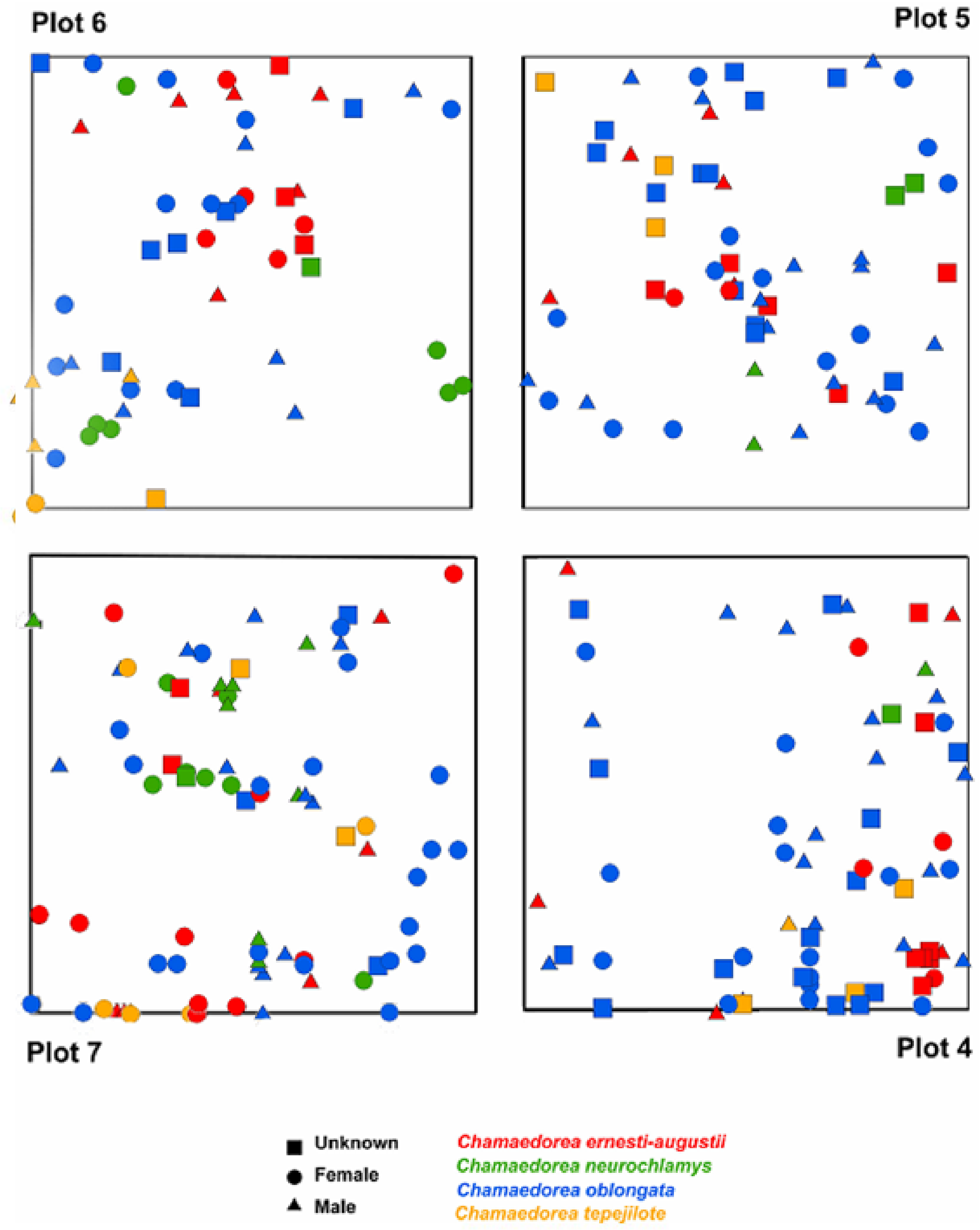


Figure 2.5
Plots 4-7, located in semi-evergreen forest. Each of the four study species is represented by a different color and the sex is indicated by one of three symbols. Note that the points represent where the stem enters the ground and not the crown of the palm, because the crown position can change over time due to such factors as bending toward sunlight and treefall.

precipitation data were obtained from several weather stations in the Cayo district of Belize. As no data for the study location was available, the data from surrounding areas was averaged.

2.8. Mortality

The next two sections present data collected on mortality and spatial distribution of the *Chamaedorea* populations.

Mortality, or conversely survival, is a critical component when investigating any population, as it has a significant impact on population dynamics. Plants, including palms, may experience mortality as the result of intrinsic factors, such as senescence, and as the result of extrinsic factors, such as predation or treefall (Sarukhán, 1978; Búrquez et al., 1987; Oyama, 1991; Martínez-Ramos & Samper, 1998; Arnold & Asquith, 2002). Data collected during this study suggest that the primary sources of mortality for *Chamaedorea* adults are extrinsic, specifically treefall and predation by small mammals.

Rates of mortality for adult individuals in tropical forests have been reported by a number of researchers. For example, Leigh (1999) stated that the annual mortality rates for all tagged trees on Barro Colorado Island (BCI), which were recorded during censuses after three, five, and seven years, were between 1.12% and 4.06%, with the highest number of mortalities occurring consistently in the lower size classes. In a study of dicot trees at BCI, Putz & Milton (1982) found mortality rates that averaged from 1%-3% per year, while for all trees, the rate was approximately 2% per year (Condit et al., 1995). Additionally, Lieberman and Lieberman investigated the mortality of trees and lianas ≥ 10 cm dbh for over a decade and calculated annual mortality rates between 1.8% and

2.24% per year per plot (plots approximately 4 ha. each). The authors of the studies described above all determined that treefall was the main cause of mortality, while animal-caused mortalities were found to be relatively low.

In their research on *Astrocaryum mexicanum*, Piñero et al. (1986) discussed how that palm contends with treefall. The authors state that after being felled by trees, individuals typically continue to grow upward, even as the lower part of the stem is prostrate along the ground. The growth thereby creates a large bend in the stem that corresponds to the time at which the tree fall occurred. Similar behavior was observed with *Chamaedorea* individuals at LCRS, when several of the study individuals were knocked over, presumably by high winds or treefall. Subsequently, these individuals were able to produce roots from their nodes and continue to flourish. In these cases, the majority of the stem remained horizontal, while the crown and any new growth were directed vertically.

A study conducted by DeSteven and Putz (1985) on Barro Colorado Island, Panama was one of the few found to contain data on *Chamaedorea* mortalities. The authors investigated the mortality rates of a number of palms obtained during a three-year phenological study, including *C. wendlandiana*. They determined that individuals of *C. wendlandiana* exhibited no animal damage to their crowns in relation to the other palms included in the study, which had death rates of up to 9.3% per annum. They concluded that this species might produce chemicals in the leaves, or possibly in floral tissues, which function to repel herbivory. Although no individuals died during their 3-year study, based on their observations, the authors suggest that when mortality does occur in *C. wendlandiana* the primary reason is likely to be treefall. One reason for this nonexistent death rate is that the majority of the palms felled by treefall did not die, instead their prostrate stems re-rooted and survived, as the apical meristem had not been affected.

For the research presented in this thesis, a total of 63 *Chamaedorea* individuals died during the two-year study period, representing17.45% of the individuals present at the beginning of the study. The primary cause of death was recorded for each of these palms. During the first year of data collection (October 2002-September 2003), 11 of the original 361 study individuals (3% of the total) died mainly to treefall and rarely to fungal infections. During the second year of data collection, 52 of the 350 individuals remaining in study plots (14.85%) died, primarily to predation by animals called ground moles.

None of the study individuals in the deciduous seasonal forest plots (plots 1-3) were killed by ground moles, while 71.15% of the mortalities in the semi-evergreen plots (plots 4-7) were the result of attacks by rodents that the locals call “ground moles.” Ground moles are a type of pocket gopher belonging to the family Geomyidae, and their scientific name is *Orthogeomys hispidus* (Reid, 1997). They are primarily nocturnal creatures that live in burrows and are rarely seen aboveground. Pocket gophers are known to cause significant damage to vegetation, as they feed on tubers, roots, and whole small trees, which they pull by the base of the stem down into their burrows.

Although the rodent predation was the main reason for mortality recorded during the second study year (October 2003 - September 2004), it is possible that some of the mortalities that occurred during the first study year may have been due to similar actions. I was unaware of this potential threat during my first study year, and therefore did not consider this when establishing the study plots. Still, the LCRS staff stated that when these rodents move in to an area, it is quite obvious due to the presence of dirt piles where each plant was removed. This was certainly the case for the study plots in which attacks were experienced. In fact, the gophers did not focus solely on *Chamaedorea*, but also preyed upon young individuals of the palms *Cryosophila* and *Sabal*, leaving the areas in which they fed devoid of adult and sub-adult understory palms. The manner in which ground moles damage plants in a particular area involves them pulling all edible plants underground for feeding before moving on to a new area. Large woody trees, such as *Manilkara chicle*, are not attacked. All four of the *Chamaedorea* study species were victimized if they were located in feeding areas. In one case, a study individual was followed for pollination observations for one week and then not visited for two days. When the individual was sought after this short break, the entire plant was removed. The only evidence of its existence was a pile of soil, an identifying characteristic of ground mole invasion, with the metal tag and a few dried pinnae at its apex.

Due to these unforeseen circumstances, the final mortality rates were far higher than I had expected. However, when individuals lost to rodent predation are removed from the analysis, mortality is in the normal range of approximately 3% for year one and 4.28% for year two. Additionally, based on the values in Table 2.2, there appears to be no relationship between species and mortality, as the total number of each species in the study population was in proportion to the number of individuals of each species that died. Therefore, the incidence of mortality was in proportion with the initial composition of the studied *Chamaedorea* population.

Conversely, there was a relationship between location and mortality, due to the fact that gophers decimate any area they invaded before moving to a new area. By plot, the mortality was between 3.84%-14.28% in plots in areas that likely were not attacked by pocket gophers. Conversely, in the plots that were documented to experience invasions, plot 5 and plot 6, the mortality rates were 36.53% and 43.33%, respectively. These mortality rates are far higher than would be found with only treefall as the cause (Table 2.3). It is not surprising that these herbivores would target locations in the semi-evergreen forest location rather than the deciduous seasonal forest plots, as the density of palms, as well as vegetation in general, is much higher than in the former forest type. Thus, treefall is concluded to be the primary reason for *Chamaedorea* mortality in areas not inundated by gophers.

A potential additional reason for the mortality in study plots occurred with the species *C. ernesti-augustii.* For only this species, the fronds of several study individuals were removed during the course of the study. As described above, the leaves are

Table 2.2 Mortality of *Chamaedorea* individuals located in the 20 x 20 m plots over the study period (October 2002 – September 2004), and the relative abundance of dead and total study plants for each species. Abbreviations: ER = *C. ernesti-augustii*; OB = *C. oblongata*; NE = *C. neurochlamys*; TP = *C. tepejilote*.

Parameter	ER	OB	NE	TP
Number of dead individuals per species	18	34	8	3
Percentage of dead individuals per species	21.1%	15.6%	20%	15%
Percentage of total study individuals by species	23.4%	60%	11%	5.5%
Percentage total dead individuals by species	28.5%	55.7%	12.7%	4.7%

Table 2.3 Mortality of *Chamaedorea* individuals from each species by plot over the study period (October 2002 – September 2004). Abbreviations: ER = *C. ernesti-augustii*; OB = *C. oblongata*; NE = *C. neurochlamys*; TP = *C. tepejilote*.

	ER	OB	NE	TP	Total number of individuals dead	Total number of individuals in plot	Percentage of dead individuals in plot
Plot 1	0	1	0	0	1	26	3.84%
Plot 2	0	5	0	0	5	35	14.28%
Plot 3	0	3	0	0	3	42	7.14%
Plot 4	0	3	0	0	3	68	4.41%
Plot 5	8	16	1	1	26	60	43.33%
Plot 6	9	5	4	1	18	52	34.61%
Plot 7	1	1	3	1	6	78	7.7%

collected by *xateros*, who sell them for use as greenery in the international floral industry. This defoliation does not appear to have affected the number of deaths in the defoliated study palm, however it remains a possibility. The reason for this supposition is that the study individuals that were defoliated and later died were located within a larger area that also was attacked by rodents. Gophers victimized all trees in the area, including defoliated and non-defoliated *C. ernesti-augustii* individuals, as well as other adult *Chamaedorea* palms. Defoliated *C. ernesti-augustii* palms that were not located in gopher-invaded plots, remained alive at the end of the study.

2.9. Spatial Distribution

Spatial pattern is an important aspect of any pollination study, particularly those that involve sympatric species, because the primary plant-to-plant interactions of any individual occur with its closest neighbors (Dale, 1999). Additionally, the relative locations of the different sexes for a dioecious species circumscribe the distribution of floral resources that are available to potential biotic pollen vectors. Therefore, spatial distribution influences a number of key pollination interactions including visitor abundance and diversity, competition between individuals for pollinators, foraging behavior of pollinators, and subsequently, the potential for effective pollination.

The spatial structure of *Chamaedorea* was examined using a Geographic Information System (GIS) (ArcGIS 9.1, ESRI), with the objective of determining whether individuals of each study species, as well as individuals of different sexes, were spatially segregated from one another. Each 20 x 20 meter plot was digitized and entered into a geodatabase. Using their Cartesian coordinates within the plots, each of the study individuals was geolocated, relevant attribute data (e.g. species, sex) was inputted, and maps of the plots produced (Figures 2.4 and 2.5). After all of the individuals were spatially located, it was possible to use the geodatabase, along with spatial statistics tools, to perform a series of analyses. The nearest-neighbor tool was used to determine if the study individuals are arranged in random, clumped (aggregated), or regular (overdispersed) patterns within their respective plots. This method compares the observed nearest distance and the expected nearest distance, which is based on the null hypothesis of complete spatial randomness (Clark & Evans, 1954). Analyses were conducted for the total set of study individuals within each plot, and then separate plot-wise analyses were performed for each of the four species.

Next, the nearest individual of the opposite sex for each study individual was identified, and the mean distance between staminate and pistillate plants for each species was measured (Figures 2.6 – 2.12). The results then were exported in tabular format and brought into SPSS 13.0 where Chi-square tests (Pearson) were performed to assess the degree of segregation between staminate and pistillate individuals (Bawa & Opler, 1977).

The nearest neighbor analyses determined that, when examined at the community level, the four *Chamaedorea* species in this study were significantly aggregated within each plot (Table 2.4). However, at the species level, none have significantly clustered distributions (Tables 2.5-2.8). The mean distance between *Chamaedorea* individuals in the study plots was calculated as 1.34 ± 1.04 meters (n = 354). When each of the study

Table 2.4 Analysis of nearest neighbor relationships between all staminate and pistillate *Chamaedorea* study individuals by plot. The r value is the nearest neighbor index, while the Z score is calculated to determine if clumping or dispersion is statistically significant ($p < .05$).

Plot	r	Z	*p*	Description
1	0.0	-9.8	$p < .01$	Clustered
2	0.0	-11.4	$p < .01$	Clustered
3	0.0	-12.4	$p < .01$	Clustered
4	0.0	-15.8	$p < .01$	Clustered
5	0.0	-14.9	$p < .01$	Clustered
6	0.0	-13.8	$p < .01$	Clustered
7	0.0	-16.9	$p < .01$	Clustered

Table 2.5 Analysis of nearest neighbor relationships between staminate and pistillate plants by plot for *C. ernesti-augustii*. The r value is the nearest neighbor index, while the Z score is calculated to determine if clumping or dispersion is statistically significant ($p < .05$).

Plot	r	Z	*p*	Description
1	1.06	0.3	-	Random
2	0.05	-4.5	$p < .01$	Slightly Clustered
3	1.5	3.0	$p < .01$	Dispersed
4	1.4	3.1	$p < .01$	Dispersed
5	1.26	1.7	$p < .10$	Dispersed
6	1.21	1.5	$p < .50$	Slightly Dispersed
7	0.99	-0.1	-	Random

Table 2.6 Analysis of nearest neighbor relationships between staminate and pistillate plants by plot for *C. oblongata.* The r value is the nearest neighbor index, while the Z score is calculated to determine if clumping or dispersion is statistically significant ($p < .05$).

Plot	r	Z	p	Description
1	1.02	0.1	-	Random
2	1.22	2.0	$p < .05$	Dispersed
3	0.85	-1.6	$p < .50$	Slightly Clustered
4	1.04	0.5	-	Random
5	-0.2	0.98	-	Random
6	-0.9	0.9	-	Random
7	0.85	-1.7	$p < .50$	Slightly Clustered

Table 2.7 Analysis of nearest neighbor relationships between staminate and pistillate plants by plot for *C. neurochlamys.* The r value is the nearest neighbor index, while the Z score is calculated to determine if clumping or dispersion is statistically significant ($p < .05$).

Plot	r	Z	p	Description
1	Too few individuals in plot to conduct an analysis.			
2	12.02	51.6	$p < .01$	Dispersed
3	2.24	4.1	$p < .01$	Dispersed
4	4.08	8.3	$p < .01$	Dispersed
5	0.94	-0.3	-	Random
6	1.03	0.2	-	Random
7	0.93	-0.6	-	Random

Table 2.8 Analysis of nearest neighbor relationships between staminate and pistillate plants by plot for *C. tepejilote.* The r value is the nearest neighbor index, while the Z score is calculated to determine if clumping or dispersion is statistically significant ($p < .05$). The species *C. tepejilote* only occurs in study plots 4-7, however plots 4, 5, and 6 contained too few individuals to conduct an analysis.

Plot	r	Z	p	Description
7	0.85	-0.3	$p < .50$	Slightly Clustered

Table 2.9 Mean distance ± standard deviation in meters for *Chamaedorea* individuals of all four study species, where N = number of individuals. The conspecific distance values are derived from study individuals located in the four 20 x 20 m plots.

Species	N	Mean Distance ± SD (meters)
C. ernesti-augustii	85	2.48 ± 1.94
C. oblongata	216	1.64 ± 1.19
C. neurochlamys	36	2.63 ± 1.66
C. tepejilote	17	4.02 ± 3.31

species was assessed separately, the average distances were also low (Table 2.9). Additionally, chi-square tests determined that there was no significant spatial association between the sexes for any of the study species (Table 2.10). Consequently, the likelihood that a staminate plant will have another staminate plant as its nearest neighbor versus a pistillate plant as its nearest neighbor is no different than what would be expected with a random distribution.

These results, and the spatial patterns they described, provide data that has direct bearing on the viability of different pollen vectors. Wind pollination is reported to be more likely when there is a relatively close spatial relationship between compatible plants, as well as a relatively open vegetation structure in general (Bawa & Crisp, 1980; Culley et al., 2002). In fact, Regal (1982) stated that the degree to which plants are segregated might be one of the most important aspects in determining the potential for wind pollination. On the hand, entomophily, rather than anemophily, may occur in a range of vegetation types, from open to closed (Whitehead, 1983).

Table 2.10 Analysis of nearest neighbor relationships between staminate and pistillate plants for each of the study species. No analysis for *C. tepejilote* was conducted due to the low number of individuals. Non-significant chi-square (x^2) values are denoted as n.s. Abbreviations: ER = *C. ernesti-augustii*; OB = *C. oblongata*; NE = *C. neurochlamys*.

Species	Base Plant	Nearest Neighbor Staminate	Nearest Neighbor Pistillate	x^2	Average distance between trees (meters)
ER	Staminate	9	18	2.705 n.s.	2.63 ± 1.99
	Pistillate	20	17		
	Total	29	35		
OB	Staminate	29	43	2.274 n.s.	1.64 ± 1.19
	Pistillate	42	38		
	Total	71	81		
NE	Staminate	8	5	3.096 n.s.	3.23 ± 2.70
	Pistillate	5	12		
	Total	13	17		

It is important to note that this study represents individuals at the scale of the study plots and distances between neighbors of the same species have been recorded at less than 0.5 m. Accordingly, analyses with smaller or larger scales, as well as in other locations, might have different results. For example, a series of 20 x 20 m plots across western Belize yielded similar spatial arrangements to those found in this study, however the plots were randomly placed, and many large patches of individual species also were found outside of plots (Bridgewater et al., 2006). This is not surprising, because spatial distribution is result of number factors. Two factors that could account for the aggregation of adult individuals are the falling of seeds close to the mother plant, and the activity of seed dispersers, which may create patches as fruit often are scattered in groups by biotic dispersers as they may leave clumps of fruit where they eat and may bury their excess food supplies (Dale, 1999).

The analyses described above also determined that staminate and pistillate plants of all study species are distributed at random with respect to one another, not segregated by sex. Based on their research on the spatial patterns of staminate and pistillate plants in dioecious species, Bawa and Opler (1977) suggest that levels of pollination and subsequently fruit set are higher when the distribution of different sexes is random rather than clumped. This spatial arrangement promotes pollination, because if the staminate plants were clustered together instead of distributed at random with respect to pistillate individuals, insect visitors might be more likely to visit staminate individuals in close proximity rather than moving to pistillate individuals, thereby resulting in lower visitation rates for pistillate inflorescences. Additionally, the intermingling of staminate and pistillate individuals, as well as the low interplant distances, allows for the possibility of wind pollination.

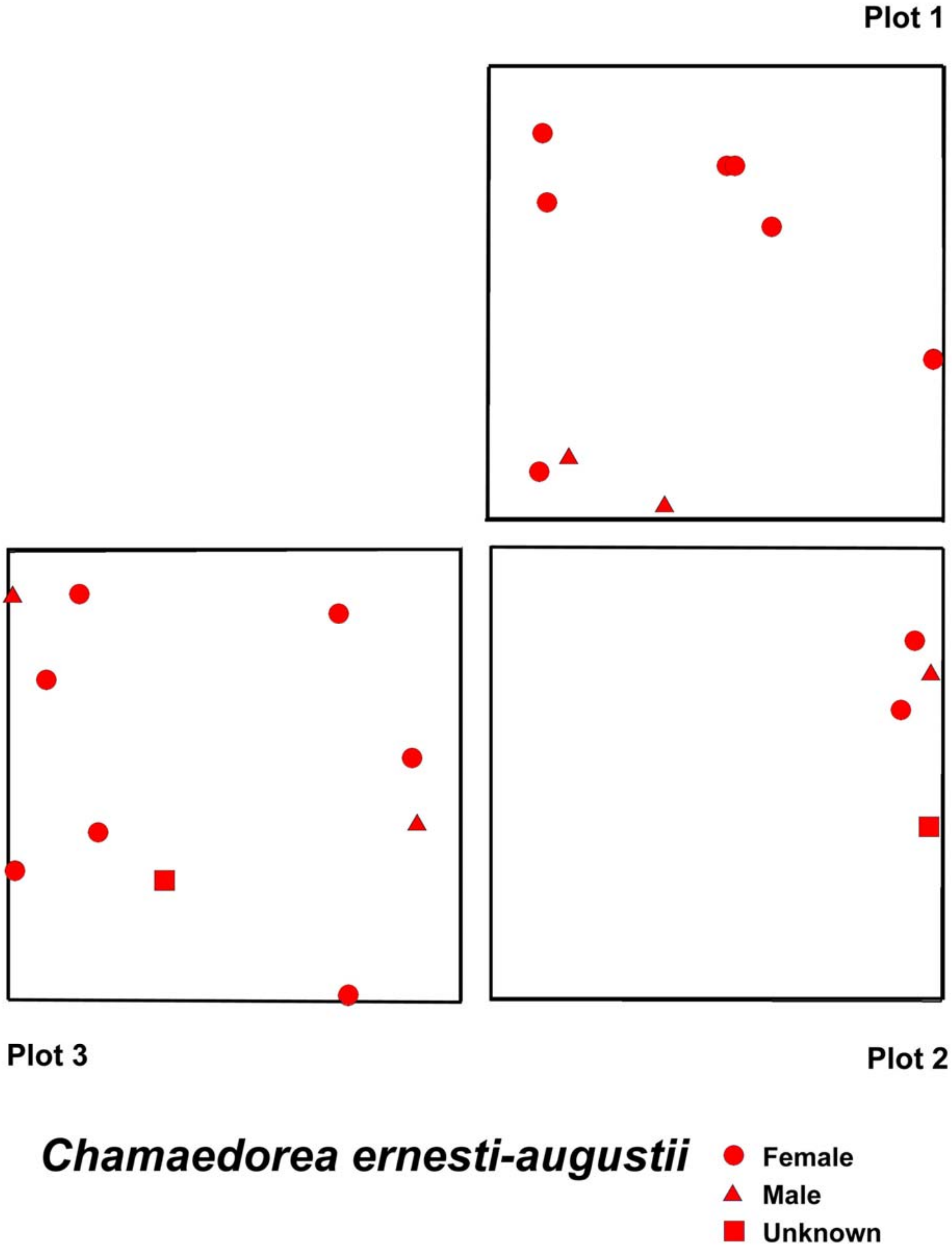


Figure 2.6
Distribution of *C. ernesti-augustii* within plots 1-3.

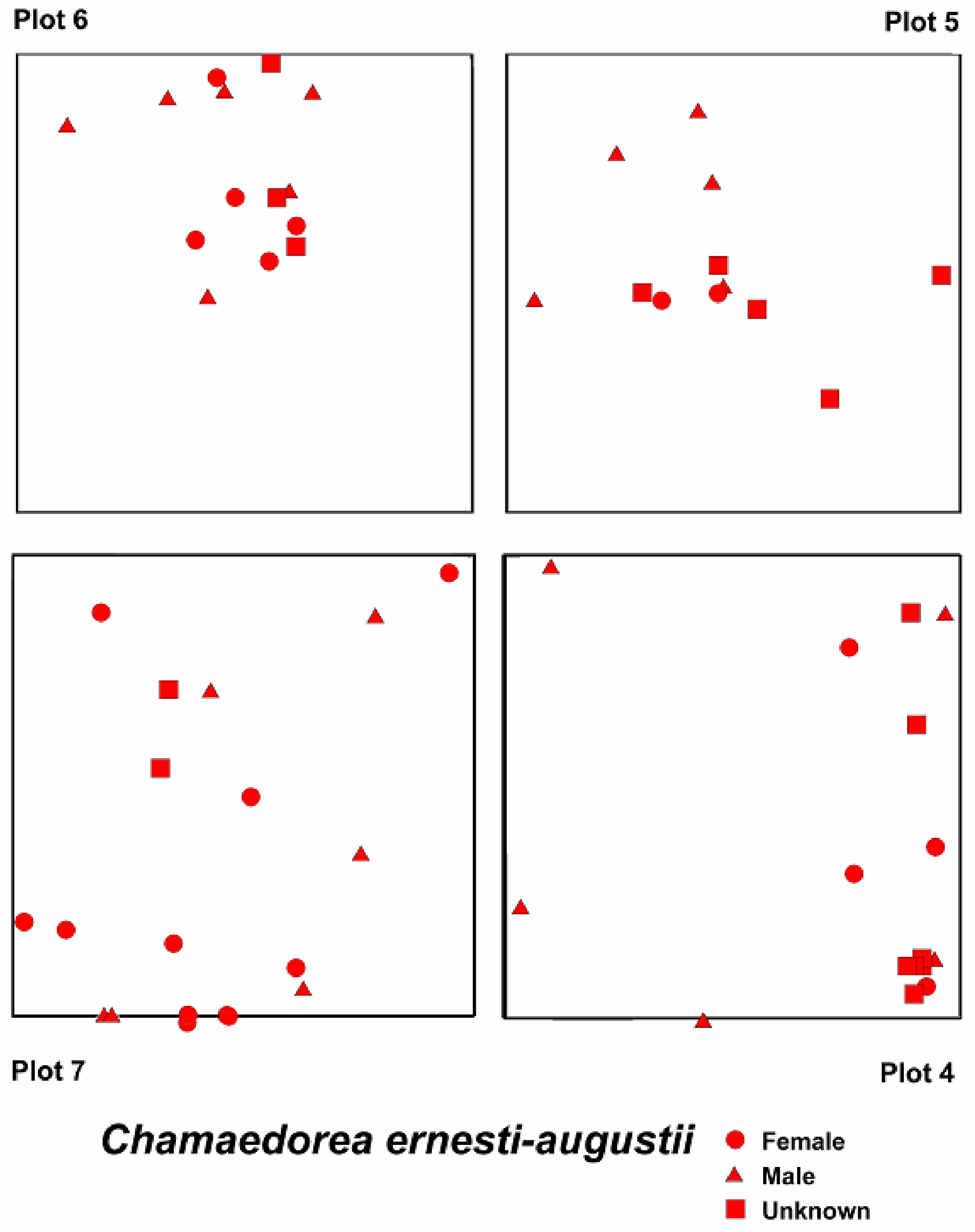


Figure 2.7
Distribution of *C. ernesti-augustii* within plots 4-7.

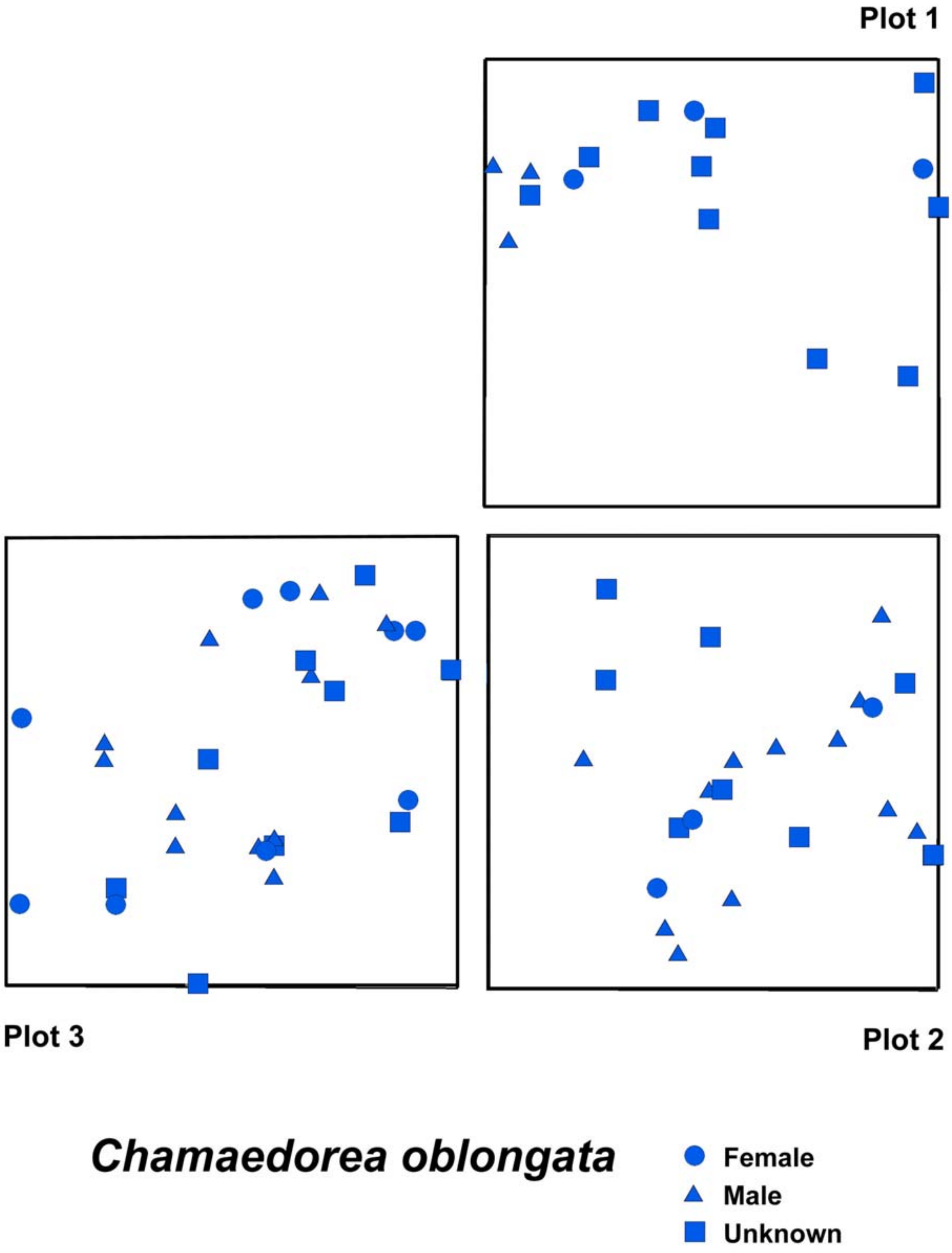


Figure 2.8
Distribution of *C. oblongata* within plots 1-3.

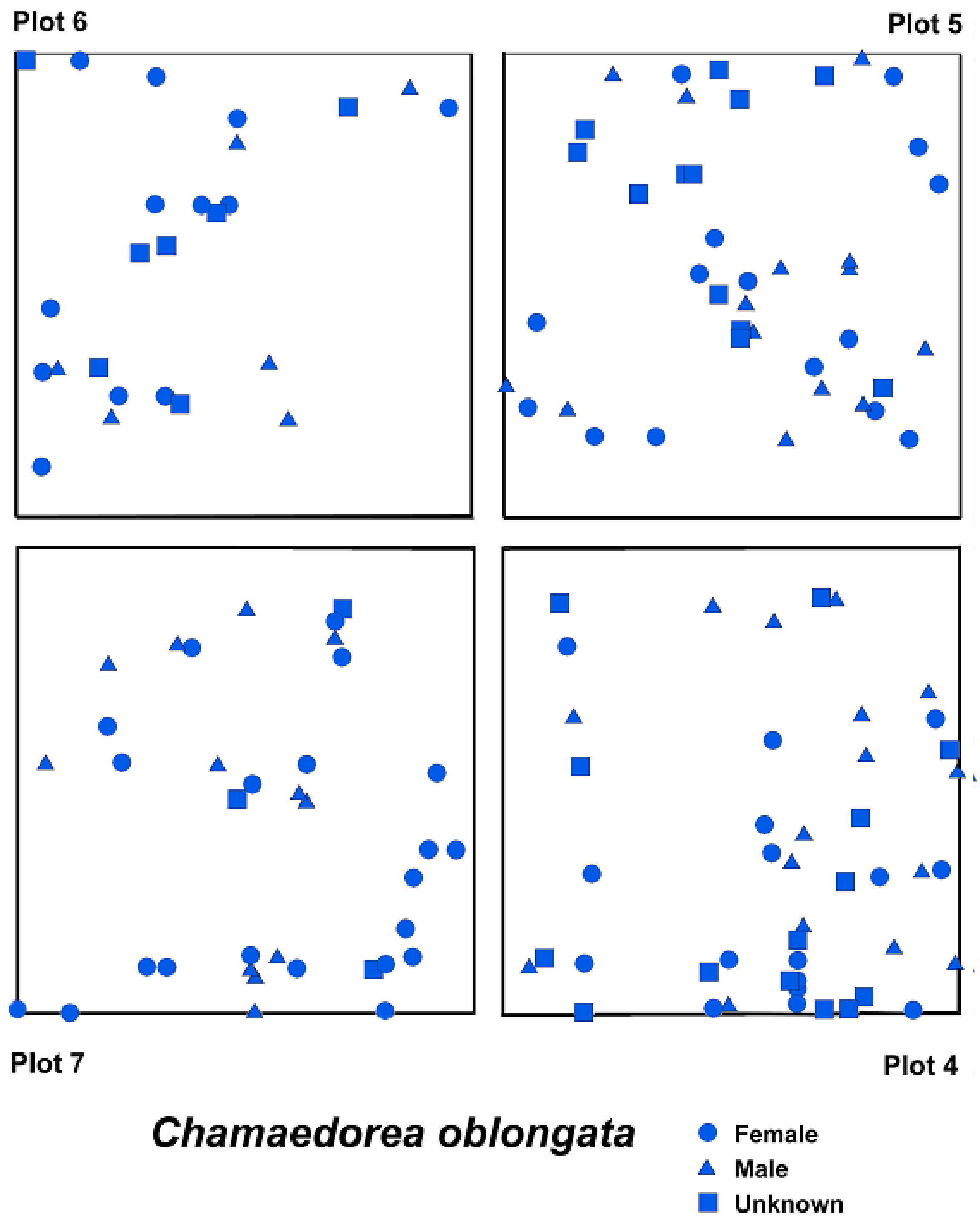


Figure 2.9
Distribution of *C. oblongata* within plots 4-7.

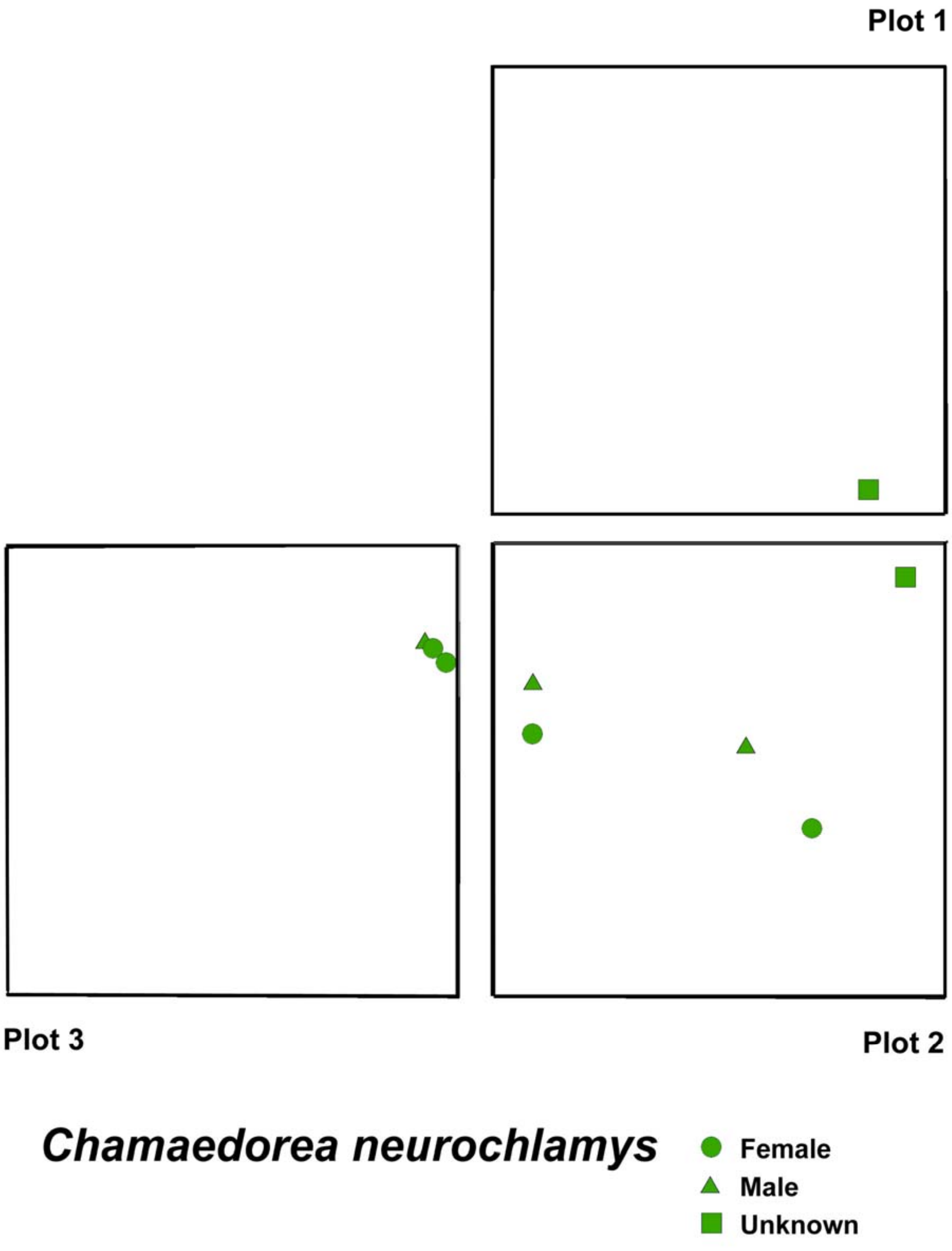


Figure 2.10
Distribution of *C. neurochlamys* within plots 1-3.

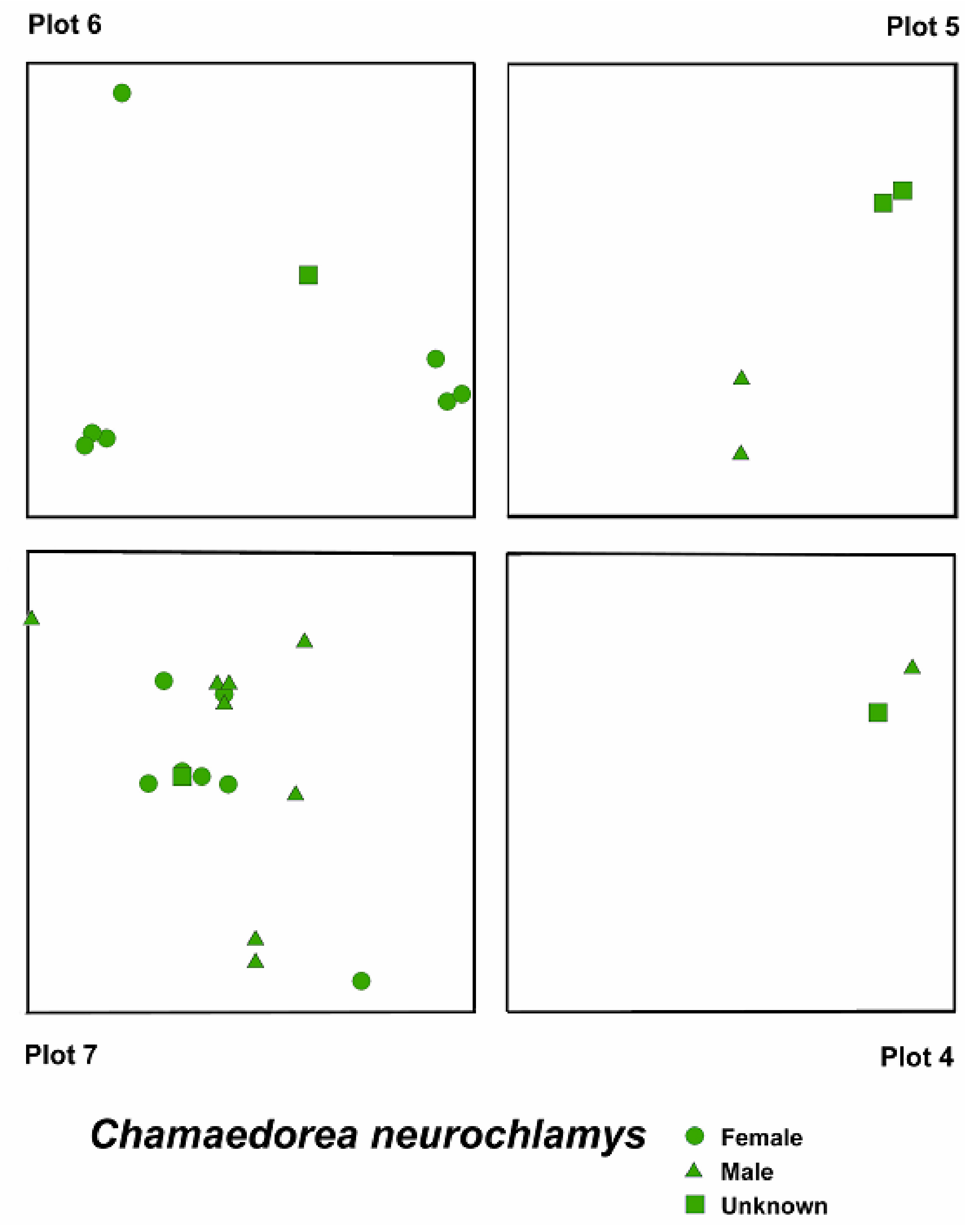


Figure 2.11
Distribution of *C. neurochlamys* within plots 4-7.

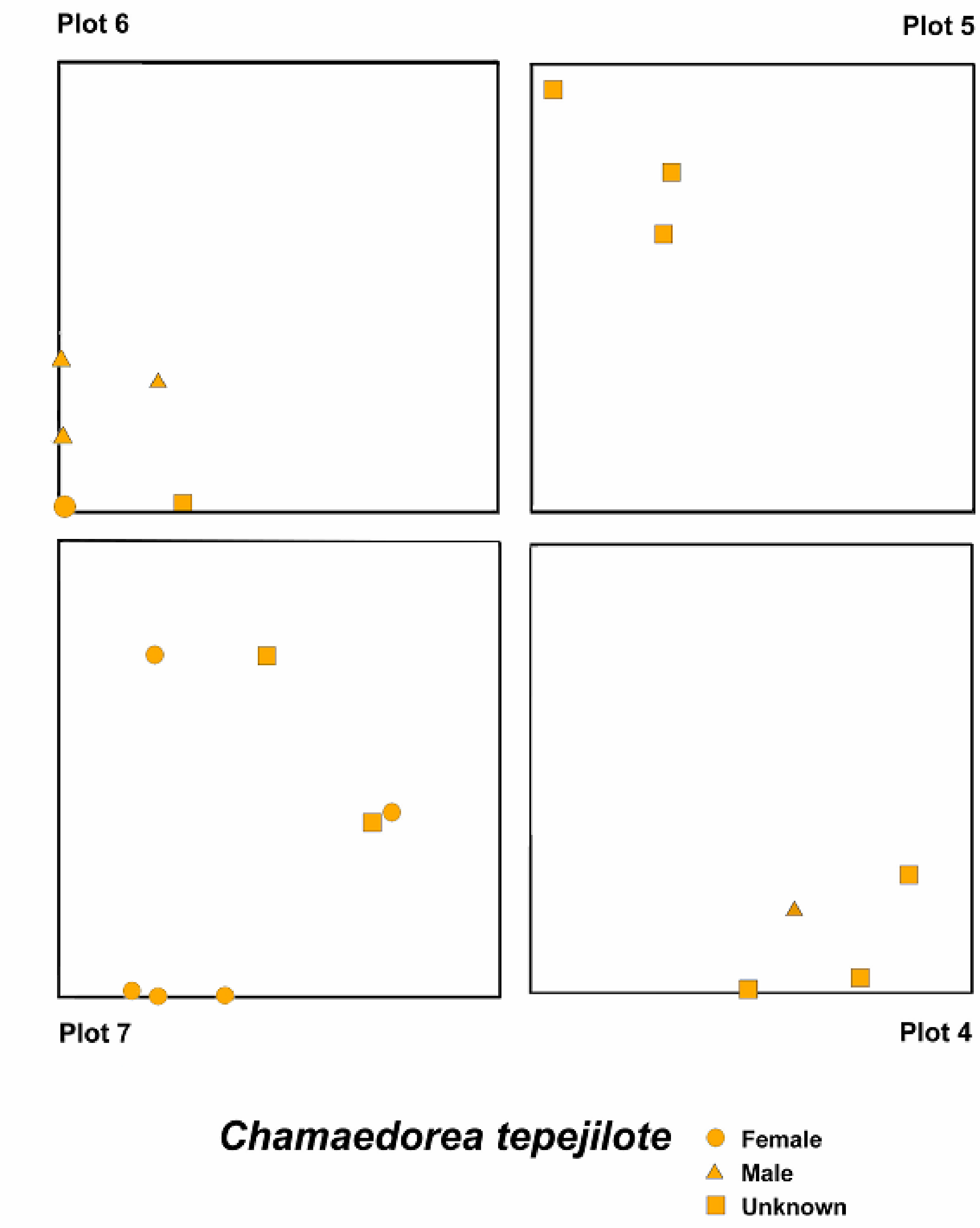


Figure 2.12
Distribution of *C. tepejilote* within plots 4-7.

Chapter 3

Flowering Phenology

3.1. Introduction

Flowering phenology refers to the diverse patterns that characterize flowering activity both within and between taxa. Patterns often vary between species of the same genus (interspecies), within a species (intraspecific), as well as between sexes (if dioecious) or sexual phases (if monoecious) in a species. These patterns also may be distinguished for a particular inflorescence or for all of the inflorescences on a particular individual. Descriptions of flowering patterns are complicated and typically involve a number of factors including the timing, frequency, and duration of flowering, which may influence the reproductive success of a population (Ratchke & Lacey, 1985; Clark & Clark, 1987; Marquis, 1988).

A number of selective factors have been proposed to influence reproductive phenology (Ratchke & Lacey, 1985; Bawa, et al., 2003). These factors include biotic factors, abiotic factors, and phylogenetic constraints (Borchert, 1983; Rathcke, 1983; Wright & Calderon, 1995). The identity and interaction of these selective forces are a subject of controversy due to the fact that so many factors may affect flowering phenology. Thus, it is difficult to isolate and define the effects of any one given factor (Frankie et al., 1974; Rathcke, 1983).

A number of climatic factors such as precipitation, photoperiod, and ambient temperature may be of importance (Rathcke and Lacey, 1985). These abiotic factors have been demonstrated to serve as triggers for flowering (Borchert, 1983; Inouye &

McGuire, 1991). Also, phenological patterns may be affected by a number of biotic factors such as pollinators, seed dispersers, and herbivores. Adaptive flowering responses, which are presumed to be the result of such interactions, have been suggested as key factors in shaping the time of flowering (e.g. Janzen, 1967; Augspurger, 1981). These responses are of great consequence to the ecosystem, as the annual timing of flowering and subsequent fruiting can have a great deal of impact on insect and animal populations by changing the availability of resources such as food and brood sites (Stiles, 1978; Ratchke & Lacey, 1985).

Pollinators may account for some aspects of flowering patterns, as these patterns influence pollinator visitation, survival, and therefore the movement of pollen (De Steven et al., 1987). These interactions are important not only at the individual, but also at the community and population levels. For example, sequential flowering of sympatric species that share pollinators may facilitate the availability of pollinators by providing them with a year-round supply of resources (e.g. nutrients, sites for oviposition) (Waser & Real, 1979; Listabarth, 1996). Additionally, plants may facilitate pollination for all taxa involved when more than one taxon blooms simultaneously such that a large number of plants presenting flowers during the same time period are able to attract more pollinators to a given area than would any of the taxa flowering alone (Rathcke, 1983). A staggered flowering pattern can effectively reduce the competition for pollinators and the chance for interspecific outbreeding that may occur when taxa with shared pollinators flower synchronously (Waser, 1983; Listabarth, 1993). Conversely, synchronous flowering behavior in a group of sympatric species could reflect pollinator spectra that are not shared or are species-specific (Henderson et al., 2000a). Thus, it is important that more research be conducted on phenological patterns and the various factors that influence flowering.

3.1.1. Palm Phenology Studies

Several previous studies have investigated the reproductive phenology of sympatric palm taxa (Beach, 1984; Ibarra-Manríquez, 1988; Bøch, 1996; Listabarth, 1994, 1996; Barfod et al., 2003). The majority of this research has found associations between specific seasons and individual species. However, at the community level, sympatric species typically were found to flower asynchronously with some overlap in flowering periods.

For example, Henderson et al. (2000a, 2000b) examined 10 species of *Bactris* in Brazil. They found the *Bactris* community was not restricted by seasonality, as flowering occurred throughout the rainy season and into the early part of the dry season. The authors also determined that at least one of the *Bactris* taxa studied was in flower at any given time for eight months of each study year, the closest related taxa were the most asynchronous temporally, and individual species had clear seasonal associations.

Another analysis that found no relationship between seasonality and flowering phenology on the community level by Listabarth (1993) observed four taxa of *Geonoma* in Peru. The author found staggered flowering patterns; a pattern wherein the four species flowered at different times of the year (i.e., not synchronously). Again, at the species level, seasonal patterns emerged. One species flowered only during the dry season, another during the wet season, a third from the wet season into the dry season, and the final species flowered during both seasons.

In these and other studies of sympatric species, it is clear that while flowering at the community level often is staggered or with only slight overlap in flowering times, typically individual taxa have seasonal associations (Henderson et al., 2000b). Henderson et al. (2000b) suggest a primary factor affecting *Bactris* flowering is biotic. They contend that different insects, which are available at different times of the year, pollinate different taxa.

3.1.2. *Chamaedorea* Phenology Studies

A study of palm community phenology that included several *Chamaedorea* taxa, was conducted by Ibarra-Manríquez (1988) at Los Tuxtlas, Mexico. Five *Chamaedorea* species (*C. elatior, C. ernesti-augustii*, *C. oblongata*, *C. pinnatifrons*, and *C. tepejilote*) were encountered, and peak flowering and fruiting months for each of the taxa were established. Overall, the peak of *Chamaedorea* flowering occurred during the dry season. However, there were taxa that flowered in the wet season, and scattered individuals were found to flower between the wet and dry seasons as well.

In their study of reproductive phenology of the palm community at Barro Colorado Island, Panama, De Steven et al. (1987) described the phenological patterns of 13 palm taxa over four years. They found that the majority of palms flowered during the rainy season, although some degree of flowering was found year-round. *Chamaedorea tepejilote* (as *C. wendlandiana*) occurred at the study site, and, like the majority of palms at this location, it exhibited a distinct pattern of seasonal flowering. However, unlike most of the taxa studied, *C. tepejilote* began to flower at the end of the wet season and continued through the middle of the dry season. As in the Henderson et al. (2000a) study, the authors suggested that flowering among these taxa is affected by biotic factors, such as the availability of pollinators and seed dispersers.

More specific phenology data is found in the existing studies of *Chamaedorea* pollination. At this time, a total of three studies have been published (Listabarth, 1992; Otero-Arnaiz & Oyama, 2001; Berry & Gorchov, 2004). Listabarth (1992) stated that *C. pinnatifrons* flowered from June through August. Individuals of this taxon therefore flowered in a seasonal manner, during the dry season. The other two studies contained more information, as they included reproductive phenology as one of the research components.

Otero-Arnaiz and Oyama (2001) collected data on the flowering phenology of 440 inflorescences from 62 *Chamaedorea alternans* individuals for a total of 30 days in Mexico. The authors found that the occurrence of anthesis peaked in mid-November, during the dry season. Although staminate and pistillate plants flowered synchronously, there were inter-sexual differences in the number of flowering inflorescences available per study day. Pistillate inflorescences were found to be in anthesis for an average of three times longer than staminate inflorescences. Otero-Arnaiz and Oyama (2001) also determined that staminate individuals produced on average twice as many inflorescences as did pistillate individuals. Therefore, although an equivalent number of staminate and pistillate plants from the study population flowered, the number of inflorescences available every study day was higher for staminate than for pistillate plants.

As one component of their study on the reproductive biology of *Chamaedorea radicalis* in Mexico, Berry and Gorchov (2004) collected data on flowering phenology for two months (the entire flowering period). The phenological stage was recorded daily for 11 inflorescences on eight pistillate plants and 10 inflorescences on four staminate plants. The authors found that, although scattered individuals could be found in flower throughout the year, the majority of flowering occurs from March-June, during the dry season and into the beginning of the wet season. Berry and Gorchov (2004) established that each study individual produced a single inflorescence. Anthesis of staminate and pistillate individuals was synchronous for the majority of the flowering season, and inflorescences of both sexes exhibited basipetal flowering sequences. Although staminate inflorescences were at anthesis for a shorter amount of time than were pistillate inflorescences, the number of staminate flowers per inflorescence was found to be significantly higher than that of pistillate inflorescences. Thus, as the number of staminate flowers greatly exceeded that of pistillate flowers and flowering was not synchronous within a given inflorescence, the authors determined that the total population duration of anthesis was actually three times longer for staminate inflorescences than it was for pistillate inflorescences.

3.1.3. Research Statement

As the first study specifically aimed at assessing the flowering phenology of sympatric *Chamaedorea* taxa, the research described here adds greatly to the previously available knowledge of the taxon's flowering patterns. For the species *C. ernest-augustii*, *C. oblongata*, *C. neurochlamys*, and *C. tepejilote,* the following questions were addressed: (1) Are flowering patterns seasonal or aseasonal? (2) Does flowering phenology vary among these sympatric species in terms of regularity, duration, and synchrony?

3.2. Collection of Phenological Data

In October 2002, monthly collection of phenological data was initiated and continued for 24 months (through September, 2004). Data was gathered from individuals in the seven plots located at the Las Cuevas Research Station (LCRS), Belize. All plots contained *C. ernesti-augustii, C. oblongata,* and *C. neurochlamys,* while *C. tepejilote* was found only in plots 4-7. Although the study plots were established at LCRS in June 2002, field assistants trained in phenological data collection were not available until October 2002, thus the difference in dates between plot establishment and initiation of data collection. Over the study period, 842 inflorescences were followed on 236 individuals. A plant was included in the individual inflorescence count for each month in which an inflorescence reached anthesis, if more than a single inflorescence was produced in succession by an individual.

In each plot, the phenological state of each study individual was recorded either by the principle investigator or one of two local field assistants during the first week of each month. As multiple observers were used to collect the data, extensive training of assistants and an illustrated code key were used to maintain consistency. On a prepared score sheet, the phenological state of each study individual was recorded as a two or three-letter code. One of the following phenological states was recorded monthly for every individual:

(1) Vegetative = no inflorescences or inflorescence buds observed.

(2) Closed inflorescence bud = inflorescence is enclosed by bracts.

(3) Developing flower buds = inflorescence is fully emerged from bracts and flower buds are maturing.

(4) Flowers at anthesis = stigmas are receptive or anthers are dehiscing.

(5) Anthesis completed = anthesis is completed.

(6) Developing fruit = fruit are green and immature.

(7) Mature fruit = fruit are black or red and mature.

Anthesis was characterized as the period of time during which stigmas were receptive for pistillate flowers and anthers were dehiscent with pollen being released for staminate flowers.

To document and quantify flowering phenology of the four sympatric *Chamaedorea* taxa, phenological data was used to calculate several phenological variables. The methodology of De Steven et al. (1987) was followed in the calculation of these measures. Two variables quantified flowering regularity (seasonal regularity and total duration of flowering), while two variables were used to assess flowering synchrony (synchrony of initiation month and mean duration of initiation). For these calculations, flowering was defined as exhibiting receptive stigmas for pistillate individuals and anther dehiscence for staminate individuals. Each study individual was assigned a flowering initiation month, which represented the month in which the first flower reached anthesis for any given individual. In several cases, individuals were not observed in flower, yet were coded as flowering during that particular month. This coding was used when a large inflorescence bud was observed at a monthly census, and at the next census a post-anthesis inflorescence was recorded. Therefore, it was possible to infer that flowering had occurred during the time between censuses.

The phenology variables are defined as follows:

(1). Seasonal regularity – the degree to which a given taxon flowered at the same on a yearly basis. Calculated as the standard deviation around each taxon's peak months of initiation.

(2). Total duration of flowering – the total number of months a taxon flowered each year. Calculated at the levels of individual and population.

(3). Synchrony of initiation month- the extent at which individuals of a given taxon flower together over the course of a year. Each taxon was assigned a mean month of initiation and then this variable was calculated as the standard deviation around each taxon's mean month of initiation. Then, the values for both study years were averaged to create a mean average index of flowering variability for each taxon.

(4). Mean duration of initiation – the average number of months in which individuals of a given taxon were in flower; from the date the first individual flowered to the date the last individual flowered.

Additionally, a regression analysis was conducted to evaluate the relationship between the amount of flowering per month and the rainfall values obtained during the course of the study. The number of individuals flowering served as the dependent variable, while rainfall was the independent variable. An ANOVA was then performed to test the significance of the regression coefficient.

A sample of staminate and pistillate inflorescences of each study species were examined for differences in the relative production of flowers by sex. The number of inflorescences produced was determined, and the number of rachillae and flowers produced per rachillae were quantified. The mean total number of flowers per inflorescence was calculated from the product of rachillae and flower counts. Independent t-tests were performed to test for differences in the number of staminate flowers on a staminate inflorescences versus the number of pistillate flowers on a pistillate inflorescence for each of the study species (Sokal & Rohlf, 1995).

3.3. Results

Climate conditions at the study location are distinctly seasonal, with a dry season that typically runs from (January) February through May (June), and a wet season that typically begins in mid-June, and continues through December (January). The regression analysis determined that there is a significant relationship between precipitation and the number of individuals initiating flowering per month ($F = 20.2$; $p < 0.001$). In total, over the study period, a total of 842 inflorescences were followed on 236 individuals. All four study taxa at LCRS exhibited annual flowering with high seasonal regularity across the two study years (Figure 3.1). Flowering was found to coincide with the end of the wet season and the beginning of the dry season. The *Chamaedorea* community experienced a peak annual flowering period from February through June, with the highest number of individuals initiating anthesis during the months of March and April (Figure 3.2).

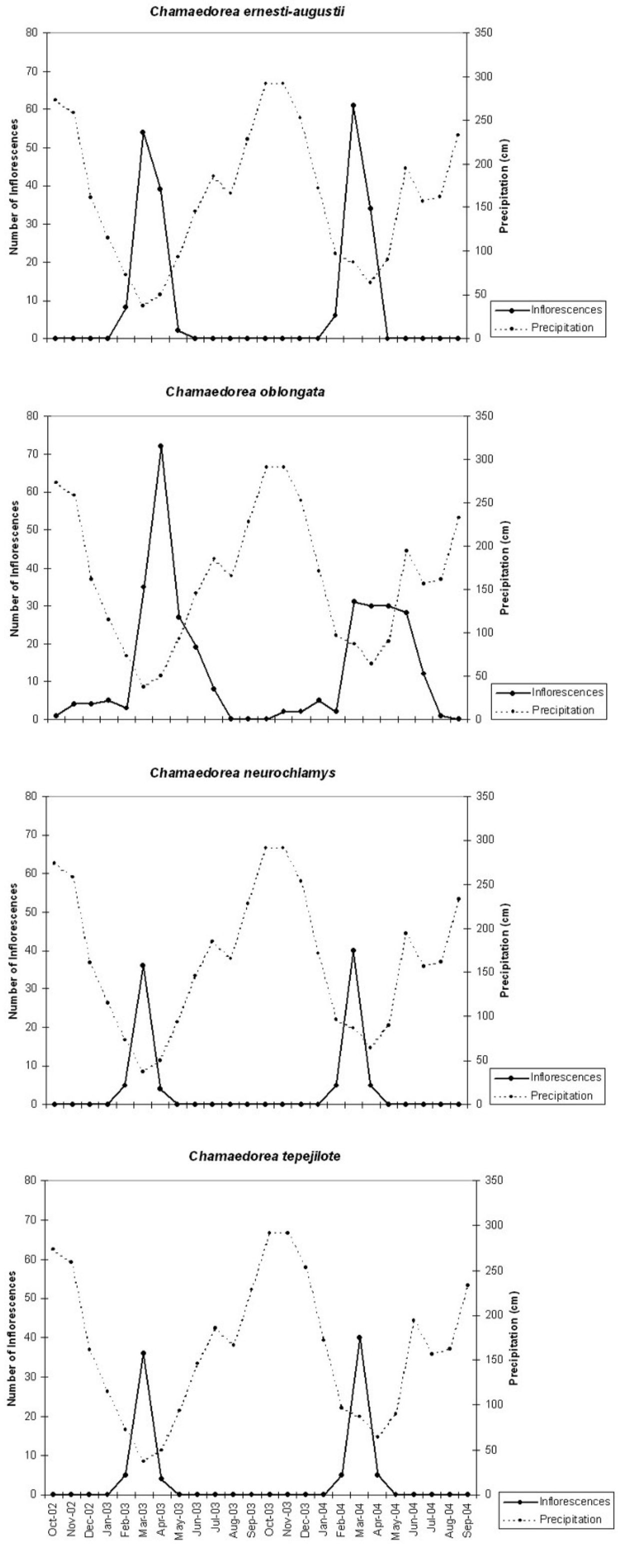


Figure 3.1

Number of inflorescences produced by each of the four *Chamaedorea* study species located in the 20 x 20 meter plots each month from October 2002 – September 2004. The dotted line represents rainfall, while the solid line represents the number of inflorescences that reached anthesis each month.

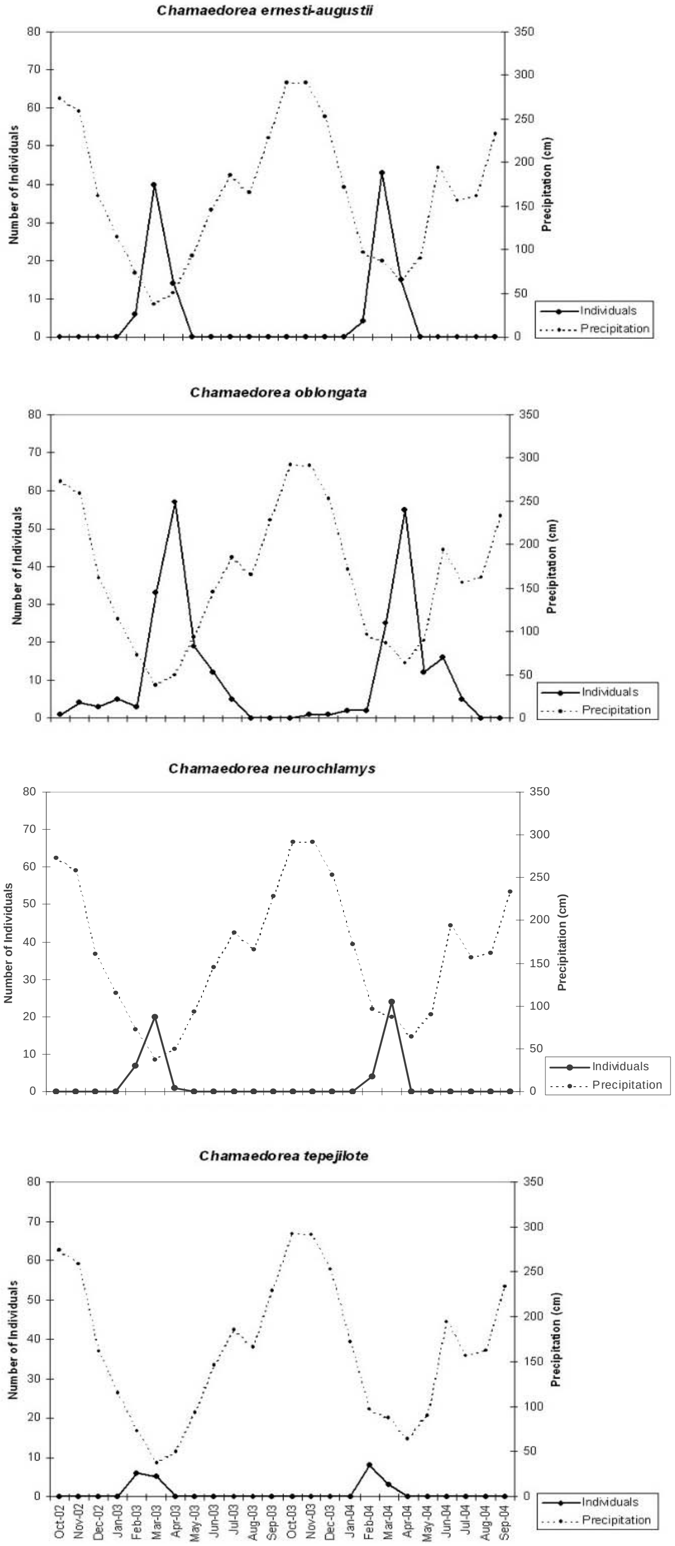


Figure 3.2

Flowering phenology for individuals of the four *Chamaedorea* study species located in the 20 x 20 meter plots each month from October 2002 – September 2004. The dotted line represents rainfall and the solid line represents the number of individuals with inflorescences that reached anthesis each month.

For one species, *C. oblongata*, scattered flowering occurred throughout most of the year. However, flowering in this taxon did peak at approximately the same time as the other three taxa. For each study year, the majority of the flowering individuals initiated anthesis during the driest months, between February and June. For all taxa, staminate and pistillate individuals were highly synchronous in terms of flowering (Figure 3.3).

The phenological data for October 2002-September 2003 indicated that the main flowering period for all four *Chamaedorea* taxa stretched from approximately February through June each year. In year one, 394 inflorescences (94.7%) of the annual total of 416 inflorescences were produced during the main flowering period. During the months of March and April, a total of 300 inflorescences, that is 72% of the total number of inflorescences produced, were recorded at anthesis. In terms of individuals, 223 or 92.5% of the individuals initiated flowering during the main flowering period. During the peak months of March and April, a total of 170 individuals, 70.5% of those that produced inflorescences, initiated flowering activity during those two months.

For the second study year, from October 2003-September 2004, the main flowering period extended from February through July, when 404 of the 426 total inflorescences bloomed (94.8%). Peak flowering occurred in year two during the months of March and April, with 307 (72%) of the inflorescences undergoing anthesis. In year two, 211 or 96% of the individuals initiated flowering during the main flowering period. During March and April, a total of 165 individuals, 75% of the reproductive individuals, initiated flowering.

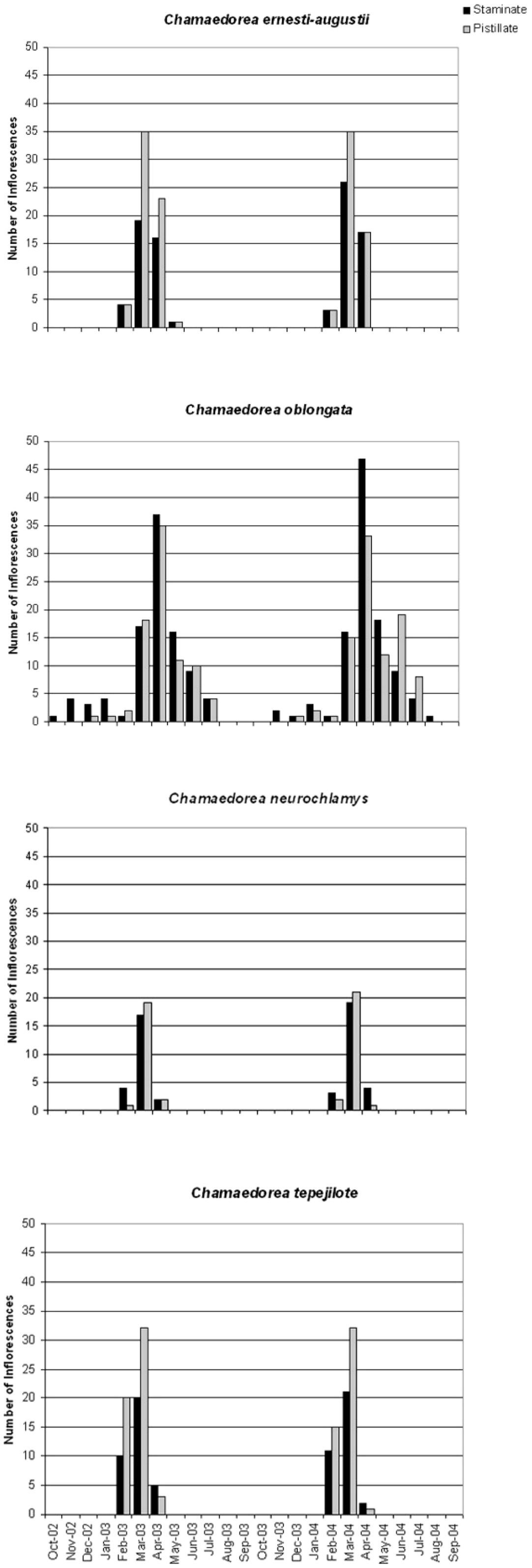


Figure 3.3
Number of staminate (black bars) and pistillate (gray bars) inflorescences produced by the four *Chamaedorea* study species each month from October 2002 – September 2004.

For the value of total flowering duration at the population level (Table 3.1), two taxa, *C. neurochlamys* and *C. tepejilote,* had relatively short total flowering periods (3 and 2.5 months, respectively). A third taxon, *C. ernesti-augustii*, had a duration of 3.5 months, while *C. oblongata* flowered for longest period of time, with a mean duration of 10 months. The total duration of flowering at the individual level was calculated as 1.5 months for *C. ernesti-augustii*, 2.8 months for *C. oblongata*, 1.0 month for *C. neurochlamys,* and 1.3 months for *C. tepejilote*. At the individual level, the staminate flowers of all four taxa were found to be at anthesis for 4-7 days. The pistillate flowers of C. *ernesti-augustii*, *C. oblongata*, and *C. tepejilote* are at anthesis for an average of 7 days, while those of *C. neurochlamys* are at anthesis for an average of 10 days.

All four taxa were found to flower in a highly synchronous manner. In other words, the within-year distribution of flowering initiation by individuals in each taxon was relatively synchronous (Table 3.1). The taxon in which the most individuals flowered together over the year was *C. tepejilote*, and *C. neurochlamys* was the second most synchronous. Both of these taxa flowered over a 2-3 month period during both

Table 3.1 Within-year flowering synchrony, seasonal regularity, and duration of flowering season for *Chamaedorea* taxa at Las Cuevas Research Station, Belize over the 2-year study period (October 2002 – September 2004). All values are expressed in months. A high standard deviation (SD) indicates low synchrony of flowering.

	Flowering Synchrony		**Seasonal regularity**	**Total Flowering Duration**	
Species	**Synchrony of initiation month (mean SD ± SD)**	**Mean duration of initiation**	**SD of peak initiation month**	**Population**	**Individual**
C. ernesti-augustii	0.0 ± 0.0	3.0	0.1	3.5	1.5
C. oblongata	1.4 ± 0.5	9.5	0.5	10.0	2.8
C. neurochlamys	0.0 ± 0.0	2.5	0.0	3.0	1.0
C. tepejilote	0.0 ± 0.0	2.0	0.0	2.3	1.3

study years. The taxon *C. ernesti-augustii* flowered in a similar manner, although the initiation month was slightly less synchronous than that found for the former two taxa. *Chamaedorea oblongata* was found to be the least synchronous, as it flowered over the majority of the year, except during the wettest months. Note however, that the flowers of all four taxa were observed to develop in a basipetal manner. Therefore, although at the population level flowering was reasonably synchronous, flowering within a particular inflorescence did not occur synchronously, instead flowers opened over a number of days.

The second measure of flowering synchrony was the mean duration of initiation of flowering (Table 3.1). This value represents the length of time that it takes for all individuals of a particular taxon to initiate flowering; from the first date that an individual initiated flowering to last date than an individual initiated flowering. It is related to the synchrony of initiation month as follows, where the first variable determines how synchronous individuals in a taxon are with reference to one another on a yearly basis, this variable provides a measurement of the amount of time it actually takes for all of these individuals to initiate flowering. The shortest durations of initiation were found for *C. tepejilote* and *C. neurochlamys*, which initiated flowering over a period of 2 and 2.5 months, respectively. The taxon *C. ernesti-augustii* was not significantly different, with a mean flowering initiation measure of 3 months. Conversely, *C. oblongata* was found to flower over a relatively larger portion of the year (9.5 months).

Finally, it was determined that the number of pistillate inflorescences per month for *C. ernesti-augustii*, *C. oblongata*, and *C. neurochlamys* are approximately the same as the number of inflorescences produced by staminate individuals (Table 3.2). However, as staminate inflorescences contained significantly more flowers than did pistillate inflorescences (*C. ernesti-augustii*, t(48) = 11.37, p < .05; *C. oblongata*, t(44) = 13.638, p < .05; *C. neurochlamys*, t(26) = 18.4, p < .05), more staminate than pistillate flowers are available at any given time during the flowering period (Table 3.3). The only exception to this rule was *C. tepejilote*. In this species, approximately two times as many pistillate inflorescences are produced relative to staminate inflorescences. Nonetheless, as staminate inflorescences produce more than four times as many flowers as pistillate inflorescences, this difference is not likely to have a significant effect on reproduction and is significant (*C. tepejilote*, t(20) = 12.106, p < .05).

3.4. Discussion

The main findings of the phenological research described here are that flowering in the study taxa, which occurs over a limited number of months during the dry season, is highly synchronized at both species and community levels. In comparing these results to those of other studies involving sympatric palm species, these results were quite different from those of Henderson et al. (2000a) and Listabarth (1993), concerning *Bactris* and *Geonoma*, respectively. The palm communities at the other study locations demonstrated relatively staggered flowering patterns, while those at my location exhibited a synchronous flowering pattern. Additionally, both of the other studies reviewed found no seasonality at the community level, yet did find clear seasonality at the species level. For the four sympatric taxa of *Chamaedorea* at LCRS however, a marked seasonality was found at both the community level, as well as at the species level.

Table 3.2 Mean number of inflorescences produced per study individual for staminate and pistillate plants of the four *Chamaedorea* species. Standard deviation (SD), number of study individual in census (N), and range of values also are included. As a clumped palm with >1 stem, values for *C. tepejilote* are per stem, not per individual.

Species/Sex	**Mean ± SD**	**Range**	**N**
C. ernesti-augustii			
Pistillate	1.53 ± 0.84	0 – 4	72
Staminate	1.42 ± 0.85	0 – 3	52
C. oblongata			
Pistillate	0.98 ± 0.78	0 – 3	136
Staminate	1.25 ± 0.74	0 – 4	130
C. neurochlamys			
Pistillate	1.07 ± 0.64	0 – 2	30
Staminate	1.58 ± 0.99	0 – 3	26
C. tepejilote			
Pistillate	10.18 ± 8.63	0 – 11	15
Staminate	5.00 ± 3.00	0 – 30	17

Table 3.3 Mean number of flowers produced per inflorescence for staminate and pistillate plants of the four *Chamaedorea* species. Standard deviation (SD), number of study individual in census (N), and range of values also are included. As a clumped palm with >1 stem, values for *C. tepejilote* are per stem, not per individual.

Species/Sex	**Mean ± SD**	**Range**	**N**
C. ernesti-augustii			
Pistillate	44.44 ± 11.34	16 - 65	72
Staminate	2180.28 ± 1050.51	734 - 4912	45
C. oblongata			
Pistillate	493.65 ± 312.12	47 - 1260	46
Staminate	2141.41 ± 879.95	520 - 4454	41
C. neurochlamys			
Pistillate	443.93 ± 173.74	176 - 807	30
Staminate	3813.69 ± 919.82	2080 - 5238	26
C. tepejilote			
Pistillate	1099.3 ± 309.92	356 - 1452	20
Staminate	5165.4 ± 1469.71	2491 - 7696	20

In terms of the available information specifically regarding *Chamaedorea* phenology, the results from my study are consistent with those recorded by other researchers. In each of the studies for which phenological data is available (DeSteven et al., 1987; Ibarra-Manriquez, 1988; Listabarth, 1992; Otero-Arnaiz & Oyama, 2001; Berry & Gorchov, 2004; Cascante, pers. comm.), the target *Chamaedorea* taxon was found to flowering seasonally, principally during the dry season. In each case, both the species studied, as well as both genders were found to flower during the same period. The results of my research are comparable, with the peak flowering period for both sexes of the four study species occurring during the dry season.

Chapter 4

Pollination

4.1. Introduction

4.1.1. Palm Pollination

The prevailing view for much of the past century has been that palms are primarily wind pollinated. The assumption of anemophily likely arose because many palms have characteristics typically associated with the wind pollination syndrome. These include numerous, small, relatively inconspicuous flowers, which tend to be light in color, and produce smooth, copious pollen (Good, 1956). However, amongst the historical references to palm pollination, there is sufficient evidence to support both entomophily and anemophily (e.g. Seeman, 1856; Delpino, 1870).

For example, Martius (1849), Wallace (1853), and Spruce (1869), suggested that the odor, nectar, and often heat production by palm inflorescences was evidence of pollination by insects. Other authors, such as Kerner (1895), Drude (1889), and Rendle (1904), considered palms to be wind pollinated, largely due to their floral and inflorescence morphology.

To further confuse the issue, several later researchers, including Wettstein (1935) and Kugler (1943), recognized both anemophily and entomophily as primary palm pollination systems. Many of these authors hypothesized that palms exhibit a primitive condition of wind pollination, with derived insect pollination in some cases or a transition from anemophily to entomophily. Unfortunately, the majority of the viewpoints mentioned above were merely theoretical, as detailed studies of palm reproduction were scarce (Tomlinson, 1979).

Over the past few decades, with the introduction of new techniques and methodologies, there has been a steady increase in the number of scientific papers concerning experimental pollination studies (Dafni et al., 2005). The palm family has benefited considerable from this trend, and several papers are published every year, which demonstrate the wide variety of pollination modes within the Arecaceae (Henderson, 2002).

Henderson's (1986) review summarized the emerging literature on palm pollination and stated "extant palms are predominantly entomophilous." He expanded upon this statement in 2002, presenting evidence that although wind pollination does occur (Anderson et al., 1988; Küchmeister et al., 1997), the majority of palms are pollinated by one or more insect visitors including bees (Listabarth, 1993; Feil, 1995; Bøgh, 1996; Hall et al., 2004), beetles (Bernal & Ervik, 1996; Ratsirarson & Silander, 1996; Anstett, 1999), flies (Búrquez et al., 1987; Olesen & Balslev, 1990; Knudsen, 1999), and wasps (Fong, 1987; Jong, 1995; Zakaria, 1997). Additionally, bats have been demonstrated to pollinate at least one species of palm (Cunningham, 1995). These studies have contributed greatly to our understanding of pollination strategies within the family and supported the idea that while some palms are indeed wind pollinated, the majority is primarily insect pollinated.

4.1.2. *Chamaedorea* Pollination

The genus *Chamaedorea* is intriguing because many taxa exhibit characters typical of both wind and insect pollination. Cook (1943a) noted that the members of *Chamaedorea* have two different types of pollen, dry and moist. The dry pollen type is described as light, produced in copious amounts, and easily disengaged from anthers at anthesis. Cook (1943a) suggested that taxa with this type of pollen might be anemophilous. Conversely, the moist pollen type is defined as sticky to the touch, relatively heavy, and typically is associated with flowers that are fragrant, exhibit a more vivid petal color than those with dry pollen, and may exude nectar. These flowers are posited to belong to entomophilous taxa.

Much of the information available on the pollination of *Chamaedorea* is based solely on observations and floral morphology (Spruce, 1869; Cook, 1943b; Barry, 1957; González-Cervantes et al., 1997). For example, Ibarra-Manríquez (1988) suggests that, based on the floral morphology, at least three of the five *Chamaedorea* species present at his survey site are probably anemophilous. In a study of the pollination mechanisms of tropical lowland rain forest trees in Costa Rica, Bawa et al. (1985) similarly concluded that *Chamaedorea tepejilote* (then *C. exorrhiza*) relies on wind as its pollination vector, on the basis of morphological features and observations of floral visitors.

Pollination studies have been published for three species of *Chamaedorea*: *C. alternans* (Berry & Gorchov, 2004), *C. pinnatifrons* (Listabarth, 1992a), and *C. radicalis* (Otero-Arnaiz & Oyama, 2001). All three of the papers concluded that wind is the primary pollen vector, although current *Chamaedorea* and Arecaceae authorities believe the majority of *Chamaedorea* to be entomophilous (Hodel, 1992a; Henderson, 2002).

Listabarth (1992a) investigated the pollination ecology of *C. pinnatifrons* in the Peruvian Amazon. The study provides a detailed description of the floral and inflorescence life cycles for both staminate and pistillate flowers. He also reported the relative abundance and timing of visitation for the main visitors. Listabarth (1992a) identified a number of floral characters that indicated an anemophilous pollination syndrome including copious, powdery pollen, yet several characteristics indicative of entomophily (e.g., fragrance production) were found as well. Determination of a pollination strategy was further complicated by the unusual staminate floral structure, petals connate apically and basally with flowers opening only by lateral slits. Listabarth (1992a) described the pollination mode of *C. pinnatifrons* as "insect-induced wind pollination." He stated that hundreds of thrips and small ptiliid beetles visited the staminate flowers, entering through the lateral slits and their activity facilitated pollen release. The clouds of pollen emitted from flowers either became airborne directly, or pollen settled on the external flower surfaces to be picked up by wind currents at a later time. Listabarth (1992a) concluded that insects are not directly involved in the pollination of *C. pinnatifrons*, yet they are needed to expel pollen from staminate flowers and therefore facilitate wind pollination.

Otero-Arnaiz and Oyama (2001) studied the reproductive biology of *C. alternans* in Veracruz, Mexico. Their conclusions, based mainly on bagging experiments and floral morphology, were that *C. alternans* is anemophilous. In terms of exclusion experiments, Otero-Arnaiz and Oyama (2001) state that they used three treatments: (1) 0.1 mm aperture bags to exclude possible visitors while allowing wind-carried pollen to enter; (2) impermeable bags to test for apomixis; and (3) inflorescences that were not manipulated to serve as a control. These experiments demonstrated that seed production did not differ significantly between the three groups, suggesting anemophily. Although they concluded that wind is the primary pollen vector for *C. alternans*, the authors did state that staminate inflorescences were heavily visited by thrips prior to anthesis. Otero-Arnaiz and Oyama (2001) also suggested that further study might show that these thrips are somehow involved in pollen release. However, in the course of their research, the authors reported no visitors of any type on pistillate inflorescences.

Berry and Gorchov (2004) examined the reproductive biology of *Chamaedorea radicalis* in Mexico. They collected daily data on the developmental stage of flowering individuals. The morphology of pollen, flowers, and inflorescences was examined and compared to known characteristics of both wind and insect pollinated plants. Flowers were observed in the field, as well as fixed and stored for later study with a scanning electron microscope. Glucose test strips were also used to test for nectar production. Bagging experiments were conducted to determine the relative importance of wind and insects as pollen vectors. Pistillate inflorescences were bagged in either a mesh (1.5 mm/aperture) to exclude insects, but not pollen carried by wind, or they were bagged in a smaller mesh (0.5 mm/aperture) to exclude both visitors and wind-borne pollen. Un-manipulated inflorescences were also included as controls. The authors found that fruit set was significantly lower in the exclusion experiments than in the controls. Based on the results of the bagging experiments and the correlation of many morphological characters with an anemophilous pollination syndrome, Berry and Gorchov (2004) concluded that the primary pollen vector for *Chamaedorea radicalis* was wind.

In addition to these pollination studies, information regarding potential pollen vectors can be found in a variety of articles. For example, the work by Fischer and Moore (1977) on the implications of multiple inflorescences in palms is relevant. The authors state that this feature is found in 6 of the 15 major palm groups. While *Chamaedorea* inflorescences typically are solitary at a node, multiplicity of inflorescences occurs in a number of taxa in the subgenus *Stephanostachys*, as well as all of the species in the subgenera *Morenia* and *Moreniopsis* (Hodel, 1992a). This feature is more common in staminate *Chamaedorea* individuals than in pistillate individuals. Fischer and Moore (1977) state that this phenomenon may serve three adaptive functions. First, as inflorescences will develop consecutively, the length of the flowering period is increased. Therefore, an individual plant will exhibit receptive stigmas or shed pollen for many weeks or even months. Second, this pattern will increase the chances that pollen will be removed from staminate plants, or that pistillate plants will receive pollen. Finally, the presence of multiple inflorescences may reduce the overall effect of herbivory on reproduction by providing a large number of structures upon which insect appetites can be satiated.

Uhl and Moore (1973, 1977) also provided evidence for entomophily when they described several structural features that may function in the protection of pollen or ovules. They found that raphide crystals are a common component in the floral structures of many *Chamaedorea* species. These crystals are irritating to predators, as well as some potential pollinators, and it is logical to assume that flowers with these structures host insect visitors. Thus, the authors suggested that these features are associated with insect pollination.

Research by González-Cervantes et al. (1997) on the development of *C. ernesti-augustii* pollen grains also is relevant for pollination studies. Staminate flowers were fixed in FAA, prepared, and examined under a scanning electron microscope. In addition, observations of anthesis were conducted. They found that upon dehiscence, pollen grains were released into the floral cavity formed by the petals; no pollen was observed on the outer floral surfaces. The authors concluded that these observations, along with the presence of a pistillode with a nectar drop, suggests an entomophilous pollination system.

Cook and Doyle (1939) reported on the floral biology and insect visitors to *C. tepejilote* (then *Edanthe veraepacis*). The authors noted that both staminate and pistillate flowers produced a strong fragrance, although no nectar secretion was recorded. They also stated that both sexes were visited by large numbers of thrips. However, insects were not mentioned as possible pollen vectors. Instead, the authors noted that pollen is able to easily sift through the petals for wind distribution. They interpreted the closely packed nature of the male flowers and subsequently narrowed apical openings as an adaptation for anemophily.

Douglas (1988) described effective hand-pollination techniques for taxa in the subgenus *Eletheropetalum*. He described in detail many aspects of floral morphology at anthesis for both staminate and pistillate flowers. Interestingly, Douglas stated that the pollen in this subgenus is dry. The author also noted that although the pollen is transported to some degree by wind currents, the primary pollen vectors are most likely insects. This conclusion is based on the fact that flowers of both sexes tend to be brightly colored (e.g. orange), as well as highly fragrant. In addition, the moist stigmas are not well exposed at anthesis.

Several brief mentions of visitors and general observations also can be found concerning *Chamaedorea* species. For example, Spruce (1869) noted that *C. fragrans* exhibited both brightly colored, orange flowers and a sweet smell during anthesis, characteristics symptomatic of insect pollination. Croat (1978) reported that *Trigona* bees and weevils collected pollen from *C. tepejilote* (then *C. wendlandiana*) in Panama. Moore (1973) called attention to the creamy-white internal color of vertically oriented bracts of *C. robertii* when at anthesis. This visually striking display, in contrast to the deep green of surrounding vegetative organs, along with its highly fragrant flowers, was pointed out as a clue toward an entomophilous breeding system. Finally, Henderson (1986) found that numerous insects, including bees, beetles, and flies, were present at both staminate and pistillate anthesis of *C. costaricana* in Panama. As both sexes produce flowers of a similar color and scent, entomophily was implied. Conversely, Fisher and Moore (1977) described the copious production of dry pollen by *C. alternans*, as did Cook (1943a) who noted that when disturbed, *C. tepejilote* releases “large clouds of white pollen”, suggesting that anemophily may play a role in *Chamaedorea* pollination.

4.1.3. Research Statement

Although the majority of *Chamaedorea* species are posited by leading authorities to be insect pollinated, the three pollination studies that have been conducted on *Chamaedorea* species concluded that those species were wind pollinated. Therefore, the objective of this research was to gather detailed information about the little known pollination biology of this genus. I suggest that many *Chamaedorea* species are primarily entomophilous, while anemophily is likely a secondary pollination system in these insect pollinated species. To test this hypothesis, the reproductive ecology of four sympatric *Chamaedorea* species was investigated in Belize, Central America. The following questions were addressed:

(1) What is the pollination system for each of the study species?
(2) What differences exist between species with respect to floral character, morphology, and floral activity during anthesis?
(3) Are there differences in the identity, diversity, abundance, and behavior of visitors between species?

4.2. Methods

4.2.1. Study Location

Pollination studies were conducted during 3 different visits to the Las Cuevas Research Station over a 2½-year period: May-June 2002, March-July 2003, and March-June 2004. Observations included both palms within seven 20 x 20 m study plots and flowering individuals located within 100 meters of study plots. Due to the potential for disrupting normal fruit set, experimental bagging treatments were performed only on flowering individuals in the vicinity of the study plots.

Four species of *Chamaedorea*, representing four of the eight subgenera in the genus, are included in this study: *C. oblongata* (subgenus *Chamaedoropsis*), *C. ernesti-augustii* (subgenus *Eleutheropetalum*), *C. neurochlamys* (subgenus *Chamaedorea*), and *C. tepejilote* (subgenus *Stephanostachys*). The study species were chosen because they exist sympatrically across the study area. Also, as a group, these species exhibit a variety of floral features and therefore are of interest from a reproductive standpoint.

Many climatic factors may influence both plants and insects because they exert an influence on the timing and duration of flowering, as well as on the presence and behavior of floral visitors (Kearns & Inouye, 1993; Dafni et al., 2005). Therefore, in addition to the precipitation data collected from weather stations throughout the study, supplementary climatological data including temperature, wind speed, and relative humidity were collected simultaneous with insect observations using a Kestrel 2000 anemometer.

4.2.2. Reproductive Phenology

The reproductive stages of individuals in the study plots were followed on a monthly basis for 24 months (October 2002-September, 2004). All plots contained *C. ernesti-augustii, C. oblongata,* and *C. neurochlamys,* while *C. tepejilote* was found only in plots 4-7. Over the two-year study period, a total of 842 inflorescences were followed on 236 individuals. If more than one inflorescence was produced in succession, a plant was included in the individual inflorescence count for each month in which an inflorescence reached anthesis.

During each monthly census, one of the following phenological states was recorded for each study individual:

(1) Vegetative = no inflorescences or inflorescence buds observed.

(2) Closed inflorescence bud = inflorescence is enclosed by bracts.

(3) Developing flower buds = inflorescence is fully emerged from bracts and flower buds are maturing.

(4) Flowers at anthesis = flowers with receptive stigmas or dehiscing anthers.

(5) Anthesis completed = stigmas no longer receptive or pollen completely released.

(6) Developing fruit = fruit are green and immature.

(7) Mature fruit = fruit are black or red and mature.

Anthesis was characterized as the period of time during which stigmas were receptive for pistillate flowers and anthers were dehiscent with pollen being released for staminate flowers (Endress, 1994).

4.2.3. Floral Characteristics and Anthesis:

In order to entice visitors to transport their pollen from anthers to stigmas, plants that are pollinated by insects rely on a number of a number of cues to attract the correct visitors, as well as to advertise the availability of rewards (Endress, 1994). Examples of floral features that attract visitors are color and odor, while the most common floral rewards are nectar and pollen (Faegri & van der Pijl, 1979).

From the plants' point of view, nectar is an ideal substance to offer as a reward. It is easily produced, and can be created quickly as demand requires. From the insects' point of view, this sugar solution is readily digested and quickly assimilated as a source of energy (Kearns & Inouye, 1993). Similarly, pollen is consumed by numerous insects, as it is a highly nutritious and well-balanced food containing protein, sizable amounts of starch, sugars, fat or oil, minerals, antioxidants, amino acids, and vitamins such as thiamin (Kearns & Inouye, 1993). Many plants, therefore, produce pollen in large quantities in order to satiate visitor appetites, while retaining sufficient supplies for potential fertilization.

These stimuli not only influence which visitors are the most likely to be present or absent at an inflorescence, but also may influence behavior once at a flower. For example, the location of rewards such as nectar may direct visitors to specific areas. Additionally, the presence or absence of specific attractants and rewards may determine how much time a particular visitor spends at an inflorescence (Proctor et al., 1996). *Chamaedorea* are especially interesting in this regard, because the genus has a highly diverse floral morphology (Hodel, 1992a). Indeed, the four species of *Chamaedorea* included in this study vary in a number of floral characteristics including flower color, scent, and corolla form at anthesis. Given that an intimate relationship often exists between floral biology and mode of pollination, floral stimuli that may attract different biotic agents and influence their behavior were investigated (Dafni et al., 2005).

The presence of nectar was tested by swabbing floral parts of both sexes with Uristix Test Strips^{TM}, which change color to indicate the presence of glucose in concentrations as low as 2% (Kearns & Inouye, 1993). To detect if floral odors were emitted, freshly picked flowers were isolated in closed glass containers to let the odor accumulate. Containers were opened after 15 minutes and any odor present was described (Kearns & Inouye, 1993). The technique was repeated 2-3 times per day to describe the fragrance, as well as document at what point the odor began, if scent intensity was consistent throughout anthesis, and how long scent lasted.

In some palms, fragrance is accompanied by a rise in temperature. This mechanism, called thermogenicity, is significant as it may promote scent emission and thereby aid in attracting potential pollinators (Henderson et. al, 2000b). To determine if thermogenicity occurs in *Chamaedorea* species, floral temperature was measured using an electronic thermometer with a small diameter probe (Kearn & Inouye, 1993). Temperatures were obtained for flowers of different-aged inflorescences before, during, and after anthesis and recorded as the difference between floral and ambient air temperature (Búrquez et al., 1987; Dafni, 1992).

Floral structure and characteristics may be an important factor in determining its accessibility to different types of visitors and therefore if any visitors are involved in the pollination process. For example, floral structure, such as pistillate flowers with small openings, may bar entry to all but the smallest visitors. Also, sexual organs may be protected to some degree from herbivory by providing alternative food sources such as staminodes and nectar-producing pistillodes (Endress, 1994; Proctor et al., 1996). For these reasons, staminate and pistillate flowers were assessed at various stages of development throughout the floral life cycle to assess floral changes.

The process of pollination involves not only the transfer of pollen from anther to stigma, but also the deposition of pollen on a stigma during its period of receptivity. Anthesis is defined here as the portion of the floral life cycle when pollen is released from staminate flowers and when the stigmas are receptive in pistillate flowers (Kearns & Inouye, 1993). Therefore, knowledge of when stigmas become receptive and how long they remain receptive is an important component of any pollination study. Stigma receptivity of *Chamaedorea* flowers was assessed in two ways: (1) by applying a solution of 3% hydrogen peroxide to pistils from flowers of various ages (Dafni, 1992); (2) by observing a sample of pistillate flowers at two-hour intervals during anthesis for changes such as differences in color and the presence or absence of nectar (Kearns & Inouye, 1993). Photographs were taken throughout the floral life cycle, from flower bud through anthesis to document floral development.

Fresh floral samples were dissected to observe floral morphology and determine changes that occur at anthesis. Flowers also were examined for evidence of structural or anatomical defenses against predation, which may influence insect visitation. For example, calcium oxalate crystals, termed raphides, have been reported to occur in various floral organs of numerous palms (Uhl & Moore, 1973, 1977) and typically function in protecting various floral tissues from predation, which may be caused by potential pollinators (Kearns & Inouye, 1993). Therefore, Uhl & Moore (1973, 1977) have suggested that the presence of raphides is associated with entomophily.

In order to analyze the relative production of flowers by staminate and pistillate individuals, several reproductive palms of each sex were selected during each of the field sessions. For each of these individuals, the number of inflorescences produced during that particular flowering period was determined. Additionally, the number of rachillae and the number of flowers produced per rachillae were quantified for inflorescences from pistillate individuals, as well as from staminate individuals of each study species. Then, the mean total number of flowers per inflorescence was obtained from the product of rachillae and flower counts. Independent t-tests were conducted to test for differences in the number of staminate flowers on staminate inflorescences versus the number of pistillate flowers on a pistillate inflorescence for each of the study species (Sokal & Rohlf, 1995).

4.2.4. Field Observations

At the beginning of each field session, a phenological survey was conducted and those individuals that were close to undergoing anthesis were noted. From this pool, several individuals of each species and sex were randomly chosen for comprehensive observation of visitors throughout the floral life cycle. As the functional unit for attracting visitors in *Chamaedorea* and other palms is the inflorescence (Henderson, 2002), the sampling unit for visitor observations was defined as the inflorescence.

Nocturnal observations were conducted on four occasions, however nocturnal insect activity was very low in comparison to diurnal activity. Therefore, subsequent observations were conducted between the hours of 6:00 a.m. and 6:00 p.m. All pollination observations were carried out on palms either within the study plots or located no more than 100 meters from the study plots.

Observations were conducted during three different field sessions, over a 2½-year period, during which approximately 11 months were spent at the study location (May-June 2002, March-July 2003, and March-June 2004). Insect visitors were directly observed and the sequence of insect visitation, and each visitor's abundance and behavior, was documented for the periods before, during, and after anthesis. During observation periods each individual inflorescence was observed for 12 minutes with 3 minutes in between observations to move to the next chosen individual. Several inflorescences were observed each day, such that each individual was observed every 2 hours. On several occasions, rachillae with visitors still in residence were brought to the laboratory in clear plastic bags to be examined more closely under a dissecting microscope.

In the field, observations were conducted on staminate and pistillate inflorescences of *C. ernesti-augustii* individuals for a total of 124 hours, *C. oblongata* for 133 hours, *C. neurochlamys* 124 hours, and *C. tepejilote* 110 hours. Specimens of each type of visitor observed were collected via killing jar, net, aspirator, or paintbrush, and preserved in 70% ethanol for later identification and examination. Additionally, as potential pollinators were identified, specimens of each were collected and stored individually in vials of 70% ethanol for examination of pollen loads (Kearns & Inouye, 1993).

As the majority of visitors collected were thrips, Dr. Laurence Mound, a thrips specialist from The Commonwealth Scientific and Industrial Research Organisation (CSIRO), Australia, identified all thrips specimens and advised on issues involved Thysanoptera. Insects from orders other than Thysanoptera were sent to the USDA for identification.

Numerous thrips samples were collected in a random manner to determine the sex of thrips on staminate and pistillate inflorescences. To collect the samples, inflorescences were quickly covered with plastic bags and tapped gently to dislodge insect visitor from the flowers. A subset of the thrips from a random sample of these collections was sent to Dr. Laurence Mound to be identified and sexed. As thrips larvae were difficult to quantify due to their small size and ability to fit into tiny spaces, as well as extremely abundant on staminate inflorescences (> 1000), they were not counted, but instead were noted as present or absent. Independent t-tests were conducted to test for differences in the number of male versus female thrips collected from the flowers of each sex during anthesis for each of the four study species (Sokal & Rohlf, 1995).

A considerable challenge to this study was to devise a manner with which to collect thrips along with any pollen they might be carrying. Standard methods for insect collection, such as the aspirator, were not effective due to the extremely small size of these visitors. Aspiration succeeded in collecting the thrips, yet it also picked up any pollen that was located on the surface of flowers and rachillae. It was determined that the best manner to collect a single thrips along with its pollen load and a minimum of loose surrounding pollen was to use a moistened camel-hair brush and place the insect directly into a vial. This method was used to collect thrips during the second and third field visits. A total of 40 thrips were collected for quantification of their pollen loads. Five thrips were caught presumably leaving staminate inflorescences of each study species, and five thrips were caught at pistillate inflorescences, presumably arriving at the inflorescences. Although it was not possible to identify pollen grains to *Chamaedorea* species, the amount of pollen could be counted accurately under a dissecting microscope.

Additionally, adhesive insect traps were placed either directly above, or within 0.5 m of flowering individuals to investigate floral visitors (Figure 4.1A). Insect traps were positioned at two staminate and two pistillate individuals from each of the four study species, for a total of 16 traps (Sticky Thrips Leafminer Trap, Seabright Laboratories, #2541). In theory, the array of insects captured by the traps should reflect, to some degree, the insects visiting the adjacent inflorescences (Webster et al., 2006). After 24 to 48 hours, the traps were removed, taken to the laboratory, and their occupants sorted to order and counted with a dissecting microscope.

4.2.5. Pollination System

Experimental bagging treatments were conducted to determine the pollination strategy of the study species and to assess the potential of any one vector as the primary mode of pollination. For the purpose of these experiments, the measure of reproductive success was fruit set, which is calculated as the percentage of flowers that develop into fruits (Búrquez et al., 1987). Where possible, different treatments were conducted on rachillae from the same pistillate inflorescence or on different inflorescences of a single individual. This methodology was enacted to reduce the presence of confounding factors, such as soil moisture. For each treatment, fruit set of the bagged rachillae, designed to exclude a suspected pollinator, was compared to the fruit set for rachillae that remained uncovered. To test for apomixis, which is defined as reproduction by non-sexual means, in this case embryo formation without fertilization, pistillate rachillae were enclosed in impermeable bags that excluded both wind currents and insect vectors, thereby preventing all pollen access, prior to anthesis (Dafni, 1992).

The potential for entomophily was investigated with two exclusion treatments. To test the efficacy of large visitors as primary pollen vectors, several pistillate rachillae of an inflorescence or entire pistillate inflorescences were enclosed in bags constructed of fine mesh (0.1 mm/100 μm per aperture) prior to anthesis; the ‘small mesh’ treatment (Figure 4.1B). These bags created an effective barrier against large visitors (e.g., bees), while allowing small visitors (e.g., thrips) and air-borne pollen to penetrate and reach the flowers (Scariot et al., 1991; Moog et al., 2002).

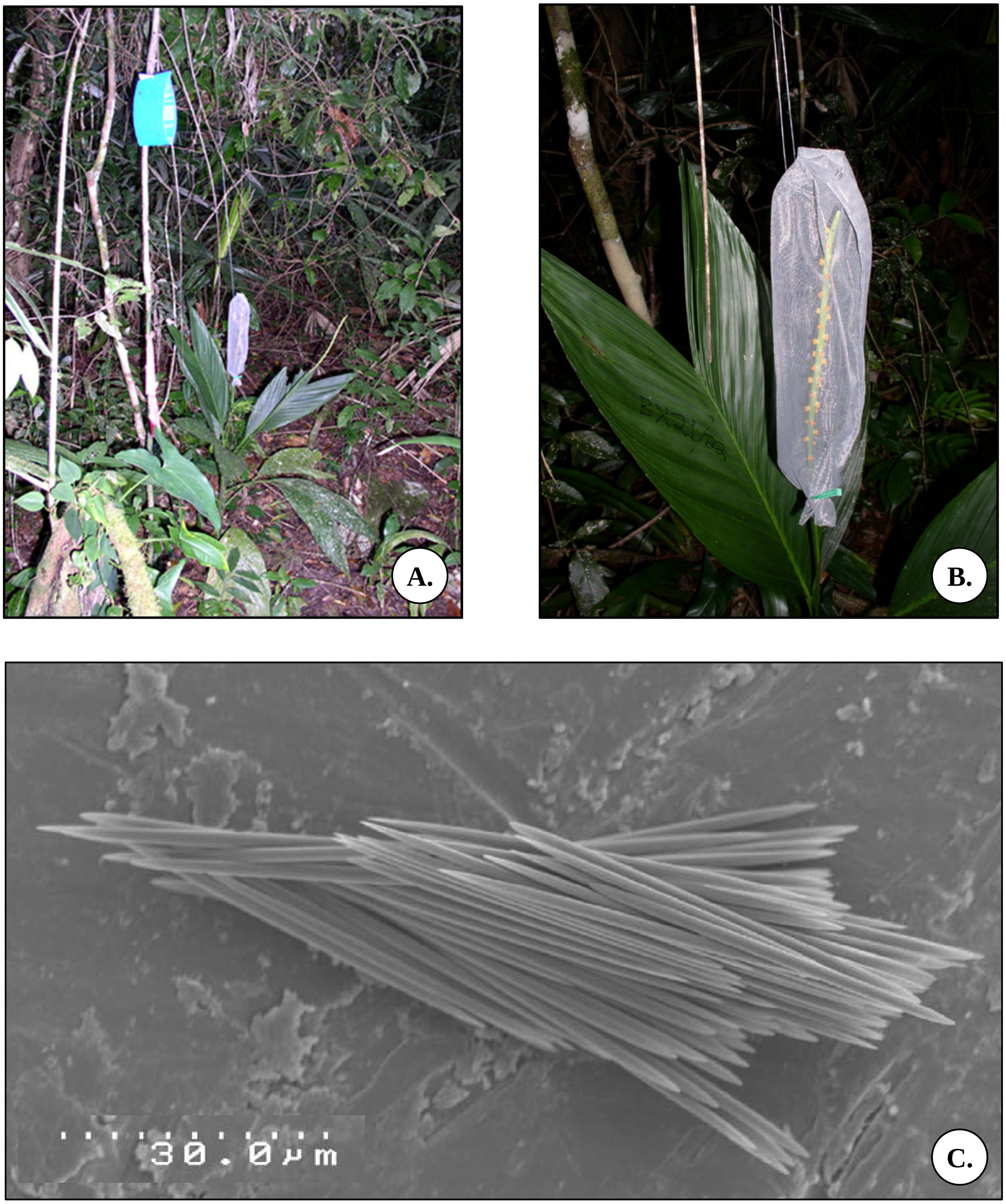


Figure 4.1
A. Sticky trap located above a pistillate individual of *C. ernesti-augustii*. **B.** Small mesh treatment bag on a pistillate inflorescence of *C. ernesti-augustii*. **C.** Scanning electron micrograph of raphides from the anthers of *Chamaedorea oblongata*.

To investigate the role of smaller visitors and wind-borne pollen, pistillate rachillae or inflorescences were covered with pollination bags created from a coarse mesh (1 mm/ 1000 µm per aperture), the ‘large mesh’ treatment. Observations confirmed that these bags allowed all small visitors access to the enclosed flowers, while excluding both air-borne pollen and larger visitors including all bees, large beetles, and large ants (Norstog et al., 1986).

The effectiveness of chosen mesh sizes was assessed by placing bags of each size over inflorescences of each sex, shaking, and removing the bags. Then, the activity of the enclosed visitors was observed as they attempted to exit the bags. This experiment determined which insects were able to move through each mesh size. The coarse mesh bags were found to create an effective barrier against larger visitors including crab spiders (Araneae), chrysophilid beetles (Coleoptera), and sweat bees (Hymenoptera). However, this size mesh did allow smaller visitors including pollen beetles (Coleoptera), staphylinid beetles (Coleoptera), ptiliid beetles (Coleoptera), and thrips (Thysanoptera), as well as air-borne pollen, access to the pistillate inflorescence. The only visitors that were able to move through the fine mesh bags were thrips. Larger visitors, even those only slightly larger, such as staphylinid beetles, were not able to travel through the fine mesh. Although it is likely that the fine mesh reduced the amount of wind-borne pollen that could reach the inflorescence, slides coated with Vaseline that were placed inside of bags for each study species indicated that some pollen passed through the bags.

To determine the effect of excluding air-borne pollen, wind currents were blocked by covering pistillate rachillae with impermeable bags; referred to as the ‘open bag’ treatment. These bags were modified to allow access to small visitors through the underside, by covering this area with coarse (1 mm/1000 µm per aperture) mesh (Stevenson et al., 1998). Upon completion of flowering, the bags were removed and the flowers subsequently scored for fruit set. The bags used were plastic, and this setup was chosen after several different materials, such as cloth and opaque paper, were tested. The clear plastic of the bags appeared to be the most applicable for these experiments, as it allowed light to reach inflorescences and allowed visitors to view the changes in flower color.

Results of each bagging treatment were statistically tested for normality using the Komogorov-Smirnov test (Sokal & Rohlf, 1995). The closed bag treatment was omitted from the analyses, as the fruit set was a constant (zero) for each case when this treatment was applied. The results for all tested treatments were found to be normal. Levene's test was used to determine homogeneity of variance, and therefore the ability to conduct parametric tests (Table 4.1). In each of the bagging treatments, the test statistic was not below 0.05, and therefore it was not possible to conduct parametric tests. As non-parametric tests were necessary, Kruskal-Wallis tests were performed to test if a significant difference existed between treatments. Where warranted, specific Mann-Whitney post-hoc tests with Bonferroni corrected significance levels were performed (Sokal & Rohlf, 1995). Three comparisons were conducted: (1) large mesh compared to control, (2) small mesh compared to control, (3) open bag compared to control. All statistical analyses were performed using SPSS 13.0 (SPSS Inc., 2004).

Table 4.1 Results of Levene's test for homogeneity of variance. For each *Chamaedorea* species, the test was conducted on the fruit set values for each of the bagging treatments. When the significance is below 0.05, non-parametric tests are necessary. Non-significant values are denoted in table as n.s.

Species	**F**	**df**	**Significance**
C. ernesti-augustii	2.081	3	.111 n.s.
C. oblongata	1.972	3	.129 n.s.
C. neurochlamys	1.964	3	.133 n.s.
C. tepejilote	1.662	3	.188 n.s.

In addition to the experimental bagging treatments, pollen traps were used to determine if *Chamaedorea* pollen was transported via wind currents in the understory environment. Microscope slides were coated with a layer of Vaseline and arranged on poles around several pistillate inflorescences (Beattie, 1971). These pollen traps (n = 18) were distributed at distances of 1, 3, and 5 meters from three staminate and three pistillate individuals of each species (Anderson et al., 1988). After 48 hours of exposure, slides were removed and examined for evidence of wind-borne pollen (Kaplan & Mulcahy, 1971; Green & Bohart, 1975).

Pollen was obtained from the bodies of captured insects by a series of agitated alcohol rinses such that *Chamaedorea* pollen could be determined. Samples then were sputter-coated and the pollen was examined using scanning electron microscopes (SEM) at Lehman College, CUNY and The New York Botanical Garden. To facilitate the identification of collected pollen, a collection of *Chamaedorea* pollen was created from individuals in the study area (Kearns & Inouye, 1993).

4.3. Results

4.3.1. Reproductive Phenology

Climatic data confirmed the presence of distinct dry season, running from (January) February through May (June), and a wet season from June through December (January). An analysis of the phenological data for the 24-month study period demonstrated that flowering coincided with the end of the wet season and the beginning of the dry season. Also, the *Chamaedorea* community as a whole exhibited a peak annual flowering period from February through June, with the highest number of individuals initiating anthesis during March and April (see Figure 3.1). In all four study taxa, both sexes exhibited highly synchronous flowering periods. Additionally, the sex ratios of all four species were similar for staminate and pistillate individuals (*C. ernesti-augustii*,1.0:1.32; *C. oblongata*, 1.0:1.06; *C. neurochlamys*, 1.0:1.35; *C. tepejilote*, 1.0:1.2).

4.3.2. Floral Characteristics and Anthesis

The sampling unit for visitor observations was defined as the inflorescence and the relative numbers of staminate and pistillate flowers per inflorescence produced by each species were calculated. The duration of flowering, that is, the floral life cycle including anthesis or pollen dehiscence, is described in the species descriptions sections (4.3.5.1. - 4.3.5.8.). Censuses determined that a similar number of flowering staminate and pistillate individuals were available each month for each of the study taxa during the main flowering period. Also, for *C. ernesti-augustii*, *C. oblongata*, and *C. neurochlamys*, the number of inflorescences per individual was comparable (see Table 3.2). For *C. tepejilote*, the only species with multiple stems, approximately twice as many pistillate inflorescences were produced per individual than were staminate inflorescences (see Table 3.3). Nonetheless, the number of staminate flowers available each month of the peak community flowering period was substantially higher than the number of pistillate flowers for all study species. Therefore, the fact that staminate inflorescences produce significantly higher numbers of flowers than do pistillate inflorescences, based on a series of independent t-tests, confirms that overall, at any point in time during the flowering period, there are more staminate flowers than pistillate flowers (*C. ernesti-augustii*, t (48) = 11.37, $p < .05$; *C. oblongata*, t (44) = 13.638, $p < .05$; *C. neurochlamys*, t (26) = 18.4, $p < .05$; *C. tepejilote*, t (20) = 12.106, $p < .05$).

The following sections describe in detail the floral development prior to and throughout the period of anthesis, as well as the identity and behavior of visitors, for each sex of the four study species. Although there are similarities in many of these descriptions, each species exhibits some degree of variation in morphology and in the identity and abundance of visitors. Therefore, staminate and pistillate inflorescences for each species are described in detail separately in the following section. The most important characteristics for pistillate and staminate flowers for each of the study species are listed in Table 4.2.

Field observations and the timing of stimuli in relation to visitation demonstrated that visitors were attracted to *Chamaedorea* flowers by fragrance cues, as well as by color changes that occurred as the flowers reached anthesis. In all cases, fragrance was emitted throughout flowering, yet its intensity decreased as the flowers aged. Although fragrance emission in some palm genera has been accompanied by a rise in inflorescence temperature (Bernal & Ervik, 1996; Henderson et al., 2000b), no thermogenicity was

Table 4.2 Characteristics of staminate and pistillate flowers for the four *Chamaedorea* species in the 20 x 20 m study plots when flowers are at anthesis. Based on Hodel (1992) and personal observations.

	C. ernesti-augustii	***C. oblongata***	***C. neurochlamys***	***C. tepejilote***
Subgenus	Eleutheropetalum	Chamaedoropsis	Chamaedorea	Stephanostachys
Pollen Type	Moist-sticky	Dry-powdery	Dry-powdery	Dry-powdery
Staminate: Fragrance	Aromatic	Aromatic	Aromatic	Aromatic
Staminate: Color	Bright orange	Yellow to green	Yellow to green	Pale yellow
Staminate: Morphology	Petals curved over stamens at apex	Petals free and spreading to base	Petals connate apically and basally, opening by lateral slits	Petals free and spreading. Flowers densely packed
Pistillate: Fragrance	Aromatic	Aromatic	Aromatic	Aromatic
Pistillate: Color	Bright orange	Greenish to yellow	Yellow	Greenish to yellow
Pistillate: Morphology	Cup-shaped petals curved over stigmas	Petals imbricate Stigma lobes exerted beyond petals	Petals imbricate Stigma lobes exerted beyond petals	Petals imbricate Stigma lobes exerted beyond petals

found for any species of *Chamaedorea*. This result is consistent with previous studies on *Chamaedorea* pollination in that no significant differences were found between the ambient air temperature and that of flowers when measured over the floral life cycle (Listabarth, 1992a; Berry & Gorchov, 2004).

Another feature that was determined to be an attractant in the *Chamaedorea* species studied is the aggregation of male thrips. Although this is actually an attractant produced by the insects, not by the plant, pistillate rachillae were found to provide a popular venue upon which aggregations could occur. Male thrips were found to aggregate in large numbers, and it has been demonstrated that they produce an attracting pheromone, which indicates the availability of mating opportunities to females (Hamilton et al., 2005; Webster et al., 2006). It could be argued that these groupings also are an attractant for male thrips, as they have a better chance of encountering receptive females when participating in an aggregation than they could alone. Similarly, these mating opportunities may be viewed as a reward to both male and female thrips for visiting pistillate inflorescences.

Rewards to visitors of *Chamaedorea* include nectar from the pistillode, stigma lobes, and potentially, septal nectaries. The possibility of septal nectaries occurring in the *Chamaedorea* species studied is based on the fact that septal nectaries have been found in several species of *Chamaedorea* (Berry & Gorchov, 2004; Askgaard, pers. comm.). While their presence is plausible, detailed SEM studies of flowers are still needed in order to determine if septal nectaries do indeed exist in flowers of the study species.

Observations also confirmed that one of the main rewards for both male and female thrips was pollen. However, as some pollen must be retained and not consumed in order for fertilization to take place, the staminate flowers of all four species were found to produce large quantities of pollen. Although copious pollen is certainly a reward for visiting thrips, it should be noted that copious pollen production also is a characteristic attributed to anemophilous flowers (Proctor et al., 1996).

Another reward identified in this research was specifically directed toward female thrips. The thrips were found to lay eggs in the staminate flowers of all four study species, and in the pistillate flowers of *C. ernesti-augustii*. In addition to providing brood sites, these flowers also reward thrips with readily available food for the developing larvae, in the form of floral tissues and pollen, (Kirk, 1996).

Although the potential of staminodes as supplying visitor rewards in the form of food sources or nectaries was investigated, it is unlikely that this occurs. The staminodes were found to be relatively small, in comparison to stigmas, or lacking altogether. They also appeared to be functionless, as visitors were not observed specifically investigating or collecting nectar from them. However, it must be noted that the staminodes tend to be tiny and in close proximity to the large stigmas. Therefore, it was difficult under the available laboratory and field conditions to determine if staminodes were indeed producing nectar.

A final floral feature assessed in this study is not considered an attractant or a reward, but instead a deterrent. Scanning electron micrographs of pollen and associated floral debris from the staminate flowers of all four study species confirmed the presence of raphides (Figure 4.1C), which may function as a defense against predation (Kearns & Inouye, 1993). Within the confines of this study, it was not possible to determine the exact structures from which these crystals were isolated, and therefore further investigation is required.

4.3.3. Environmental Characteristics

As described in Section 4.3.1, all four study species began to flower at the end of the wet season and continued into the dry season. During this period, the typical day was slightly cool in temperature until approximately 7:00 – 8:00 am, and then became warmer as the sun began to move directly overhead. The midday hours were warm to hot and sunny, at times light rains occurred in the early afternoon for an hour or two. It was noticeably cooler in the late afternoon, and very cool by the time that the sun went down, usually between 5:00 pm and 5:30 pm.

The average temperature during the hours of highest insect visitation (9:00 am – 1:00 pm) was 28.49° C ± 3.69° C (n = 35). Average humidity during the same hours was 74% ± 14.18% (n = 35). Additionally, high humidity may increase the density of pollen grains, thus lowering the potential for wind pollination (Whitehead, 1983; Kearns & Inouye, 1993). These data are also significant with regards to the most abundant visitor, thrips. Thrips require medium to high humidity in order to survive, typically this indicates a relative humidity in the range of 70%-75% (Lewis, 1973). Additionally, they do not fly when it is dark, preferring instead to remain inside flowers or in other enclosed areas until the sun is out and light intensity is high (Lewis, 1973; Kirk, 1996).

Wind speed values are an especially important measurement for this study, as it is has been suggested that little wind reaches the understory, therefore decreasing the chance of anemophily (Whitehead, 1983). It was determined that the average wind gusts during insect visitation were 0.57 kt (SD = 0.17 kt, n = 35), while the maximum wind gusts were measured at 1.27 kt (SD = 0.39 kt, n = 35). These wind speeds are enough for wind dispersal of pollen, especially pollen that is small and dry in nature.

In addition, the fact that *Chamaedorea* individuals tend to occur in dense stands and thereby have a clumped distribution (see Chapter 2), suggests that pollen flow between individuals is not as restricted as previously believed and supports the possibility that some degree of anemophily may occur (Bawa, 1990). An important criterion of wind pollination is small, dry, relatively smooth pollen, and the *Chamaedorea* pollen of the species studied measures between 20-35 µm; the typical range for anemophilous species is 20-40 µm (Whitehead, 1983). Also, for the *Chamaedorea* species studied, all except *C. ernesti-augustii* exhibit dry, powdery pollen (Figure 4.2A). Only the pollen produced by *C. ernesti-augustii* is found to be sticky. The potential insect pollen vectors, thrips, take flight easily in still to breezy air, and therefore the recorded wind speeds pose no limitations to thrips flight. Thrips are only deterred by extremely high wind velocities, primarily of speeds in excess of 35 kt (Lewis, 1973).

4.3.4. General Field Observations

Although detailed descriptions of the visitors to both staminate and pistillate flowers of each species follow, a few general field observations may be made. First, the most abundant period of insect visitation occurred during daytime hours, especially mid-morning into the early afternoon, from approximately 9:00 am–1:00 pm

Observations at night found very low visitor activity. Nocturnal visitors included spiders, ants, and a few crickets, the latter of which were observed only prior to anthesis. Thrips were present in the staminate flowers of all four species, as well as the pistillate flowers of *C. ernesti-augustii*, after petals began to open and prior to anthesis. However, no movement between flowers or plants was observed during the dark, cool nights, as thrips preferred to remain inside the flowers. These observations are consistent with those of other researchers who have found that the highest density and activity of thrips occurs during the daytime (Lewis, 1973; Kirk, 1996; Kiers et al., 2000; Terry et al., 2005).

4.3.5. Species Descriptions

For each of the four study species, inflorescence buds develop at stem nodes over a period of several months to one year prior to flowering activity. A large number of the inflorescence buds that develop do not survive until anthesis (32%-85%, n = 232), instead dying prior to reaching 3 cm in length (pers. obs.). Those that do survive grow larger (Figure 4.2B), and after two to three months on average, split open apically to reveal the rachillae clustered inside (Figure 4.2C).

Over the course of the next several weeks, the rachillae change color from pale yellowish-green to green, increase in diameter, push out of the bract, and spread out (excepting spicate *C. ernesti-augustii* pistillate inflorescences). This process occurs in both the staminate and pistillate inflorescences of *C. ernesti-augustii*, *C. oblongata*, and *C. neurochlamys*. Although pistillate *C. tepejilote* inflorescences progress similarly, the staminate ones develop in a different manner, which is described below.

Once rachillae have spread to their full breadth, a few more weeks are required for the tiny dark areas, visible from the time that rachillae are released from the inflorescence bracts, to develop in to flower buds, and for the flower buds to develop to the point that anthesis occurs. The average amount of time for each of these processes is summarized in Table 4.3 for each sex of the study species. Additionally, the visitors observed at each sex and species are listed in Table 4.4.

Table 4.3 Average time elapsed between the opening of inflorescence buds and the start of anthesis for staminate and pistillate inflorescences of each *Chamaedorea* species. Weeks to emerge = amount of time needed for rachillae to release from inflorescence bract and spread out; Weeks to develop = amount of time needed for flower buds to develop, this phase ends at anthesis.

Species/Sex	Weeks to Emerge	Weeks to Develop	Total Weeks
C. ernesti-augustii			
Pistillate	4-6	3-4	7-10
Staminate	2-3	5-6	7-9
C. oblongata			
Pistillate	3-4	3-4	6-8
Staminate	2-3	3-4	5-7
C. neurochlamys			
Pistillate	2	2	4
Staminate	2	2-3	4-5
C. tepejilote			
Pistillate	1-2	2	3-4
Staminate	NA	NA	NA

4.3.5.1. *Chamaedorea ernesti-augustii*: Staminate

4.3.5.1.1. *Chamaedorea ernesti-augustii*: Staminate Floral Development

While the first activity associated with flowering occurs when the inflorescence bract splits and rachillae begin to emerge, the emphasis here is on the development of flowers from bud through anthesis. By the time that the staminate rachillae have reached their final size and length, they are perpendicular to the rachis, yet not completely straight. Typically, each rachilla is somewhat pendulous, curving down slightly from the middle portion to the apex (Figure 4.3A).

Flower buds occur in loose spirals a few centimeters from one another, and are slightly sunken into shallow depressions in the rachillae. The small flower buds, which

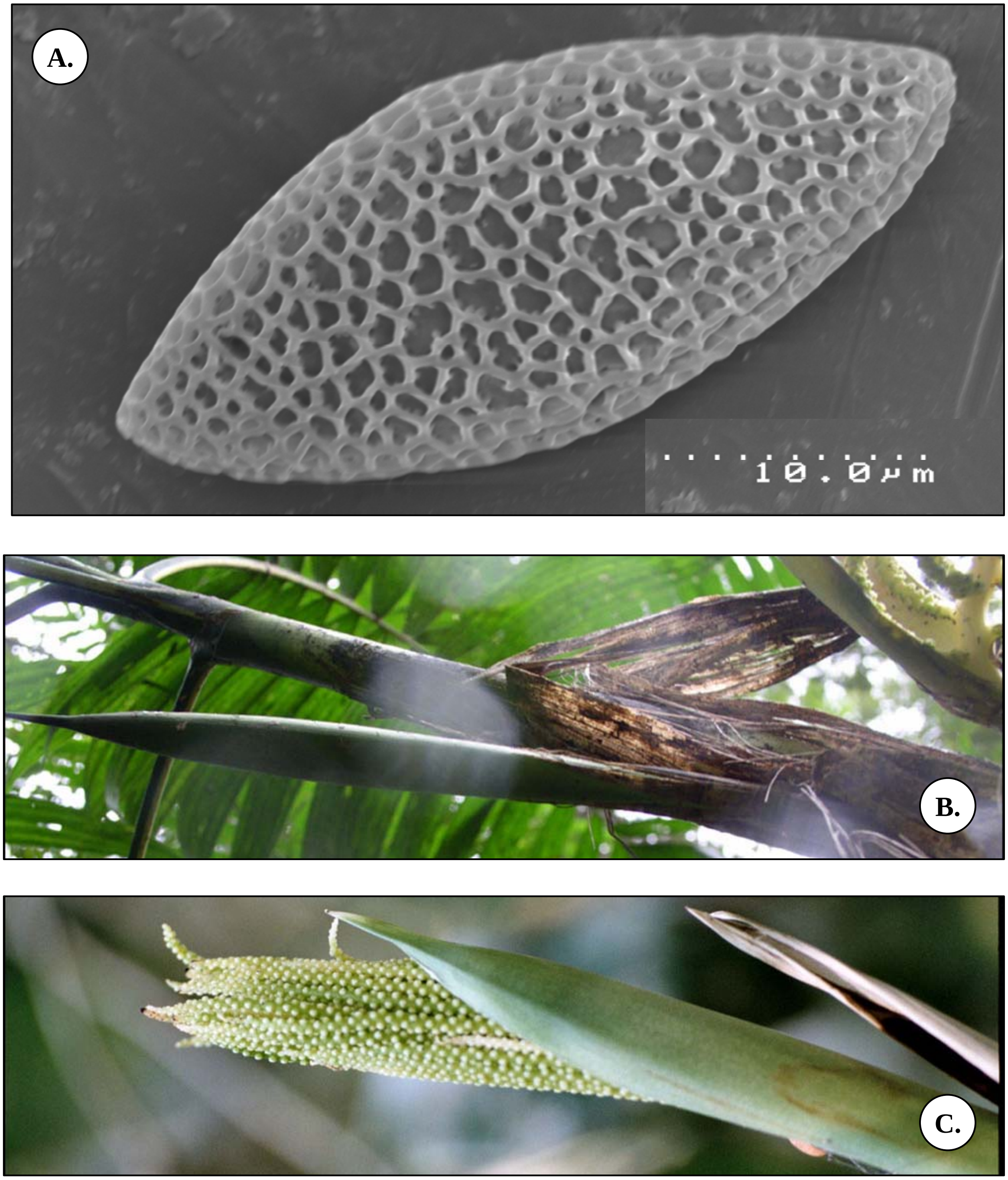


Figure 4.2
A. Scanning electron micrograph of *C. oblongata* pollen grain. **B.** Two closed inflorescence buds of *C. tepejilote*. **C.** Open inflorescence bud of *C. oblongata* with rachillae emerging.

Table 4.4 Relative abundance of visitors collected at staminate and pistillate inflorescences of *Chamaedorea* spp. at Las Cuevas Research Station, Belize. Abbreviations: ER = *C. ernesti-augustii*; OB = *C. oblongata*; NE = *C. neurochlamys*; TP = *C. tepejilote*. Presence and abundance of visitors is indicated as follows: rare (-); common (+); abundant (++); not recorded (°).

	Pistillate Inflorescences				**Staminate Inflorescences**			
Order/Family	**ER**	**OB**	**NE**	**TP**	**ER**	**OB**	**NE**	**TP**
Thysanoptera								
Thripidae	++	++	++	++	++	++	++	++
Hymenoptera								
Halictidae	+	+	+	+	+	+	+	+
Formicidae	+	+	+	+	+	+	+	+
Braconidae	-	-	-	-	-	-	-	-
Chalcididae	-	-	-	-	-	-	-	-
Hemiptera								
Cicadellidae	°	-	-	°	-	-	-	-
Araneae								
Thomisidae	-	-	-	-	+	+	+	+
Archaeognatha								
Machilidae	°	-	-	°	°	-	-	°
Coleoptera								
Curculionidae	°	-	-	-	-	-	-	-
Coccinellidae	°	-	°	°	-	-	-	-
Chrysomelidae	°	-	-	-	-	-	-	-
Nitidulidae	°	-	-	°	+	+	+	++
Cleridae					-	-	-	-
Cerambycidae	-	-	-	-	-	-	-	-
Staphylinidae	°	°	°	-	-	-	-	++
Diptera								
Drosophilidae	-	-	-	-	+	+	+	++
Syrphidae	-	-	-	-	+	+	+	++

are visible as rachillae assume their final orientation, appear only as white areas. As they develop, the white calyx continues to be the most prominent feature, with a growing red triangular aperture at the center of the flower. Over time, the dark red corolla becomes more visible and rises up past the level of the sepals (Figure 4.3B).

As anthesis nears, the large, dark red to red-orange flower buds exhibit a tri-lobed appearance, sitting just above the rachis on top of the collar of white sepals (Figure 4.3C). The parting of petals begins at their apices and it typically takes one to two days for petals to open from apex to base. As the petals part, their color changes gradually until it is a bright, almost fluorescent, orange. At this point, the pistillode is the most prominent feature and occupies the majority of the open triangular space between petal apices. The anthers remain inside of and below the height of the petals. From the time that the petals begin to part, a sweet to somewhat fruity fragrance is noticeable. Although it is faint at first, the aroma becomes very strong by the time the anthers dehisce. Additionally, floral development is highly dependant upon the position of flowers on individual rachillae and the position of those rachillae. This is because anthesis is basipetal at both the inflorescence and rachillae levels.

When the anthers dehisce, the petals have opened such that they are thick, fleshy, and bright orange in color, not in contact with one another, free apically, and arch slightly over the stamens. The pistillode is hyaline to whitish, exerted beyond the petals approximately 1 mm and expanded apically, where it is flat. Nectar is present on the pistillode as confirmed by tests with Uristix Test Strips^{TM}. In the day or two after anthesis begins, the anthers are highly visible, as approximately half of them extend such that they are exerted slightly and lie in the spaces between the petals (Figure 4.3D).

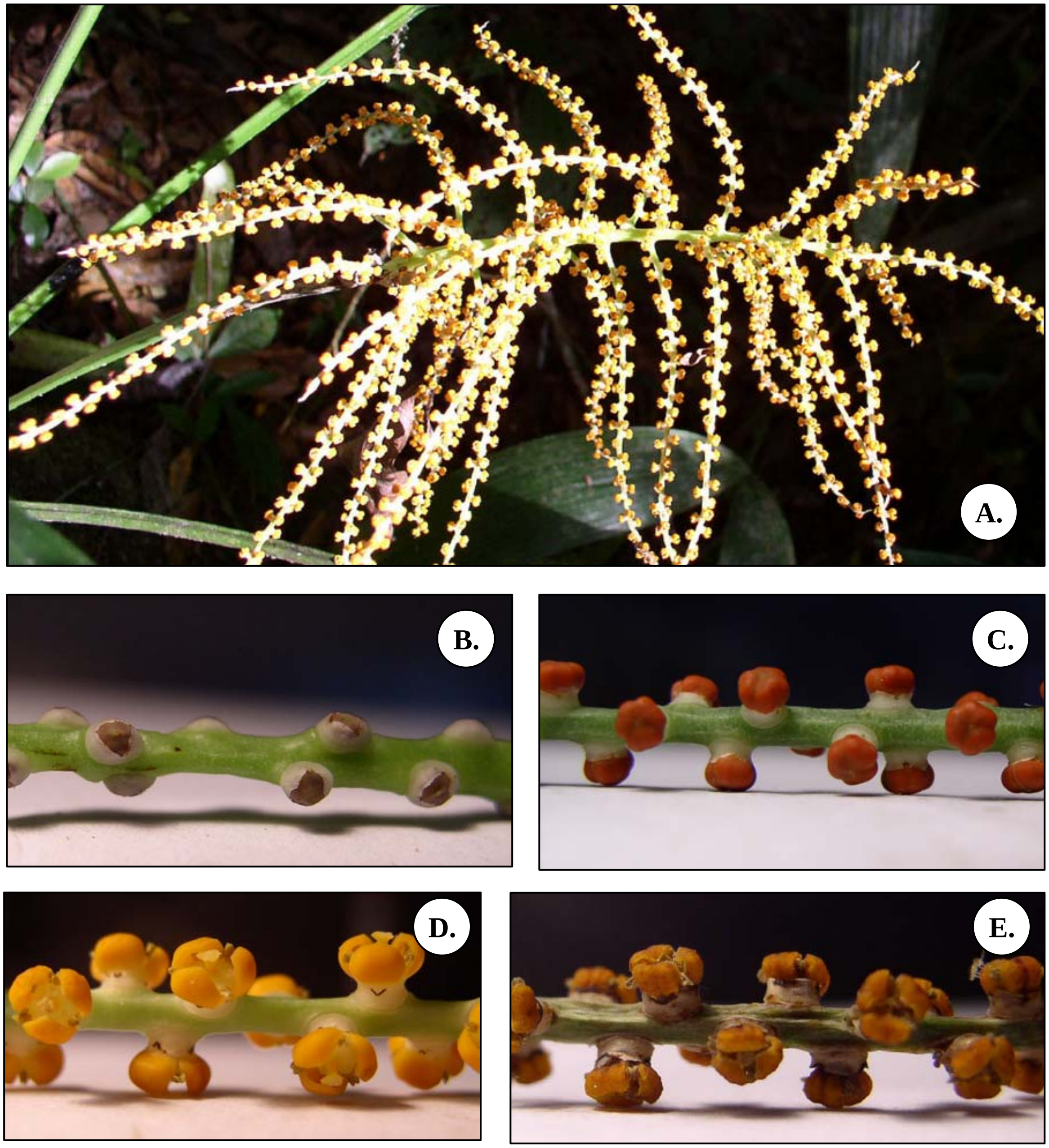


Figure 4.3
Development of staminate *C. ernesti-augustii*. **A.** Inflorescence with flowers in early anthesis. **B.** Small flower buds showing white calyx and dark red corolla in center. **C.** Large, tri-lobed flower buds with ring of white sepals. **D.** Open, bright orange flowers at anthesis, with anthers visible between petals and prominent pistillodes. **E.** Petals change color from bright to dark orange after anthesis as the flowers dry up and lose their fleshy nature.

As dehiscence occurs, the majority of pollen grains are released into the floral chamber formed by the petals. With the release of pollen, the anthers begin to change from white to brown as they dry. The flowers are highly fragrant during peak visiting hours, typically between 9:00 am - 1:00 pm, which also are the warmest hours of the day.

By approximately the third day after the onset of anthesis, the petals begin to change color from bright orange to dark orange and lose their fleshiness as they lose moisture (Figure 4.3E). This process will continue over the next two to three days as the remainder of pollen is shed. Also, the rachillae lose their plumpness as they too dry out. The attracting odor becomes weaker as anthesis progresses, and when the petals have dried up, tests demonstrate that the pistillate no longer produces nectar. When anthesis is complete, the dried, brown flowers often remain attached to their rachillae, although strong winds or falling branches may knock some to the ground.

4.3.5.1.2. *Chamaedorea ernesti-augustii*: Staminate Visitation

From the time that the petals first begin to part, insects can be found visiting staminate inflorescences. At this point, the flowers are dark red to reddish-orange in color, the anthers are intact, and the white apex of the pistillode fills the triangular aperture created at the center of the flower. A sweet but faint fragrance is emitted. Although the space between petals is small (~1mm), large numbers of thrips squeeze through these openings to enter the flowers. Thrips are not only the first visitors, but also the most abundant visitors throughout the life of the inflorescence. The primary thrips activity at this point in the floral life cycle appears to be oviposition, based on the fact that pollen is not yet available, and examination of flowers under a dissecting microscope reveals eggs implanted in the fleshy petal tissues. Within four days of their first opening, thrips larvae can be found inside flowers. After pollen becomes available, thrips activity includes not only ovipositing, but also visiting staminate inflorescences to feed on pollen.

For thrips, the majority of their time is spent inside of flowers, especially in the cooler morning hours. When a flower is touched, on average two to five thrips will emerge from the openings between its petals. As it gets hotter and the sun hits the inflorescences, more thrips are seen moving from flower to flower. They tend to visit several flowers, spending at least 3 minutes in each flower they enter. Thrips censuses conducted between 10:00 a.m. and 12:00 p.m. typically yield more than 50 individuals per rachillae. This is the period of highest thrips visitation. As the sun goes down and the temperature drops, so too does the number of thrips drop. Thrips are rarely observed on rachillae after 5:00 - 6:00 p.m., although some do remain inside of flowers overnight. This behavior pattern continues over the next two to three days while the petals continue to separate and develop a bright orange color.

It is interesting to note that at least half of the thrips visitation occurs prior to anther dehiscence, when the flowers are still relatively closed. However, in most inflorescences, pollen will still adhere to them, as anthers have often been opened by insect activity. This fact was confirmed by capture and examination of thrips leaving staminate flowers early in the floral life cycle. By the time that the flowers are open, with petals fully parted, the interior visible, and the anthers dehisced and exserted, thrips tend to occur in lower numbers. Therefore, they presumably prefer flowers that exhibit relatively closed corollas.

In addition to thrips, staphylinids are early guests to staminate inflorescences. They visit in far lower numbers however, with no more than three observed on a single inflorescence at any given time. Conversely, bees can be found in high numbers throughout the floral life cycle and constitute the second most abundant visitors. At least two species of bees investigate the inflorescences; yet do not remain for long periods of time when the petals are just beginning to separate. Bees are likely attracted to the fragrance and the developing orange color. They are observed collecting nectar from the pistillodes (Figure 4.4A). Later, after anthers have dehisced, numerous bees (up to 12 on a single inflorescence) of several species visit to gather pollen in the 'baskets' on their hind legs (Figure 4.4B). They may remain at an inflorescence for up to 30 minutes, moving from flower to flower and visiting flowers on several rachillae before departing. Bees can be found on the inflorescences throughout the day, digging in anthers to extricate pollen. This behavior occurs in all but the most extreme weather conditions. Regardless of whether they are present in the early or later period of anthesis, the bees tend to prefer those flowers that have opened to the greatest extent.

Other prominent visitors are ants of at least three species. Ants have been recorded in higher numbers on staminate inflorescences of *C. ernesti-augustii* (typically > 50 over the floral life cycle) than on any of the other study species. Unlike bees, ants do not appear to be interested in the anthers; instead the typical ant arrives and remains outside of the flower, standing on the petals to probe the pistillodes of several flowers before departing (Figure 4.4C). As the flowers open and anthers begin to dehisce, initially on flowers at the apex of the inflorescence, both ants and bees become more numerous and the overall volume of insect visitors increases dramatically. This increase is due to the striking and highly visible display of bright orange flowers, as well as the increase in fragrance intensity. As the temperature continues rises throughout the morning, a variety of visitors arrive including bees, ants, beetles, wasps, flies, and spiders. Thrips are in residence, yet in somewhat lower numbers than prior to anther dehiscence. Although many of the visitors, including ants and bees, will become dusted with pollen after it has been released from the anthers, they visit pistillate flowers in such low numbers and so rarely contact stigmas that they are not considered primary pollinators.

Wasps, flies, beetles, and spiders were all recorded as minor visitors but few transported pollen to the pistillate inflorescences. Each of these insects was observed throughout the peak visitation hours in medium (when anthers dehisce) or low (prior to or days after anther dehiscence) numbers. Wasps also were observed at inflorescences, although they did not appear to be interested in the pollen. It is presumed that they visit in order to find prey to parasitize (Jon Martin, pers. comm).

When the anthers dehisce, flowers begin to dry out, and petals become drier and less fleshy. During this period, the main visitors are ants and bees. However as the petals become even drier and more reduced in size, the ants and bees are not as abundant as flies. Flies are present throughout the floral life cycle, from the time that the flowers open and petals are free, through the drying of flowers. However, they are the most numerous and often the only visitors found at flowers that are a few days past complete pollen removal.

A variety of beetles visit the staminate inflorescences including those from the following families: Cleridae, Coccinellidae, Curculionidae, Nitidulidae, and

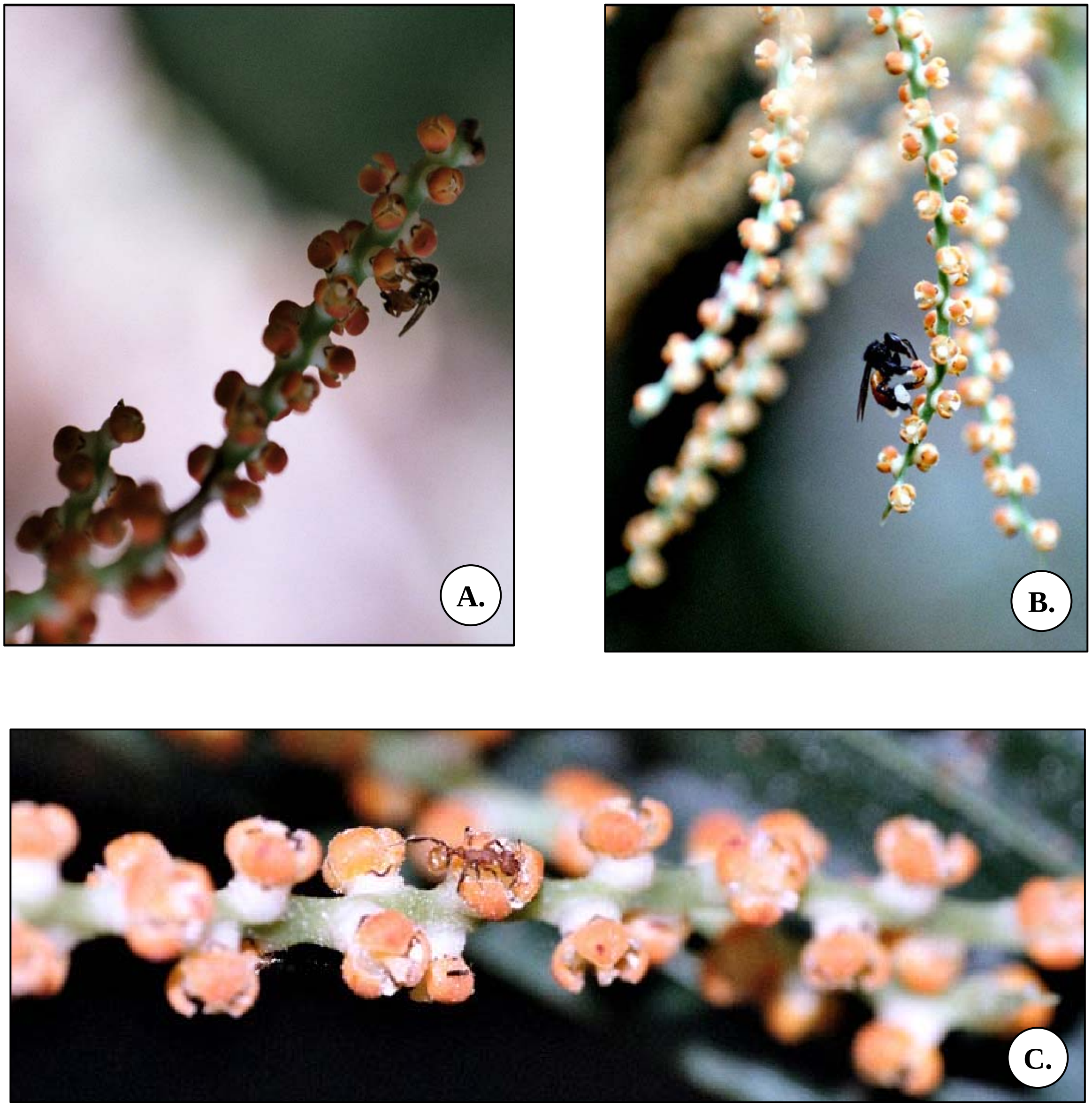


Figure 4.4
Visitors to staminate *C. ernesti-augustii*. **A.** Sweat bee collecting nectar from pistillode. **B.** Sweat bee collecting pollen, note the pollen in baskets on the bee’s rear legs. **C.** Ant probing flower. Thrips also are visible.

Tenebrionidae. Beetles move from flower to flower, feeding on pollen and floral tissues. They are observed from the time that the petals are fully open and the anthers have dehisced. Conversely, they are rare during the late stages of the floral life cycle, when pollen has been dispersed and the flowers are rapidly drying.

Spiders arrive at inflorescences either prior to or on the day that petals begin to part. Up to eight spiders can be found on a single inflorescence. Only crab spiders were observed to visit and they typically remain in a single location throughout their tenure on an inflorescence. Spiders were not observed entering flowers or touching reproductive organs, but instead were located on the rachis, rachillae, or rarely, on the exterior portions of the petals, waiting for prey.

4.3.5.2. *Chamaedorea ernesti-augustii*: Pistillate

4.3.5.2.1. *Chamaedorea ernesti-augustii*: Pistillate Floral Development

The pistillate inflorescences of *C. ernesti-augustii* develop somewhat differently from the pistillate inflorescences of the other three study species. They are typically spicate, unlike the other species, which have inflorescences with many rachillae. Rarely pistillate *C. ernesti-augustii* inflorescences have 2-4 rachillae. Yet, within the general vicinity of LCRS (~3 ha.), only four such individuals were encountered.

The inflorescence bud is slender. When it reaches its full length of approximately 9-12 cm, the end of the bract splits open and the white rachis begins to emerge (Figure 4.5A). At this point, the areas where flowers will develop are evident as dark red circles spaced at intervals much further apart along the rachis than those of staminate inflorescences. Also, they remain either flush with the rachis or slightly sunken into the rachis. Thus, while the inflorescence is developing, it is possible to see the elliptical areas where flowers will be located.

After the rachis has extended fully from its bract, it increases in width and changes from white to light or medium green in color. The petals begin to be visible at the center of each elliptical area, where a three-lobed group of dark red petals can be seen pushing up through the white sepals (Figure 4.5B). Grooves or lines where the petals will part become more and more obvious as the flowers develop. The small buds are dark red in color and they remain dark red to dark reddish-orange until anthesis. In fact, in most cases, the petals will begin to open while flowers are still dark red in color (Figure 4.5C). Peroxidase tests show that the stigmas are not yet receptive when flowers have petals relatively dark in color and petals only slightly parted.

The flowers located closest to the apex of the rachis tend to be larger and more developed than those at the basal portion and anthesis occurs in a basipetal fashion. It is not uncommon for the apical flowers to begin receiving visitors into their open flowers a few days prior to the time that basal flowers begin to open. It takes approximately 3 days for all of the flowers to fully open and become bright orange.

In comparison to those of the other three sympatric species, *C. ernesti-augustii* possesses the thickest petals. However, the biggest difference in these pistillate flowers lies in their morphology. This species is the only one in this study in which insects are required to enter the flowers in order to effect pollination. At anthesis, the stigmas are not exposed outside of the petals and are situated in the floral cavity created by the bases of the 3-4 mm long petals (Figure 4.5D). Therefore, they stigmas can only be accessed by moving deep into the flower.

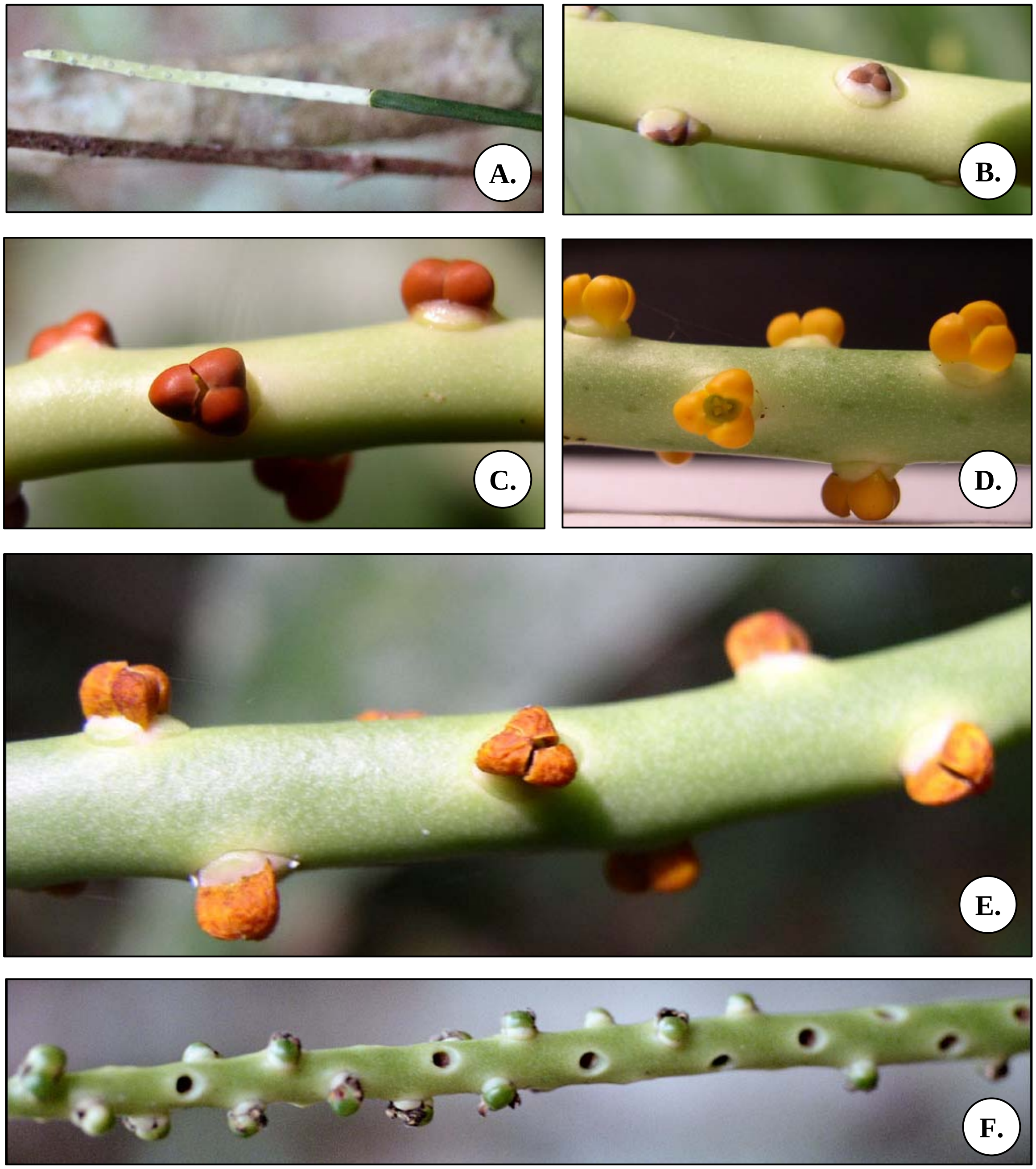


Figure 4.5
Development of pistillate *C. ernesti-augustii*. **A.** Inflorescence, just emerging from bract. **B.** Small flower buds, a three-lobed group of dark red petals can be seen pushing up through the white sepals at the center. **C.** Large, dark red flower buds, with petals just beginning to open. **D.** Bright orange flowers at anthesis with white stigmas visible inside. **E.** Post-anthesis flowers with thin, brittle petals and dried sepals. The drying petals curl inward and cover the interior of the flower. **F.** Developing fruit are visible pushing up past the remnants of petals and sepals.

By the time that they are open to their full extent, the petals are free at their apices and most of the way to the base, where they are valvate basally for approximately the bottom one-third of their length. Additionally, the petals have become bright to almost fluorescent orange in color. This color is quite striking against the green of the rachis and leaves, as well as the browns and greens of the surrounding forest. Peroxidase tests at this point confirm that the stigmas are receptive. Also, tests for nectar demonstrate that sugary exudates are being produced by the stigmas and possibly elsewhere. I was not able to determine if the nectar came entirely from the stigmas, or if some also is produced by the staminodes. A strong, sweet fragrance is emitted during the entire time that the stigmas are receptive. Typically, the scent is noticeable, but weak, when the first flowers turn orange, but it gains in strength as the flowers open and change color and more flowers open up. Neutral red tests indicate that the fragrance is primarily produced at the tips of stigmas, as that area is heavily stained. However, the scale-like staminodes located just outside of the stigma lobes also stain red and therefore are involved in odor and/or nectar production.

Both the petals and the flower itself are raised up off of the rachis and sit atop a collar of white sepals. When viewing flowers from the top, the moist stigmas are visible, although they are not distinguishable when a flower is observed from its side. The stigmas are large, triangular, and white to hyaline. Typically, the stigmas are receptive for 3 to 5 days.

As anthesis nears its end, the petals begin to dry out, a process that will continue for approximately a week. The fragrance becomes weaker and eventually ceases to be emitted. Concurrently, the stigmas change in color from white to dark brown, and ultimately to black, signaling the end of anthesis. Also, the stigmas cease to be receptive and no nectar is detected. The petals become progressively darker, moving from bright to dark orange, then to reddish-orange, to red, and then finally to black. Having lost much of their size, the flowers with their thin, brittle petals and dried sepals now constitute about half the size that they were at anthesis. Additionally, the petals curl inward as they dry, once again covering the flowers' interiors (Figure 4.5E). Many flowers fall off the rachis as they dry. Within a week after the flowers dry out, those that have been fertilized are obvious, as their swollen ovaries push up past the remnants of petals and sepals (Figure 4.5F). Eventually, any flowers that were not fertilized will fall off the rachis, leaving a shallow elliptical depression.

4.3.5.2.2. *Chamaedorea ernesti-augustii*: Pistillate Visitation

As described above, the primary difference between the pistillate flowers of *C. ernesti-augustii* and those of the other study species is that visitors enter into the floral chamber created at the base of the petals. This is not possible in the other study species, as the petals are tightly appressed to the large stigmas and thus no floral chamber exists. Therefore, any insect that would serve as a pollinator must enter the flower and move to the base of the petals in order to make contact with the stigmas.

The most abundant visitors by far are thrips, which constitute approximately 95% of the visitors to an inflorescence. As soon as the petals begin to crack open on the first flower, thrips arrive (Figure 4.6A). Thrips are most active just prior to and in the early stages of anthesis and are found in their highest numbers during the sunniest parts of the day. Thrips are rarely found in flowers that are bright orange and fully open. They appear to prefer the dark red to dark orange flowers that have only slightly parted petals. Therefore, when the flowers nearest to the rachis' apex open their petals, an activity that occurs before those at the base, the basal flowers experience high rates of visitation. At times thrips begin to visit when the openings between petals are so small they are the only insects able to enter the flowers. By 9:00 a.m., dozens of thrips can be observed on a single inflorescence of average size. An estimate of the number of thrips that visit an inflorescence is no less than 100 and typically betweem 500 to 600 individuals. This quantity is, of course, dependant on both the size of the inflorescence and number of flowers it produces.

After entering the pistillate flowers, female thrips feed on stigmatic exudates and oviposit inside of the flowers, planting their eggs in the bases of the thick, fleshy petals. The resultant larvae can be found in flowers and crawling on the rachis 5-6 days after flowers have begun to open (Figure 4.6B). Thrips are easily observed moving from flower to flower, however at least 50% of the visitors are inside of the flowers at any time. Typically, they remain inside of one of more flowers for the majority of their stay at an inflorescence. The thrips that are not inside of flowers tend to aggregate on the rachis, presumably for mating (Figure 4.6C). Although it often is not possible to see into the floral interior during the highest period of thrips visitation, several thrips leave each flower when the inflorescence is shaken. When they are prepared to leave an inflorescence, thrips will move to the top of the rachis, or they take flight from the petal apices.

Thrips abandon the apical flowers as their petals part further, and they visit instead those flowers that are located in the middle and basal portions of the inflorescences, which are in the process of opening. It takes approximately 3-4 days for all of the flowers on an inflorescence to open, and thrips are observed each of these days on the youngest flowers during daytime hours.

As the flowers open and turn bright orange, other visitors may be observed at inflorescences including ants, sweat bees, beetles, flies, and crab spiders. When the majority of the inflorescence has bright orange flowers with open petals and the scent is at its strongest (about 2-3 days after petals begin to part), ants are often seen as visitors. Ants walk up the inflorescence and move from flower to flower, probing for nectar. Although several of those collected did carry pollen, it was a small amount of pollen, and typically no more than fifteen ants are seen over the inflorescence life cycle.

More numerous than ants, between 20 and 25 sweat bees are observed throughout an inflorescence's flowering cycle. Due to their size, sweat bees typically do not enter the flowers, but instead stand on the petals and put their heads in the flowers to collect nectar (Figure 4.6D). They tend to visit two or more flowers, and often alight on an inflorescence, probe inside a flower, leave, hover above the inflorescence, and then fly down to visit a different flower. As with ants, the sweat bees do carry pollen, but the majority of their pollen is located in the baskets on their back legs. They tend to only put their heads into the flowers, and although they do have small amounts pollen on their heads, their contribution to pollination is probably minimal.

Visitation by beetles is rare, with no more than five observed during the flowering of an inflorescence. Also visiting in low numbers, a few parasitic wasps may be found at inflorescences when flowers are most open. Only twice were flies observed on pistillate

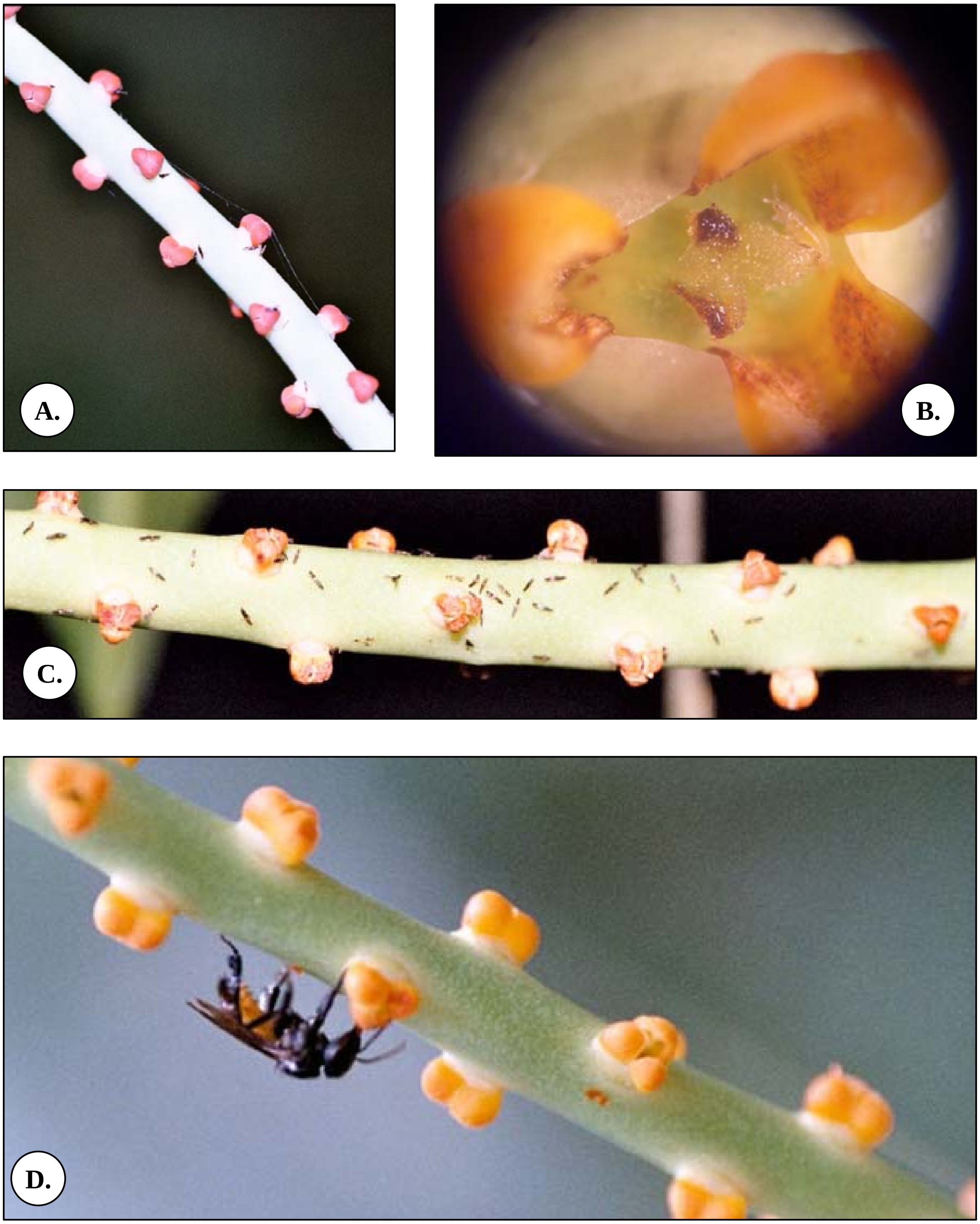


Figure 4.6

Visitors to pistillate *C. ernesti-augustii*. **A.** As petals begin to open on the first flowers, thrips arrive at the inflorescence. **B.** Flower (x 20) with a newly-hatched larva visible inside. **C.** Thrips aggregated on rachis. **D.** Sweat bee visiting flowers at anthesis.

inflorescences. None of these insects (beetles, wasps, or flies) were observed inside of pistillate flowers or in contact with stigmas. In contrast to their abundance at staminate inflorescences, only one or two crab spiders visited a pistillate inflorescence over the floral life cycle. Presumably, the amount of prey was too low to attract larger numbers of spiders.

4.3.5.3. *Chamaedorea oblongata*: Staminate

4.3.5.3.1. *Chamaedorea oblongata*: Staminate Floral Development

When the staminate rachillae have assumed their full size, they are spread out slightly from the rachis for few centimeters and then become pendulous from the middle to the apex (Figure 4.7A). Anthesis will occur basipetally, with the flowers on both the topmost rachillae and those at the apex of each rachillae opening first. The flower buds occur in dense spirals, and are positioned every few centimeters, however they do not touch one another.

As anthesis approaches, flower buds change in color from dark to light green or greenish-yellow (Figure 4.7B). At this point, they have three obvious grooves where the three petals will part. Also, the flower buds are plump, appearing almost ready to burst open, and sit atop a green collar of sepals. Sepals are approximately 2-3 mm in height, and the apex of each is distinctly white in color.

The closer they get to opening, the lighter in color the petals will become. This change in color begins at the base of the petals and moves to the top. Even before flowers begin to open, many have a band of yellow at the petal bases. However, some flowers never become yellow, but instead remain light green or greenish-yellow until they begin to dry. The thick petals begin to part at the apex and over the next 1-2 days, they spread apart slightly down to their bases. When they are completely free from one another, the petals' curved shape creates a chamber at the base of the flower's interior.

The prominent, apically-lobed, light green pistillode is visible through the opening at the center of the flower. It is only slightly shorter than the height of the petals. The stamens, composed of large, light yellow to white anthers with short, green filaments, are also exposed, as they lie just inside of the petals. It will take 3-4 days for all of the flowers on an inflorescence to open their petals. A fragrance is emitted from the time that the first petals begin to part. This fragrance is pleasant and can be described as somewhat musty, yet sweet, and it becomes progressively stronger and as more of the flowers open their petals.

Three or fours days after the petals separate, the anthers dehisce (Fig. 4.7C). Similar to all aspects of floral development, the beginning of anthesis occurs in a basipetal manner. It is important to note that some anthers may have been ruptured prior to dehiscing due to insect activity. Throughout the dehiscence period, the flowers are strongly fragrant, particular from mid-morning to early afternoon. As they open, the stamens lie both between and inside of the petals (Fig. 4.7D). Typically, a few of the anthers are exerted past the petals, while the remaining ones open within the cupped portions at the interior base of the petals. At the apex of the pistillode, nectar may be observed approximately one day prior to anthesis, and it will remain until 2-3 days before the flower abscises.

After the anthers dehisce, the petals begin to dry. This is visible, as petals become dark green or black first at their apices and margins and then down to their bases. As they lose moisture, they become less fleshy and somewhat less curved, and move further apart from one another (Fig.4.7E). The white anthers also begin to dry out and take on a brownish tinge. At this point, they are the most prominent aspect of the flower and they occupy most of the space inside the flower. At the onset of anthesis, the pistillode is highly visible, yet it loses volume as it dries and becomes brown to black in color. Finally, the fragrance that began to be emitted when the flowers opened, weakens progressively, until it is unnoticeable as the flowers dry. The drying process will take approximately three days. When they are completely dry, the flowers are dark green to black in color, the pistillode is shriveled and blackish, and the petals are spread out and open to an angle of a 45 degrees from the base of the flower (Fig. 4.7F). At this point, many flowers still have pollen available. Within one week, the majority of flowers will fall off, leaving only the thin, brittle, dark brown rachillae hanging from the plant.

4.3.5.3.2. *Chamaedorea oblongata*: Staminate Visitation

As was observed with the other species, thrips are the most abundant visitors to the staminate inflorescences of *C. tepejilote*. They begin to arrive the first day that the petals begin parting. Those rachillae with opening flowers tend to have 25-50 thrips, with the majority of the visitors congregating inside a small number (~35%) of the flowers that have their petals parted a few millimeters. No more than five thrips at a time may be found in a single flower. At this point, the flowers are greenish-yellow to yellow and the large unopened anthers are visible in the openings between the petals from the sides of the flowers. Although not yet dehisced, a few of the anthers have been ruptured

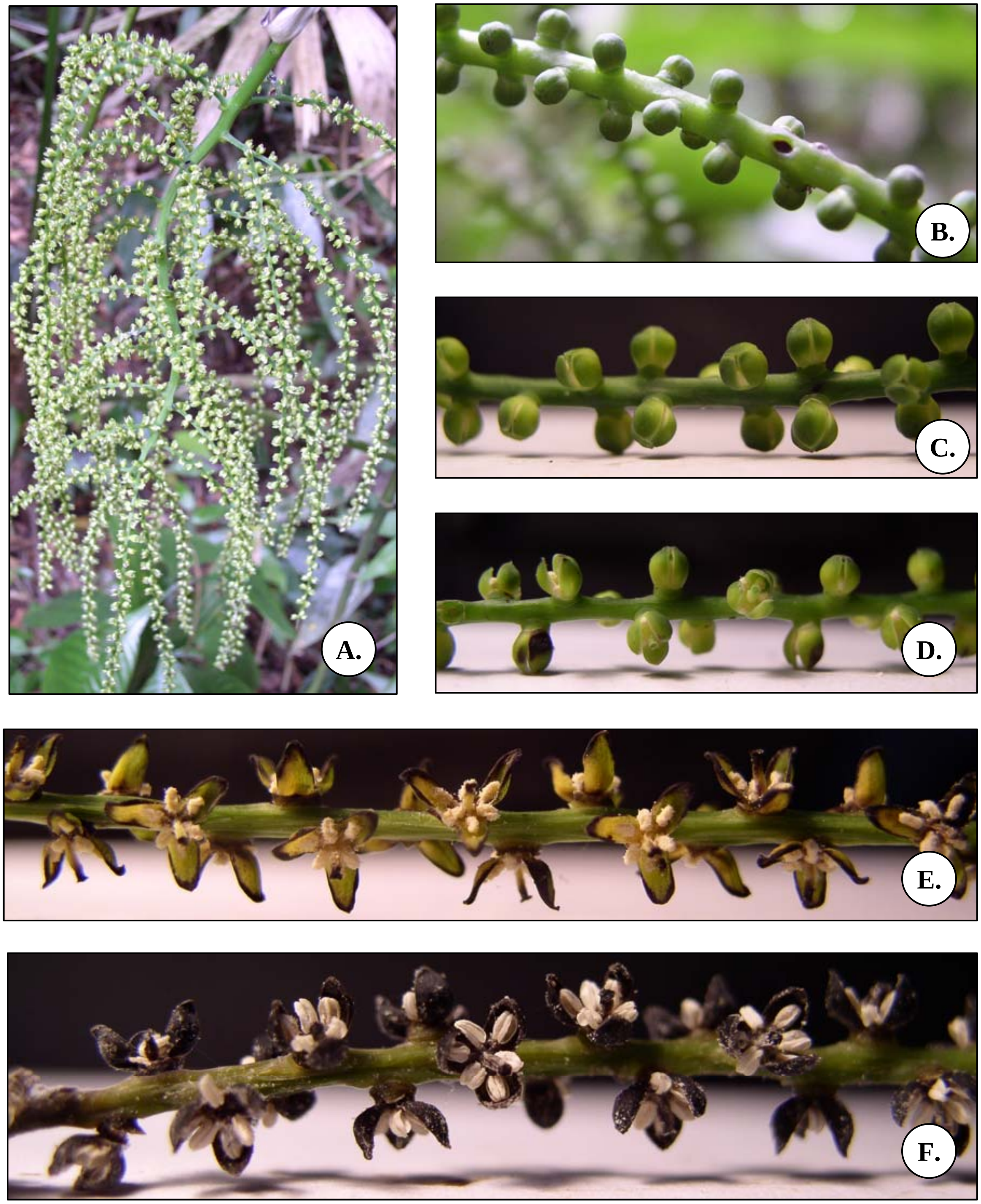


Figure 4.7
Development of staminate *C. oblongata*. **A**. Inflorescence with flowers at anthesis. **B.** Large flower buds. **C.** Petals just beginning to part. **D.** Early anthesis, petals opening and anthers beginning to dehisce. **E.** Later anthesis, with the flowers beginning to turn black in color. **F.** Flowers black and dry. The majority of pollen has been removed.

by visitors seeking pollen, and pollen can be seen spilling out onto the outer surfaces of the petals and the rachillae, as well as into the floral chamber.

By the second day after petals have begun to part, thrips visitation is greatly increased. As early as 6:00 a.m. thrips may be observed inside flowers, and it is likely that they were visitors that had remained inside overnight. As the day progresses and the temperature and light intensity increases, the fragrance produced by the staminate flowers becomes very strong and attracts numerous thrips to the inflorescence (Figure 4.8A). By 8:30 am, hundreds of thrips may be seen swarming over the inflorescence, entering and exiting the flowers and moving between them. In addition, there is often a cloud of insects around the inflorescence and by 10:00 am the fragrance is strong from up to a meter away.

Once inside of the floral chamber formed by the petals, thrips may oviposit, laying their eggs in the fleshy tissues at the base of the petals. If a number of eggs are already present in a flower, the female thrips will investigate other flowers or move to a different individual in order to find a suitable site. This is likely due to the fact that each flower can only support the food needs of a limited number of larvae. Several days later, after the pollen has been removed, larvae will be present both inside flowers and covering the rachillae. As pollen is an important food source for mating and ovipositing thrips, both male and female thrips enter flowers and begin to feed on available pollen if visitors prior to dehiscence have ruptured the anthers. As the anthers dehisce and pollen is distributed throughout the floral chambers, the thrips are covered with pollen. When flowers have fully opened and are beginning to dry out and turn darker in color, thrips visitation becomes low. By the time that the flowers are completely black and dry, thrips larvae are numerous and no adult thrips may be observed.

Unlike *C. ernesti-augustii*, staphylinid beetles were not observed to visit staminate inflorescences of *C. oblongata* during the study period. However, several other types of beetle, including weevils, pollen beetles, ladybird beetles, and longhorn beetles, visited in large numbers. Beetles visit staminate flowers at all stages of development, with over 20 beetles of different species often found at an inflorescence during the mid-morning hours. Leaf beetles sit on rachises prior to anthesis, and ladybird beetles are common visitors after the petals have parted (Figure 4.8B). However, longhorn beetles and pollen beetles are the most numerous beetles present during the period of anther dehiscence, both of which feed on pollen. The longhorn beetles are especially prevalent and up to a fifteen have been observed at an inflorescence at a single point in time. Pollen beetles are smaller and therefore not as easily counted during observation periods. Both types of beetle tend to visit only those flowers with fully open anthers, where they push their heads into the flower chamber to consume pollen. As with the other insects moving between post-dehiscence flowers, longhorn and pollen beetles tend to be covered with pollen and distribute it across any floral structures they contact including the petal exteriors and the rachillae between flowers (Figure 4.8C). After all pollen has been completely removed from the anthers, visits by beetles become infrequent.

Sweat bees are common visitors during peak visitation hours when the floral fragrance is at its strongest (Figure 4.8D). Up to a dozen bees have been recorded simultaneously visiting a single inflorescence, and they tend to visit numerous flowers during each foraging bout. The bees stand alongside a flower and probe the interior with their head and often front legs (Figure 4.8E). Collected pollen is readily observed to accumulate in the bee's pollen baskets.

The other visitors recorded at staminate inflorescence include ants, wasps, flies, and spiders. Numerous ants (up to eight recorded at one time) walk up the palms' stems and along the rachillae throughout anthesis. They remain at inflorescences for long periods of time probing the pistillode of one flower after another, seemingly unnerved by the other insect activity around them. Conversely, one of two parasitic wasps visits inflorescences every few hours, yet they do not alight for more than a few minutes (Figure 4.8F). They likely deposit their eggs into their preferred hosts and then leave the inflorescence.

From medium bud stage through anthesis, small numbers of flies were viewed visiting the flowers. The largest number of flies (>50 per observation) were present after all pollen had been dispersed, as flowers were drying out and falling off the inflorescences. Flies are also found at staminate inflorescences of *C. oblongata* where they lay eggs in flower buds, which in turn stimulate the development of galls, typically 1-2 weeks prior to anthesis. In approximately 30% of the inflorescences inspected (n = 273), from 5%- 60% of the flower buds are Diptera.

Finally, spiders, particularly crab spiders, are as ubiquitous at inflorescences of *C. oblongata* as they are at staminate inflorescences of the other species studied. Spiders arrive a day or two before the first flowers part their petals or the day that flowers first begin to open. They will remain at the inflorescence throughout its floral life cycle, often with one spider in residence on each of the rachillae, presumably waiting for prey.

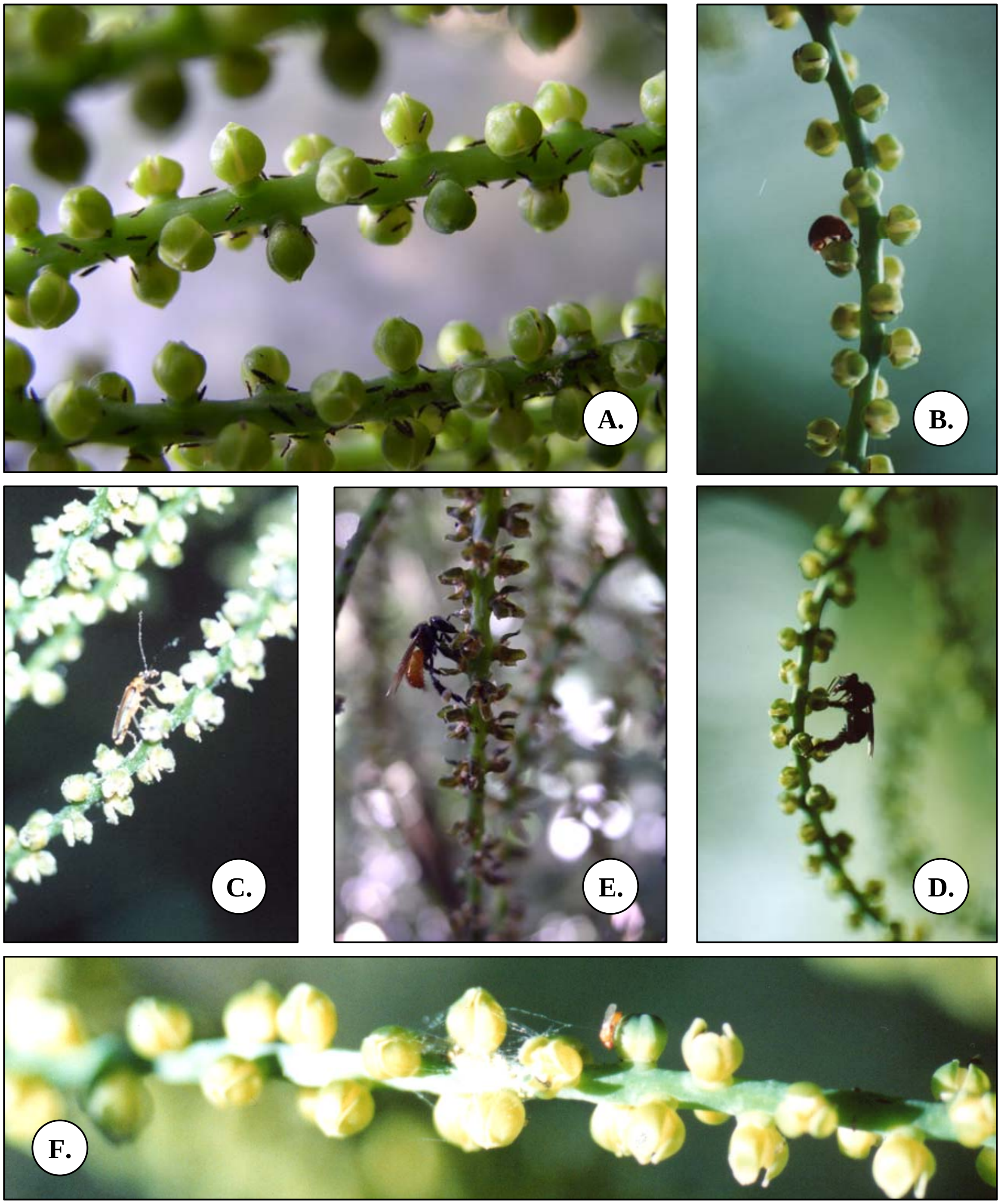


Figure 4.8
Visitors to staminate *C. oblongata*. **A.** Staminate *C. oblongata* swarming with thrips, and with the petals just beginning to open. **B.** Ladybird beetle. **C.** Longhorn beetle. **D.** Sweat bee. **E.** Sweat bee with pollen baskets on legs. **F.** Wasp.

4.3.5.4. *Chamaedorea oblongata*: Pistillate

4.3.5.4.1. *Chamaedorea oblongata*: Pistillate Floral Development

Unlike the staminate rachillae, the rachillae of pistillate *C. oblongata* are distinctly stiff and relatively straight, projecting out perpendicularly from the rachis (Figure 4.9A). Within two weeks of opening, the light green flower buds reach a medium size (1.0–1.5 mm diameter) and begin to protrude from the rachillae. As the buds become larger in size and volume, they change color from green to greenish-yellow to yellow. The sepals are green and will remain so throughout anthesis. At the flower level, the petals lighten from base to apex, with the whole process taking approximately 2-3 days. This basipetal manner of color change also occurs at the rachillae and inflorescence levels for approximately one week. As anthesis nears, the petals begin to part at their apices; the moist stigma lobes are often visible inside of petals (Figure 4.9B). Petals are thick, yet not as fleshy as those of the male flowers, and they lie tightly appressed to the large stigma lobes beneath them. At this point, the flowers are rounded at the bottom and taper at their apices where the yellow petals part. However, in some cases, the petals will open when they are still greenish-yellow in color.

At the same time as the petal apices are parting, creating a triangular aperture in the center of the flower, the stigmas extend beyond the petals, a process which takes place in a basipetal manner both within each rachillae and the inflorescence as a whole. It takes 1-2 days for the stigma lobes to reach their full extent. When fully exerted they are above the petals (Figure 4.9C). The prominent stigmas are hyaline in color and glisten because of stigmatic exudates. Tests for sugar in the stigmatic exudates and peroxidase tests, conducted while stigma lobes are in the process of extending, confirm that the flowers are receptive and therefore anthesis has been initiated.

From the time that the first petals begin to separate at their apices, a faint fragrance is emitted that grows stronger over the next few days (days 3-4 of anthesis). The odor produced by pistillate flowers is similar to that of staminate flowers, yet never as strong. It can be described as slightly musty, fruity, and somewhat sweet. During the first 3-4 days of anthesis, the scent is at its strongest from approximately 9:00 am until 1:00 pm, and it fades each day in the late afternoon. As anthesis progresses, the floral fragrance is slightly less potent each day, such that by approximately the 6th day the fragrance is faint even during mid-morning hours by the 8th or 9th day it is absent.

By the 3rd or 4th day of anthesis, the flowers begin to dry out. As this occurs, the exposed stigmatic surfaces begin to turn dark brown to black and are less moist (Figure 4.9D). Although the stigmas are dark in color and gradually reduce the production of exudate to none, many flower remain receptive through the 8th or 9th day after anthesis initiation. Also, dark spots start to appear on the petals as they lose moisture, and the petal margins may darken as well. Approximately 50% of the flowers have brown spots by the 5th day of anthesis, mainly those flowers on the rachillae toward the basal portion of the inflorescence. As the flowers finish anthesis, all of the stigma lobes are brown or black in color and eventually the petals becoming totally brown as they dry. Within one week after anthesis ends, immature fruits are noticeable on those flowers that have been fertilized (Figure 4.9E).

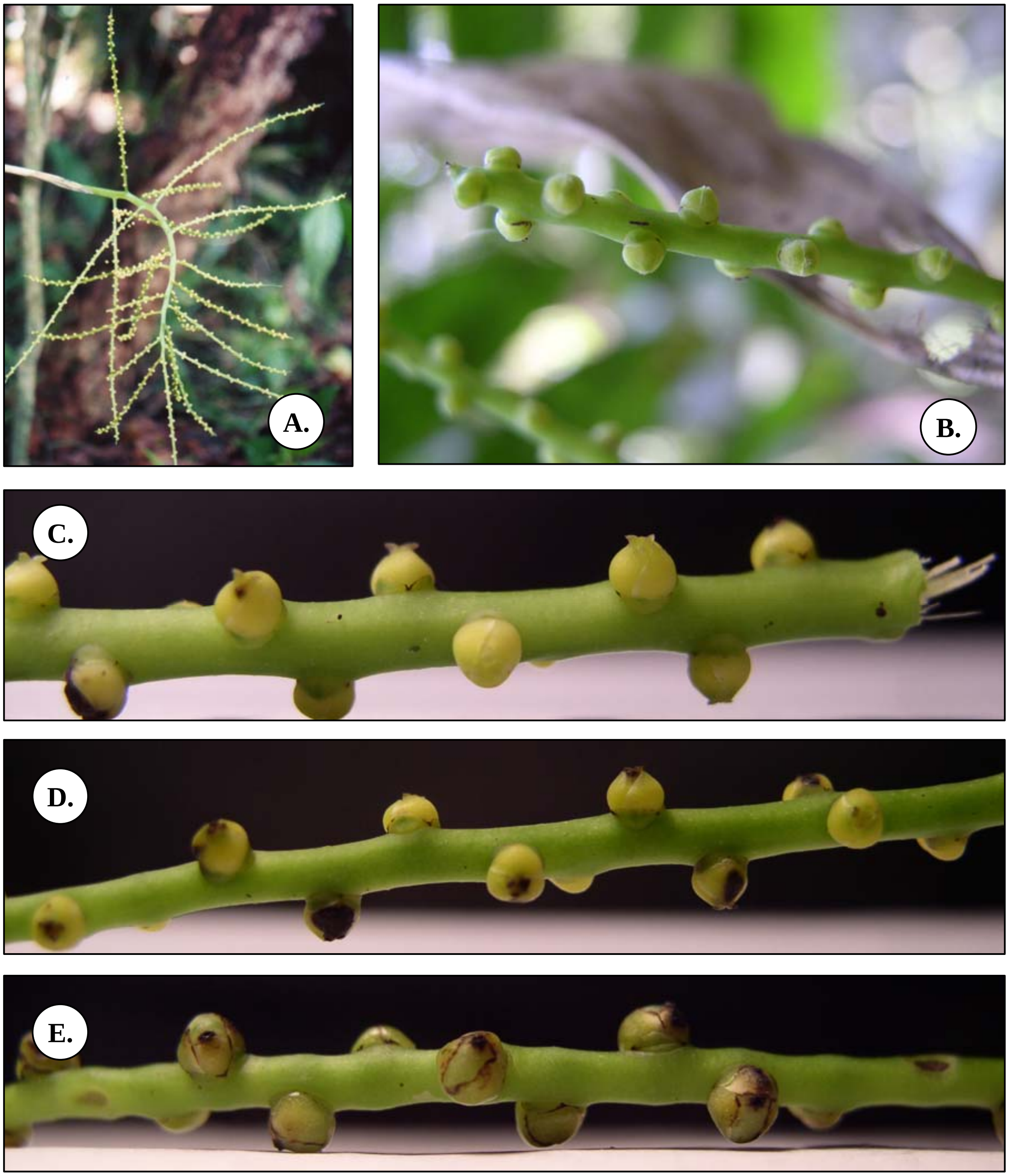


Figure 4.9
Development of pistillate *C. oblongata*. **A.** Inflorescence. **B.** Flowers with their petals just beginning to part at the apices. **C.** Flowers at anthesis with exerted stigmas. **D.** At the end of anthesis, the flowers have stigmas that are black and dry. **E.** Immature fruits.

4.3.5.4.2. *Chamaedorea oblongata*: Pistillate Visitation

The most abundant visitors to pistillate inflorescences are thrips (Figure 4.10A). A few thrips may be observed at pistillate flowers from the time that the first petals begin to open. The floral attractant at this point is likely to be the faint fragrance emitted by the flowers, because at this stage the petals are often still greenish in color. Typically, less than 10 thrips typically are observed during the 1st day that flowers begin to open, yet the numbers increase steadily over the next few days. The highest numbers are found the 2nd, 3rd, and 4th days after flowers open, with up to 300 captured from a single inflorescence during peak visitation. When their numbers are high, thrips congregate on the sides of flowers and on the rachillae between flowers. They are also observed alighting on and moving directly across stigma lobes. By the 5th days after the start of anthesis, thrips continue to visit, but in smaller numbers than previously, typically less 20 on an inflorescence at any given time.

Although thrips comprise more than 80% of the floral visitors to a pistillate inflorescence over its life cycle, several other insects do also visit. A number of beetles including longhorn beetles, ladybird beetles, and weevils visit each pistillate inflorescence. Both longhorns and ladybird beetles inspect several flowers, often visiting more than one rachillae, probing the stigma lobes, and consuming stigmatic exudate (Figure 4.10B). Weevils also appear to be attracted to the sugary exudates, but they also eat floral tissues (Figure 4.10C). In fact, after a weevil visits a flower, the damage is evidence by brown spots visible on the petals.

Both flies and wasps visit the pistillate flowers, however they are not common. Typically only 2-5 are observed during anthesis, and these insects alight on inflorescences for less than one minute on average. All of the wasps captured at pistillate inflorescences were identified as parasites on other insects. Additionally, although not observed, flies visit prior to anthesis. This is obvious, because flower galls stimulated by the larvae of ovipositing flies occur in pistillate flowers, but only approximately 10% of the flowers are victimized.

Other minor visitors included ants and spiders. Up to five ants may be observed walking along rachillae over the course of a day (Figure 4.10D). They stop at numerous flowers and probe the stigmas to presumably collect exudates. Crab spiders arrive usually one day prior to the start of anthesis and remain throughout the floral life cycle. Although they are in residence, the spiders rarely contact stigmas. They tend to stay in one place while waiting to prey on other floral visitors. Additionally, during anthesis, bristletails may sit at the base of rachillae or on the rachis, but they do not interact with the flowers. Even more often, bristletails were found on immature and mature fruit, causing visible damage to the developing fruit.

4.3.5.5. *Chamaedorea neurochlamys*: Staminate

4.3.5.5.1. *Chamaedorea neurochlamys*: Staminate Floral Development

After emerging from the inflorescence bract and extending to their full length, the rachillae of *C. neurochlamys* are pendulous (Figure 4.11A). Approximately one week before opening, the flower buds are plump, club-shaped, and lines are visible where the petals will part (Figure 4.11B). They rest upon prominent green sepals, whose apices are lighter in color than the rest of the calyx. The flowers on the basal rachillae tend to be more developed than those at the apex of the inflorescences. During floral bud

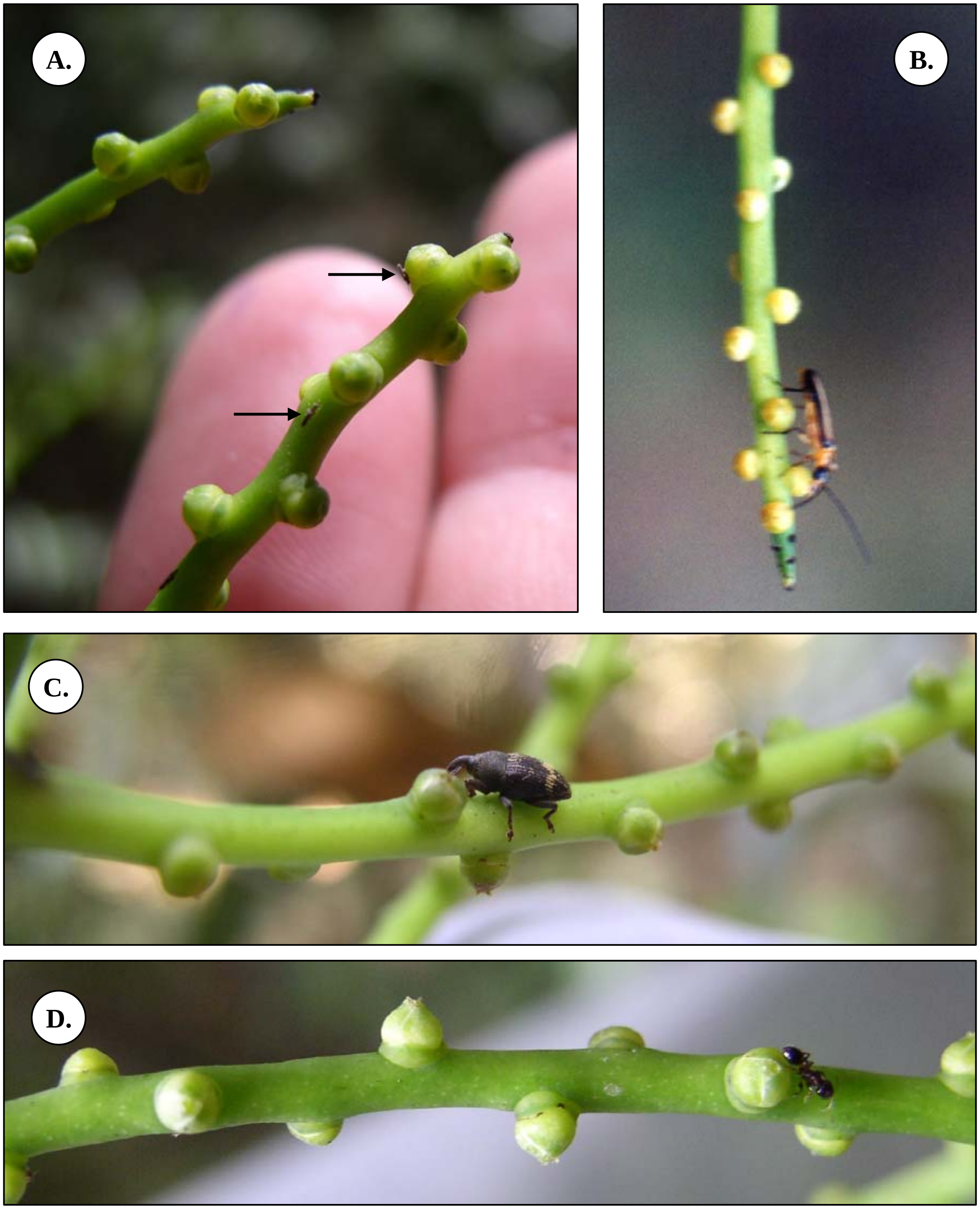


Figure 4.10
Visitors to pistillate *C. oblongata*. **A.** Early anthesis with thrips at apical flowers of a rachilla (arrows). **B.** Longhorn beetle. **C.** Weevil. **D.** Ant.

development, the color changes from a dark green, to a yellowish-green, and just prior to anthesis to a pale yellow. The thick, fleshy petals begin to get lighter in color starting with the basal portion of the petals, such that the petal bases might be yellowish-green, while the remainders of the petals are dark green. Thus, color change occurs in a basipetal manner, and similarly, floral development is basipetal both within rachillae and in the inflorescence as a whole.

Petals are connate basally and apically and are attached to the 3-lobed pistillode at their apices. Due to this morphology, the petals open by lateral slits and a relatively protected floral chamber is created inside of the petals (Figure 4.11C). Although they are open only a few mm at this point, by the time that dehiscence occurs, the openings between the petals are much larger. As the petals part, they also continue to change color, becoming yellow to bright yellow. Also, prominent nerves are visible as anthesis progresses, and even more so when the petals begin to dry in later in anthesis.

With the flowers developing, the lateral apertures become wider and the large, white anthers are conspicuous inside of the flowers, often filling up the entire opening created as the petals separate. The pistillode is rarely visible as the prominent anthers obstruct the view. Although the pistillode may produce nectar, it was not detected with the test used. Typically, it takes between 3- 5 days for the petals to fully part, and, at that stage, the anthers dehisce. At the time of dehiscence, the anthers are somewhat exposed, either filling the spaces between adjacent petals or slightly protruding through the openings between the petals (Figure 4.11D). The anthers open such that pollen is released toward the exterior, rather than the interior of flowers. The dry pollen will therefore often be both inside the floral chamber, as well as on the outside of petals.

Although a fruity fragrance is emitted as soon as the petals begin to part, the odor becomes very strong just prior to and for 2-3 days after the anthers dehisce. The aroma will remain discernable for another few days, yet fades as the flowers age and the stigmas lose receptivity. By the time that flowers have dried up, no fragrance is produced.

As soon as the anthers dehisce, the flowers begin a rapid drying process. As they lose moisture, the petals once again become dark green in color, and eventually black (Figures 4.11E and 4.11F). Also, the lateral slits become even larger as the petals shrink in volume. An inflorescence was considered to be past anthesis when the pollen had been released from flowers and the flowers and rachillae were dry and brittle. The flowers will remain on the dried inflorescence, unlike those of *C. oblongata*, which were knocked off by a slight motion. This is likely due to the differences in staminate floral morphology, where the flowers of *C. neurochlamys* are a held together by the adnate pistillode and petal apices, rather than free and open at anthesis. Dried inflorescences with intact flowers may be found on staminate individuals even a year after flowering, thus providing a useful identification tool (Figure 4.11G).

4.3.5.5.2. *Chamaedorea neurochlamys*: Staminate Visitation

Visitors begin to arrive at staminate inflorescences the first day that the petals begin to separate. The most common visitors are thrips, which may be observed throughout the floral life cycle. On the first day, when less than half of the flowers have begun to open, 300-500 thrips may be observed on the inflorescence. Thrips are able to move easily into the flowers through the tiny lateral apertures and then maneuver around the large intact anthers. For this reason, they are one of the few types of visitors at this

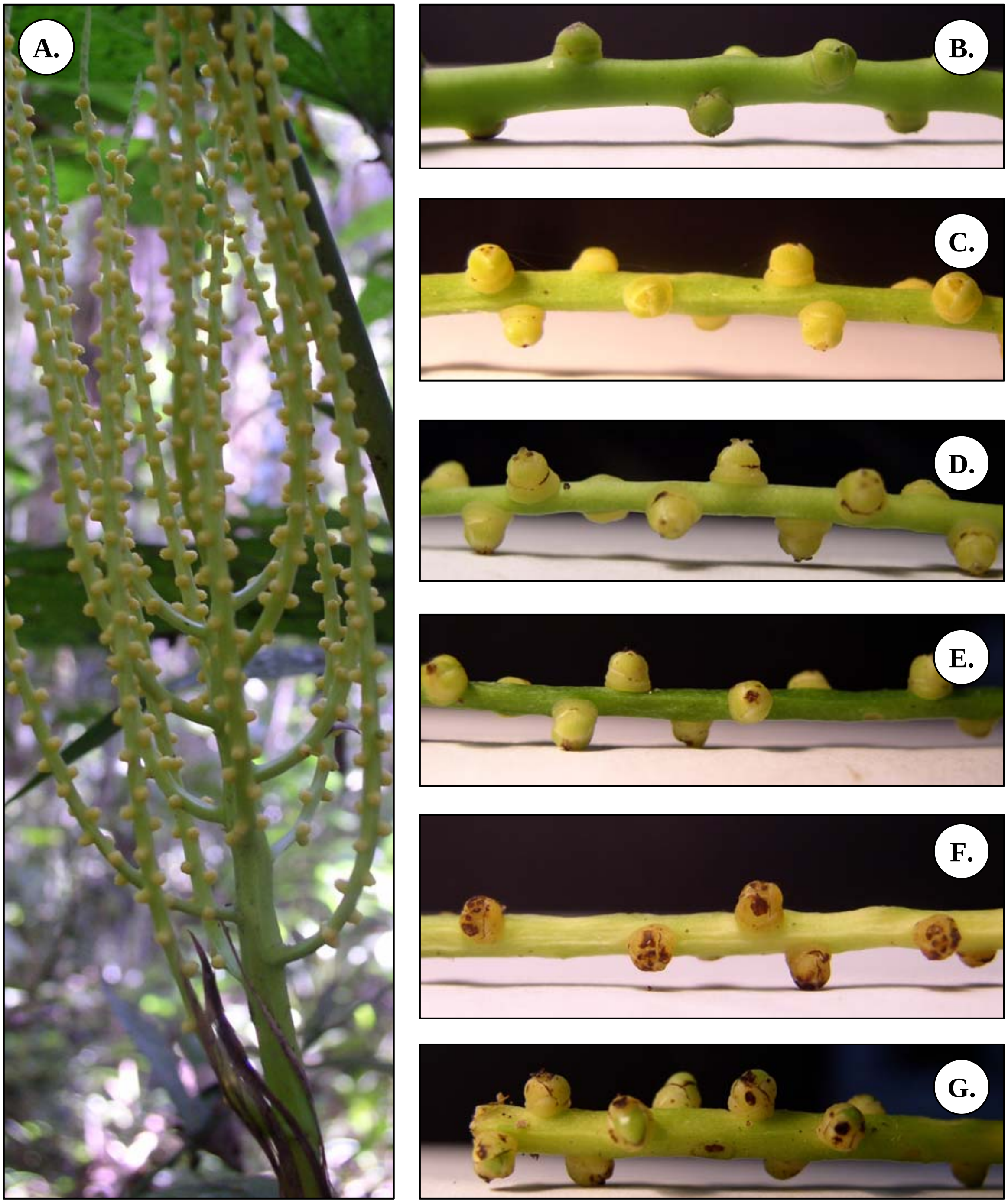


Figure 4.11
Development of pistillate *C. neurochlamys*. **A.** Inflorescence. **B.** Flowers with green petals just in the process of parting. **C.** Stigmas emerging and projecting up past the petal apices. **D.** Exerted stigmas at anthesis. **E.** Later anthesis, stigmas becoming brown. **F.** Post-anthesis flowers with brown stigmas and spotted petals. **G.** Immature fruits.

stage of flowering, because none of the other visitors are small enough to gain entry to the flowers. By the 2nd day after the petals bean to open, thrips can be seen moving from flower to flower, although the majority are located inside of flowers (Figure 4.12A). As the anthers have not dehisced at this point (although some may rupture due to insect activity), the main reasons for thrips visitation are oviposition and mating. Microscopic examination of flowers collected during the first day of flowering determined that thrips lay eggs in the fleshy petal tissues as soon as petals are even slightly parted. Within 4-5 days of the first flowers opening, numerous larvae may be seen on the rachillae. By the time that the anthers have dispersed their pollen and the flowers are dried up, thousands of larvae congregate on the rachillae and rachis (Figure 4.12B).

Prior to peak visitation hours (before approximately 9:00 am), few thrips are seen outside of the flowers. However, if flowers are jostled, a number of thrips (up to 8 have been recorded) emerging from each opening of the flower. By 9:00-10:00 am, as the temperature begins to rise, large numbers of thrips arrive at the flowers. In one visitor census, at 11:00 am, over 3,000 thrips were collected from a single inflorescence. Typically, during peak visitation hours, a cloud of small flying insects, composed mainly of thrips, can be seen surrounding a staminate inflorescence that has open flowers. After the anthers dehisce, the thrips are coated with pollen and they leave trails of it on the rachillae as they move between flowers. The number of thrips visiting drops as anthesis proceeds and by the time that the flowers are drying out, less than 200 adult thrips are found at an inflorescence. Only larvae are present on the dry black flowers.

The second most abundant visitors are beetles, and several different types, including pollen beetles, ladybird beetles, and weevils, may be found at staminate flowers. The majority of these beetles visit staminate flowers after the anthers have dehisced and either probe inside the flowers or enter them in order to feed on pollen. However, a few weevils may be found damaging flowers while they are still in bud. Hundreds of pollen beetles may be observed during the hours when flowers are most fragrant, from approximately 10:00 am to 1:00 pm. These small beetles are able to enter those flowers that have fully open lateral slits, and when they emerge they are covered with pollen.

Sweat bees are also common at staminate *C. neurochlamys* flowers. Although they are too large to enter the flowers, the bees are able to extract pollen from them. At least two species of sweat bee visit the inflorescences after dehiscence. Up to 18 bees have been observed at a single inflorescence simultaneously collecting pollen and storing it in the ‘baskets’ on their back legs. After the anthers are empty of pollen, bee visits are rare. If a bee does alight on an inflorescence, it will not stay for any length of time. Typically, it probes a few flowers after which it flies off.

Other insects that visit the inflorescences during anthesis include ants, wasps, and flies. Ants visit the staminate flowers, but in relatively low numbers (~2-5 at one inflorescence), and they rarely are observed entering flowers. This is likely due to the fact that the pistillodes are not easy to access. Still, as they walk along the rachillae and around flowers, they do pick up some pollen and therefore are capable of transporting small amounts to pistillate flowers. A number of wasps, primarily parasitoids, are also visitors. The wasps do not enter flowers, but instead may alight on a rachillae or hover above it seeking insects upon which to lay their eggs. Several flies are observed to visit

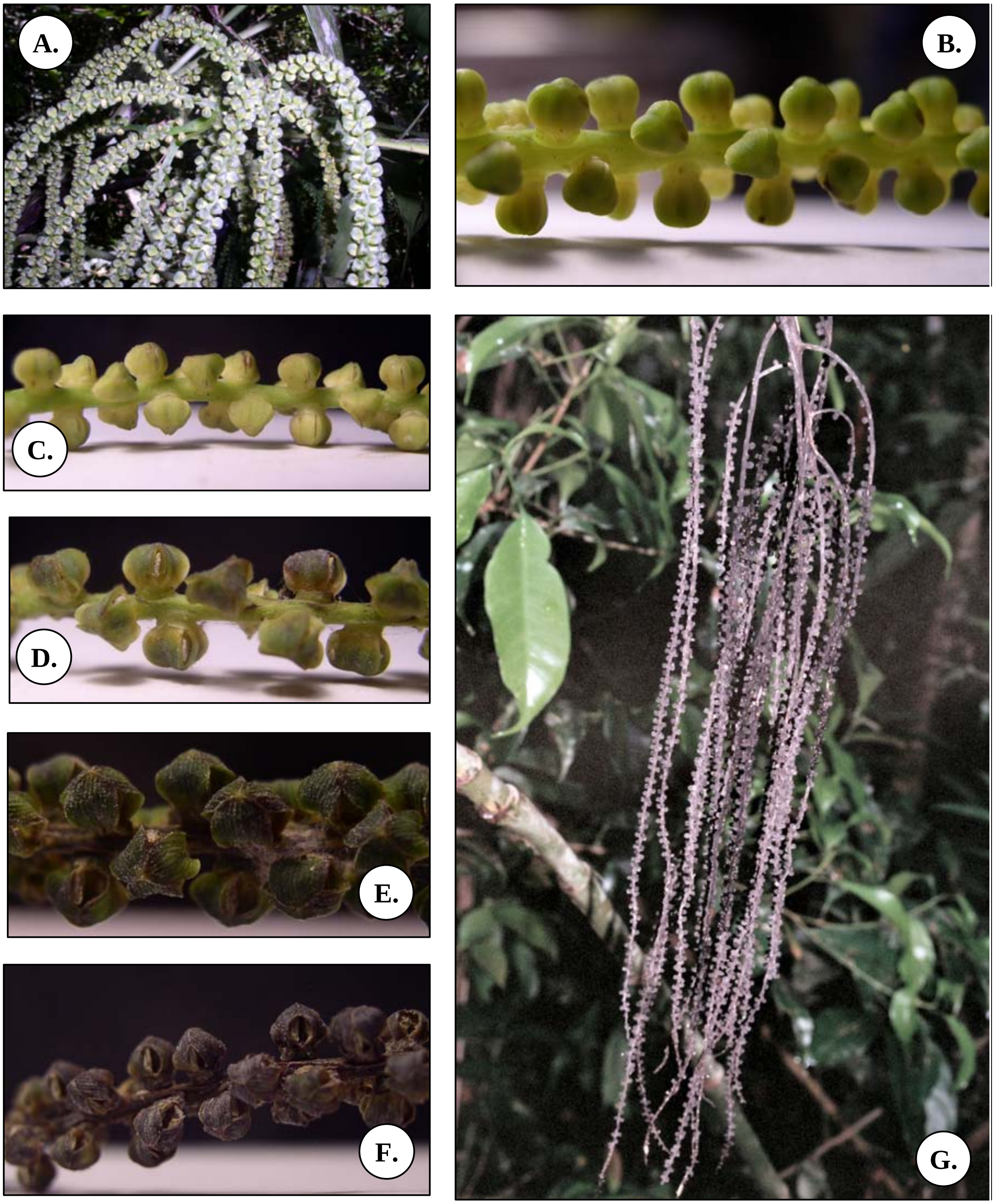


Figure 4.12
Development of staminate *C. neurochlamys*. **A.** Inflorescence at anthesis. **B.** Club-shaped buds. **C.** Petals begin to open. **D.** Petals part at their sides and anthers are visible. **E.** Drying green to black petals. **F.** Post-anthesis flowers with black, dry petals and large openings between petals. **G.** Dried inflorescence with flowers still attached to the rachillae.

when flowers are highly fragrant, although their activities while at inflorescences has not been determined.

Crab spiders actually are the first visitors, arriving even before thrips. A few spiders tend to take up residence at an inflorescences a day or two prior to any of the flowers opening and remain until the flowers begin to dry up. During anthesis, it is not uncommon to find a spider on almost every rachillae at some point in time. As many as 9 spiders have been found on an inflorescence at one time. Although they are common visitors, spiders rarely have any contact with flowers and are unlikely to move pollen between plants.

4.3.5.6. *Chamaedorea neurochlamys*: Pistillate

4.3.5.6.1. *Chamaedorea neurochlamys*: Pistillate Floral Development

As the rachillae push out of the inflorescence bract, they typically curve out from the rachis and then lengthen such that they are vertically oriented and the inflorescence resembles a candelabra (Figure 4.13A). This distinctive shape is an indicating feature when attempting to differentiate the pistillate inflorescences of *C. neurochlamys* from those of *C. oblongata*. Additionally, the sepals of *C. neurochlamys* are a few millimeters wider than those of *C. oblongata* pistillate flowers. The sepals raise the flowers off the rachillae to a larger degree than seen in other pistillate flowers. The flowers also are longer and more rectangular in comparison to those of *C. oblongata*, which have rounded petal bases.

The flower buds enlarge to their full size and change from a greenish-yellow to pale or bright yellow in color as anthesis approaches. Although flowering may be irregular, it typically proceeds in a basipetal manner at both inflorescence and rachillae levels, with flowers on the basal rachillae reaching receptivity prior to those at the apex.

As anthesis nears, the petals part slightly at their apices to reveal the stigma lobes (Figure 4.13B). Over the next 2-3 days, the petals are forced to open further as the stigmas push up past them (Figure 4.13C). Nectar and peroxidase tests demonstrate that from the time that stigmas begin to rise above the petals they are receptive. However, when the petals have just parted and stigmas are slightly visible, but have not begun to emerge, they are not receptive. When the stigmas have exserted past the petals to their full extent, they are most prominent part of the flower (Figure 4.13D).

By the 4th or 5th day after the first petals began to part, the majority of flowers exhibit clear-colored, moist stigmas with numerous papillae that are exerted well beyond the yellow petals. Nectar tests confirm that a sugary exudates is present on the exposed stigmas. A fragrance is emitted, faintly during the early days of anthesis, but becomes stronger as anthesis continues. The aroma is of medium intensity and not as strong as that of the staminate inflorescence, yet similarly pleasant and somewhat sweet and fruity as the pistillate flowers. The fragrance is emitted at its highest levels during the peak hours of insect visitation, which coincide with the hours of peak sunlight and the warmest hours of the day.

Over the next few days, flowers begin to develop brown spots on their petals and the stigmas gradually turn brown and then black (Figures 4.13E and 4.13F). As the stigmas lose moisture they decrease in volume, covering less of the exterior petal surfaces. The aroma becomes less noticeable as anthesis progresses, such that a week after the flowers first opened, it is only perceptible to the human nose within six inches of the inflorescence. In is interesting to note that many flowers continue to be receptive, based on peroxidase tests, even as the stigmas begin to dry up and darken in color. In fact, pistillate flowers may remain receptive for up to two weeks. At the end of receptivity, and therefore anthesis, those flower that were effectively fertilized have ovaries that begin to swell into developing fruit (Figure 4.13G).

4.3.5.6.2. *Chamaedorea neurochlamys*: Pistillate Visitation

The visitors to pistillate flowers of *C. neurochlamys* are similar to those of *C. oblongata*, albeit in somewhat lower numbers. Over 90% of the visitors to pistillate inflorescences are thrips. They arrive soon after the petals begin to part and the stigmas exert, and are present for the next 7-8 days. The first day, when not all of the flowers are receptive and the fragrance is relatively faint, thrips are infrequent (< 10 thrips). Thrips abundance is highest during the first 2-3 days of anthesis, with 30-50 thrips visiting at any one time during peak visitation hours. Over the remaining 5-6 days of receptivity, the number of thrips decreases, such that visits are rare during the last day or two. At the inflorescence, some thrips are observed moving from flower to flower, and in the process they walk across the large, exposed stigma lobes. Thrips will also form aggregations on the inflorescences, with the population spaced along the rachillae between flowers, presumably awaiting mating partners.

Several other insects visit during the flowering of a pistillate inflorescence, although in far lower abundance than thrips. A few beetles, including ladybird beetles and weevils, visit a number of flowers, some on different rachillae, where they spend time probing the stigma lobes, presumably to collect the sugary exudates. They also have

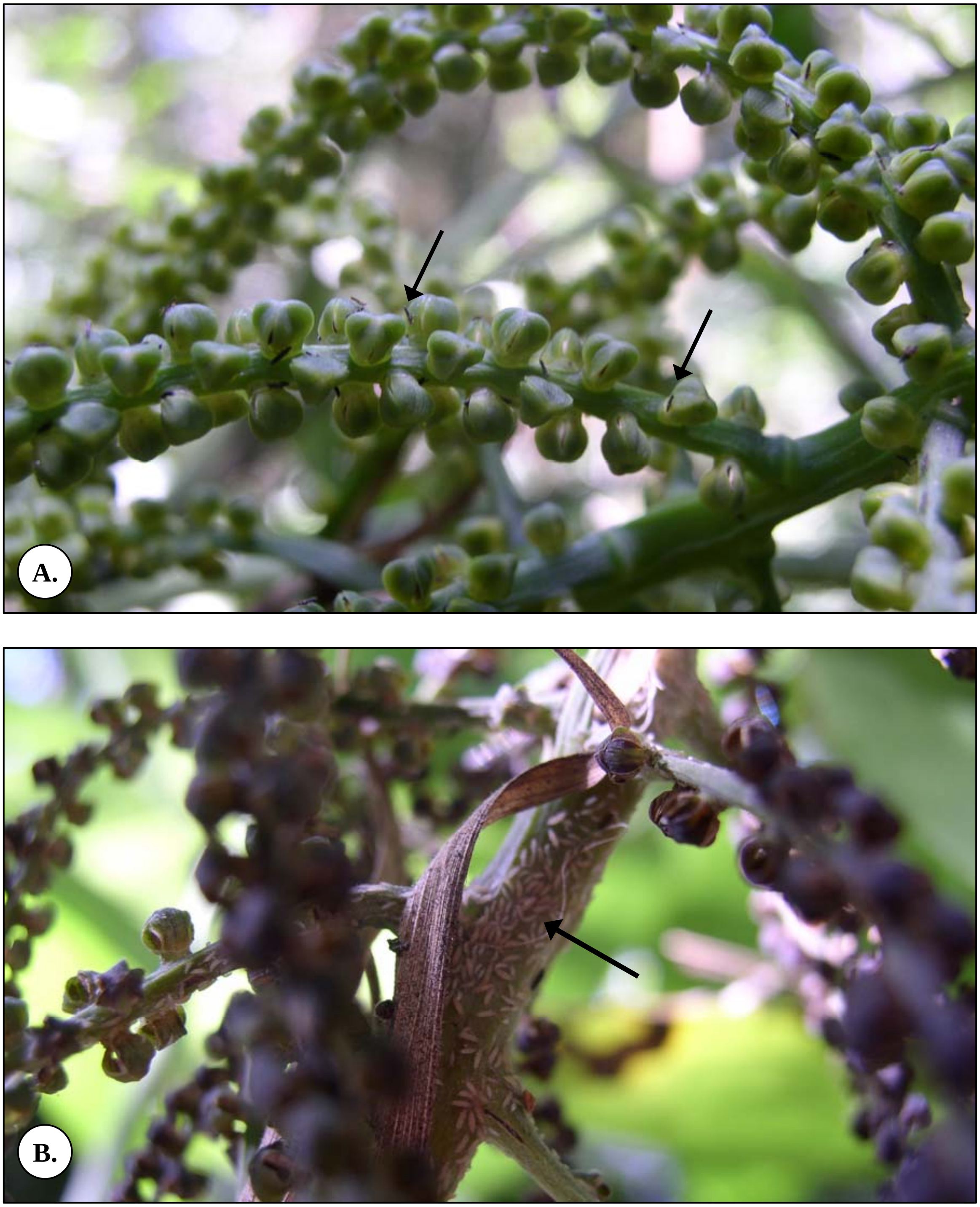


Figure 4.13
Visitors to staminate *C. neurochlamys*. **A**. Petals in the process of parting prior to pollen release, with many thrips visitors (arrows). **B.** Thrips larvae on rachis (arrow).

been observed consuming floral and vegetative tissues. As the number of beetle visitors is low (< 30 over the life of the inflorescence), the damage that they inflict tends to be quite low.

A few sweat bees may visit the pistillate flowers when they are at anthesis. They also visit in low numbers, typically with no more than a single visit every hour during the first few days of anthesis, and rarely after the 3rd day. Bees alight on the rachillae and tend to investigate the stigmas of 2-3 flowers before leaving the inflorescence.

Other visitors that are present in low numbers include ants, wasps, flies, and spiders. Ants walk up the inflorescence and are observed collecting stigmatic exudates. Wasps and flies also visit the pistillate flowers, however they rarely make contact with the stigmas. Their presence is uncommon, typically less than 5 are observed during the course of an inflorescence's life cycle. A few crab spiders will arrive just prior to anthesis and remain until the petals become dry. These visitors do not move between flowers, but instead remain in one place awaiting prey.

4.3.5.7. *Chamaedorea tepejilote*: Staminate

4.3.5.7.1. *Chamaedorea tepejilote*: Staminate Floral Development

The first activity associated with flowering occurs when the inflorescence bract splits lengthwise and rachillae begin to emerge between 6:00 am and 1:00 pm as the sun rises and the day becomes warmer. The bract from which rachillae have been released remains oriented vertically. The outer portion of the tough bract is a medium to dark green, and the interior portion of the bract is creamy-white (Figure 4.14A).

The rachillae are tightly packed inside the bract. Upon release, one by one, they begin to bend toward the ground, such that they will eventually be pointing downward (Figure 4.14B). Rachillae therefore will end up hanging in pendulous fashion. By the end of the first day, all of the rachillae are pendulous.

Flowers are tightly packed on rachillae and they cover the entire length of each rachilla. Upon release, the portions of the outermost rachillae that touch the bract exhibit green flowers. The rachillae that are located toward the interior are yellowish-green in color (Figure 4.14C). The triangular petals are closed, each meeting the others at the middle of the flower.

The flowers begin to change color during the first day after bract opening. Flowers on the apical rachillae and on the apical portions of rachillae begin to change from green to yellowish, and over the course of anthesis will change to pure yellow in color. Over the next two days, all flowers will change color to yellow, signifying their receptivity. Anthesis therefore proceeds in a basipetal fashion. This occurs not only on individual rachillae, but also the inflorescences as a whole; basal rachillae reach anthesis prior to those located apically. As the temperature rises throughout the morning, the rachillae continue to become pendulous.

By the beginning of the second day after bract opening all rachillae are pendulous. Also, flower color continues to change from green to yellowish-green to yellow depending on position on the inflorescence. By the afternoon of the second day, the apical portions of the top rachillae are distinctly yellow in color (Figure 4.14D). The inflorescence emits a faint fragrance throughout the morning and the aroma strengthens slightly by the early afternoon. Later, as the sun sets, the fragrance tapers off. It is a pleasant, yet somewhat sweet and fruity fragrance. Throughout the period of anthesis, the flowers continue to emit this strong fragrance during peak visitation hours.

During the mid-morning, flowers slowly open as temperature warms up, however they will part only slightly at petal apices. In these flowers, the prominent pistillode can be seen exceeding the thick, triangular petals. Depending on how far the petals have parted, in some flowers, only the pistillode can be viewed in the open area (Figure 4.14E). In other *C. neurochlamys* flowers, the anthers surround the pistillode and crowd the opening created by the parting petals. Tests for nectar demonstrate that nectar is being produced at the pistillode. In many cases, anthers begin to dehisce even while petals are still greenish-yellow. However, in some cases, not all of the anthers are even visible when they dehisce, because some remain below the height of the petal apices.

By the third day after the inflorescence bract opened, the majority of anthers have begun to dehisce. As they open, the anthers appear to push the petals further apart and may cover the pistillode as they push up just past the height of the petal apices. In their fully opened state, typically the whitish anthers are exerted well past the petals, may block the pistillode from view, and are the most prominent structure visible in a flower. The petals at this time are becoming more yellowish than greenish. Although the petals begin to be pushed further apart at their apices, they remain touching one another at their sides. At this time, all flowers have petals that are yellow to yellowish-green. Any flowers that are still yellowish-green tend to be found in the basal one-fourth of the rachillae and the lower portion of the inflorescence. After all of the anthers have dehisced, the white to cream-colored anthers fill the both the opening at the petal apices and the area above the petals (Figure 4.14F). They exceed the greenish-yellow to pale yellow petals by approximately 0.2 mm. During this stage, the flowers are highly fragrant.

As the anthers are dehiscing and pushing up past the petals, this activity, along with that of numerous visitors, results in pollen being dusted across all exposed portions of the inflorescence including the petals, the rachillae, and often the bracts and peduncle. In some cases, the pollen is so abundant that it can found in large amounts on leaves located directly underneath inflorescences (Figure 4.14G).

During the fourth and fifth days, flower petals begin to change color from yellowish to pinkish-red or dark red, typically with the color change moving from the base toward the apex in a basipetal fashion. At this point in anthesis, the most prominent feature is still the cream to white colored open anthers that exceed the petals. Very little space is visible between the groups of anthers, because they have opened and exceeded the petals, spreading the petals as they opened. The petals tend to be dark red to reddish-purple at their bases and yellow to yellowish-green for the top one-half of their length (Figure 4.14H). At this point in the floral life cycle, the petals are not a thick or fleshy as they were at the beginning of anthesis. They begin to dry out, a process that will continue over the next two to three days. Also, the bract develops brown portions and begins to lose some of its rigidly, slumping slightly as the days advance. Yet, fragrance continues to be emitted, although it has loses some of its strength. The inflorescences continue to be fragrant until all of the flowers have become dry and brown.

After five days, the majority of flowers are reddish-brown, pink and brown, or brown in color. Flowers continue to dry out and eventually the inflorescence loses the

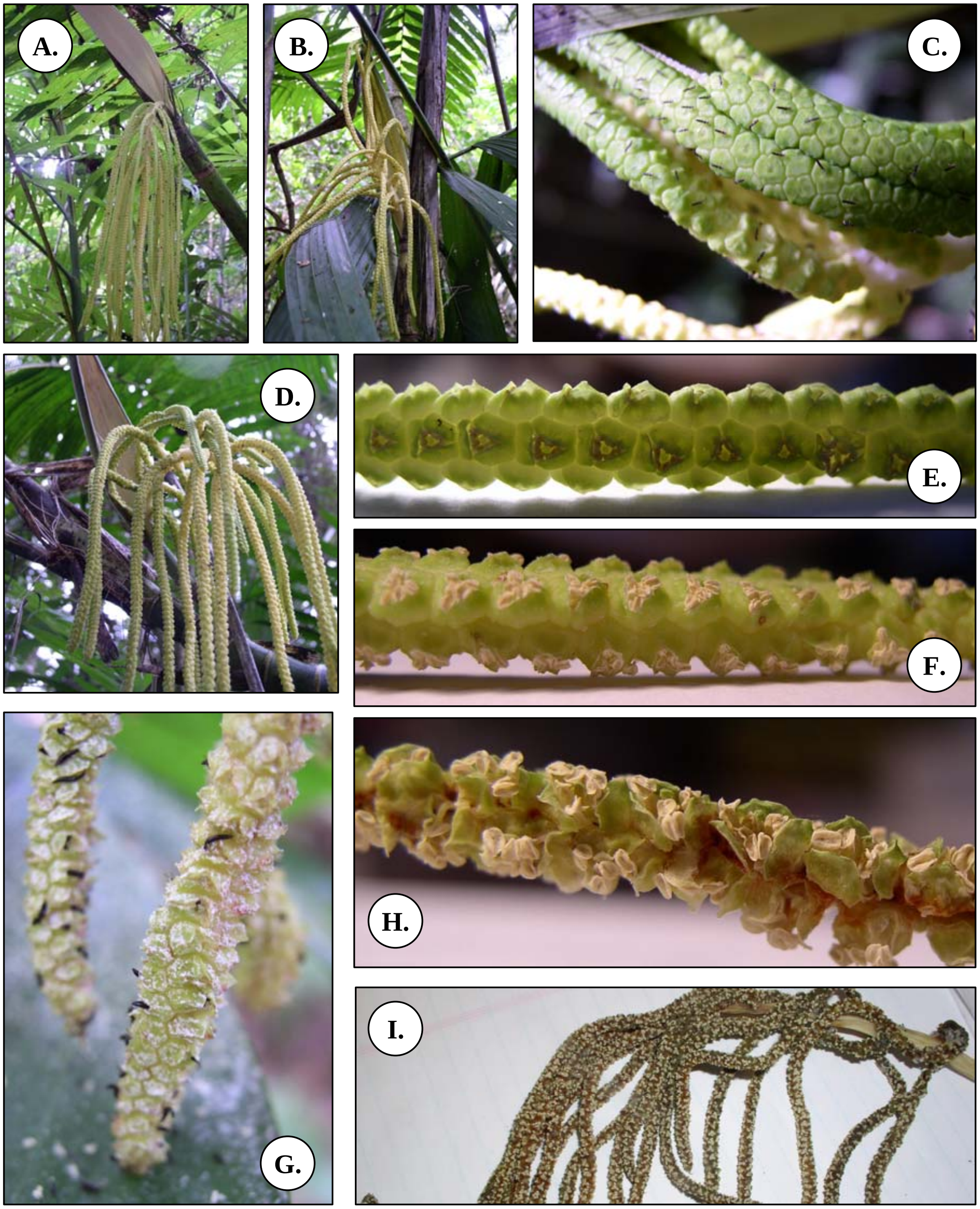


Figure 4.14.
Development of staminate *C. tepejilote*. **A.** Inflorescence with vertically-oriented, white bract. **B.** Rachillae becoming pendulous. **C.** Unopened flowers. **D.** Inflorescence at anthesis. **E.** Flowers opening and pistillodes prominent. **F.** Anthers fill the open space at the apex of each flower. **G.** Flowers at anthesis, with pollen covering floral exteriors. **H.** Post-anthesis flowers with petals turning pink and red in color. **I.** Brown, limp rachillae of a post-anthesis inflorescence.

majority of its volume (less than half the volume when at anthesis), becoming a group of limp, brown rachillae with the brown flowers still attached (Figure 4.14I).

4.3.5.7.2. *Chamaedorea tepejilote*: Staminate Visitation

Thrips arrive immediately upon opening of bracts (Figure 4.15A). As the day progresses and the temperatures rises, staphylinid beetles also begin to arrive. During the time that the rachillae move to their pendulous orientation, the most abundant visitors are thrips and staphylinid beetles. The number of thrips is roughly double that of staphylinids, however the difference in size between the two visitors (staphylinids are much larger) likely allows an inflorescence only to support a smaller number of beetles. It is interesting to note that at this point, the flowers have not even opened and petals are still tightly appressed. Visitors must burrow in between the closed petal to enter the flowers and as the day heats up, more and more visitors arrive. Approximately four hours after the bract opened and rachillae emerged, a single capture of all visitors to one inflorescence captured over 400 visitors. Similar captures were conducted during the second, third, and fourth days of anthesis, and typically more 5000 visitors were captured, over 80% of them thrips.

As the anthers begin to dehisce, the volume of insect visitors increases dramatically and the fragrant is so strong that it can be detected by the human nose from a meter away. Also, the visual display is large and consists of many rachillae and yellow flowers. Numerous visitors are observed during the anther dehiscence portion of flowering including thrips, staphylinid beetles, several other beetle taxa, sweat bees, flies and wasps, and several crab spiders (Figure 4.15B).

To assess visitor behavior closely, rachillae were brought to the laboratory in clear plastic bags to be examined more closely under a dissecting microscope. In comparison with the other study species, it was more difficult to determine visitor activities inside of the *C. tepejilote* staminate flowers due to the closely packed nature of flowers. Thrips are at their more numerous during the first few days of flowering, typically during the first 2-3 days after the bract opens (Figure 4.15C). Therefore, thrips were observed at all times on the exterior of the flowers, climbing from flower to flower, often covered with pollen. Typically, three to five thrips may be found inside of each flower. However, the open anthers are so large and obstructive it is difficult to ascertain visitor behavior once they are inside of flowers. The thrips are known to feed on pollen, as well as oviposit in the fleshy petal tissues (Mound, 2005). Thrips typically remain inside at a particular inflorescence for over 20 minutes, yet may also be observed visiting many flowers on a rachillae. At a single flower, visits of up to 15 minutes have been recorded.

As thrips oviposit within the staminate flowers, three to four days after the inflorescence bract first split, their larvae are visible both inside of the flowers and on the rachillae. They continue to visit throughout anthesis until one to two days after all the pollen has been shed and the flowers are completely open and yellow.

In terms of the second most abundant visitor, staphylinid beetles, a typical flower during peak anthesis hosts two to three staphylinids (Figure 4.15D). Staphylinids begin to arrive shortly after an inflorescence bud opens and remain throughout anthesis. Often, additional beetles were observed to approach and probe a particular flower. However, they tended to move on to another flower if two or three beetles were already present.

Due to the larger size of staphylinids, it was possible to observe at least a portion of them easily. As a staphylinid probes a flower, often only its abdomen is visible projecting out just past the petal apices. They are likely to be eating pollen, as staphylinids are documented as pollen consumers, and some species are predators or parasites on other insects (Borrer et al., 1992). Staphylinids are observed to remain in the staminate flowers for long periods of time, usually moving along a single rachilla and probing numerous flowers before moving to a different rachilla. They also mate and lay eggs in the staminate flowers, although not as abundantly as thrips.

Sweat bees are also highly attracted to the fragrant flowers (Figure 4.15E). Several taxa visit to collect pollen, moving from flower to flower and may visit flowers on several rachillae during a single visit. The typical visit lasts from 10-15 minutes, and up to 20 bees of various taxa may be observed at a single staminate inflorescence at one time. Also, several different taxa of small beetles visit the staminate inflorescences, upwards of 25 at a time during mid-morning hours, feeding on floral tissues, rachillae tissues, pollen, and nectar including pollen beetles (nitidulids) and leaf beetles (chrysomelids), all of which usually are found within the first day after anthers begin to dehisce (Figure 4.15F).

Less numerous visitors include crab spiders and flies. Crab spiders tend to arrive prior to petal opening and lie in wait of prey (Figure 4.15G). They remain on an inflorescence for the majority of the day and a large inflorescence can host up to a dozen spiders, usually on different rachillae. Flies typically visit in smaller numbers during early anthesis. However, as the flowers begin to turn reddish-purple and then brown in

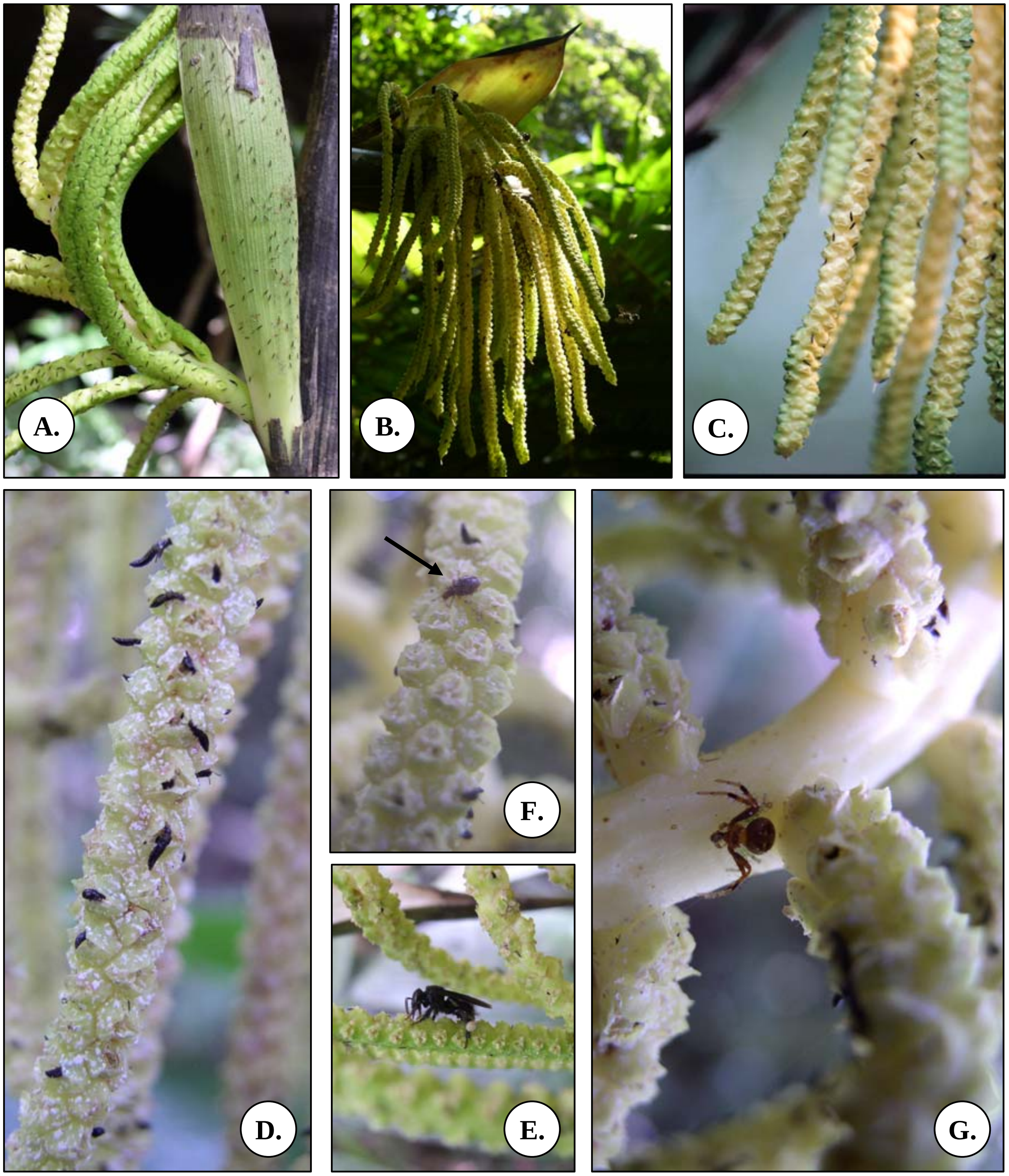


Figure 4.15
Visitors to staminate *C. tepejilote*. **A.** Thrips cover the unopened flowers, as well as the inflorescence bract. **B.** Inflorescence in anthesis with many visitors. **C.** Rachillae with anthers not yet dehisced, however many thrips are present. **D.** Staphylinid beetles on flowers at anthesis. **E.** Sweat bee. **F.** Pollen beetle (arrow). **G.** Crab spider.

color, the number of flies increases. In fact, on post-anthesis inflorescences, the majority of visitors are flies and thrips larvae.

4.3.5.8. *Chamaedorea tepejilote*: Pistillate

4.3.5.8.1. *Chamaedorea tepejilote*: Pistillate Floral Development

As the flower buds develop, they reach their largest size (2-3 mm diameter), and the thin petals lighten from a dark green to a yellowish-green, and then often to yellow in color. As with staminate inflorescences, both within rachillae and inflorescences (Figure 4.16A), the flowers develop in a basipetal fashion.

When flowers are fully developed, the stigma lobes will push through and past the petals filling the triangular opening that they create in the middle of the flower where the three petals meet. At anthesis, the stigma exceeds the petals, and the distal portion of the large stigma lobes is recurved over the petals. As the stigmas protrude out of the opening in the petals, and the petals are appressed to stigma lobes, these flowers do not create a floral chamber that may be entered by visitors.

Pistillate flowers of *C. tepejilote* are receptive for seven to nine days. During the first few days of anthesis, the prominent stigma lobes are hyaline to white and moist with stigmatic exudates (Figure 4.16B). The rachillae are green in color. Additionally, flowers will be highly fragrant, with the fragrance becoming noticeably between 9:00 a.m. and 10:00 a.m. and reaching its peak around noon. The aroma is not as strong as that of the staminate inflorescence, yet it is a similar, somewhat sweet, fruity fragrance.

In the afternoon, the fragrance fades as the sun and light begin to fade. The odor is similar to that emitted by staminate individuals of *C. tepejilote*. Nectar and peroxidase tests demonstrate that stigmas are receptive from the time the stigmas begin emerge (and therefore at anthesis), until two or three days after they begin to turn brown in color. When the petals have just parted and stigmas are visible, yet have not risen above the petals, tests show that they are not yet receptive.

Approximately three to four days after becoming receptive, noticeable brown spots begin to appear on the petals. Although the flowers will remain receptive for a few more days, they no longer emit a strong fragrance. As the anthesis period ends, larger portions of the petals will be brown. Also, the stigmas will dry and become brownish-black in color, signaling the end of anthesis (Figure 4.16C). After anthesis, those flowers that were not fertilized fall off the rachillae, while the ovaries of fertilized flowers begin to swell within a few days; the developing fruit pushing past the petal remnants (Figure 4.16D).

4.3.5.8.2. *Chamaedorea tepejilote*: Pistillate Visitation

From the time that the petals part and stigmas begin to emerge, the flowers and rachillae are covered with visitors. The majority of visitors to pistillate *C. tepejilote* were thrips and staphylinid beetles. In fact, these insects constituted over 95% of the visitors during anthesis. For the first two or three days of anthesis, that is thrips visitation is at its peak from approximately 9:00 a.m. until 12:00 p.m. Often, a swarm of hundreds of thrips is visible hovering around an individual with open flowers (that is petals parted and stigmas exserted). Thrips land on pistillate inflorescences and remain there for long periods of time (Figure 4.17A). They move between flowers and investigate their stigma lobes, as well as stand stationary on the rachillae, likely waiting for mating opportunities

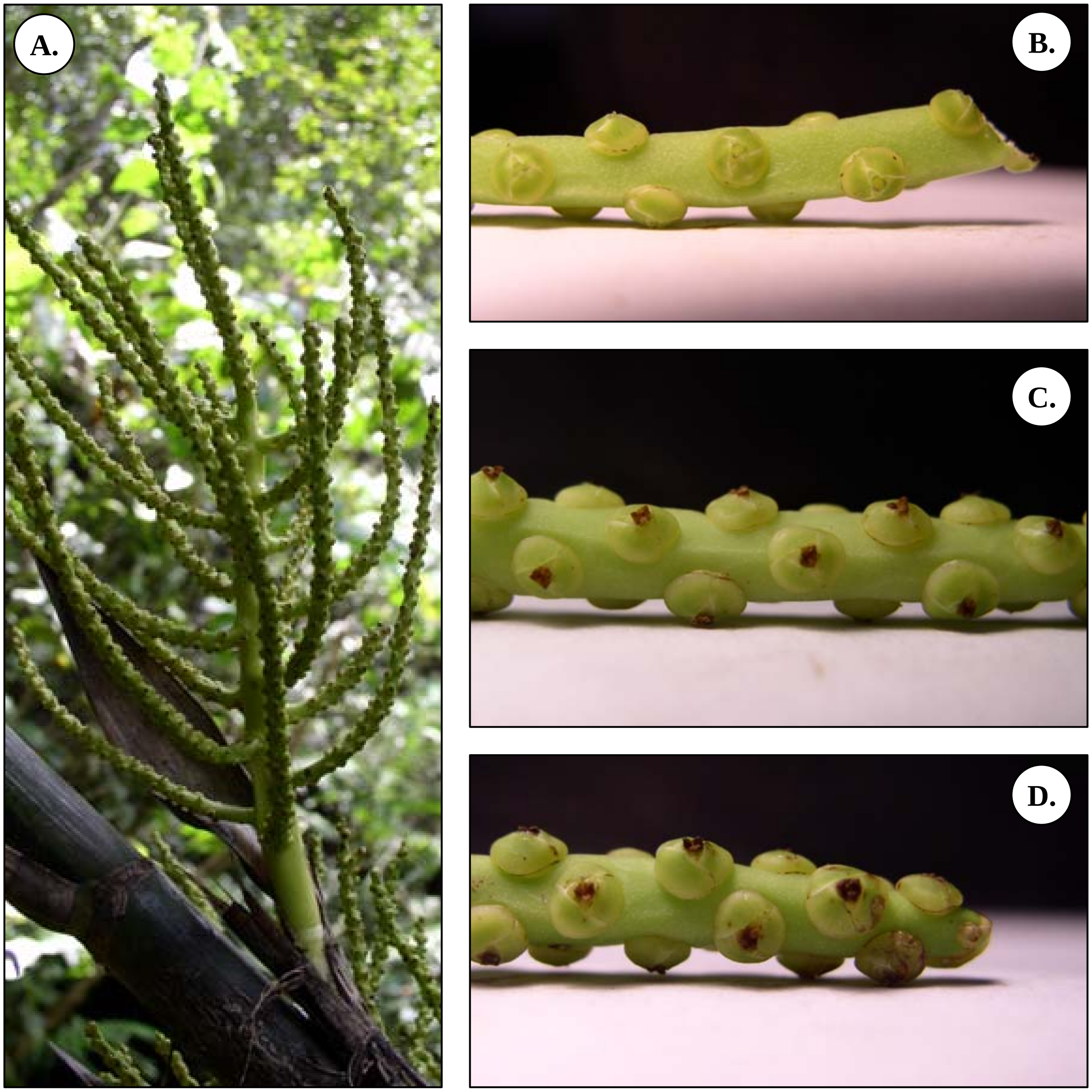


Figure 4.16
Development of pistillate *C. tepejilote*. **A**. Inflorescence. **B.** Flowers at anthesis with clear stigmas. **C.** Later anthesis flowers with brown stigmas. **D.** Immature fruits visible under the petal and stigmatic remnants.

(Webster et al., 2006). These aggregations of thrips tend to quite large, with over three hundred thrips observed spaced across a single rachilla (Figure 4.17B). Although the pistillate inflorescences of the three other species studied also host thrips in sufficiently high numbers to be considered aggregations, the groupings are most visible on *C. tepejilote*. Even as the stigmas begin to turn brown and dry up, thrips may still visit for a few more days (Figure 4.17C). As anthesis progresses, the daily abundance of thrips becomes progressively lower and tapers off as all rachillae have finished anthesis.

The pistillate inflorescences of *C. tepejilote* host a visitor not observed at any other pistillate *Chamaedorea*, staphylinid beetles (Figure 4.17D). Although the number of staphylinids is lower than that of thrips, staphylinids are the second most abundant visitors to pistillate flowers at anthesis. Throughout the mid-morning hours when flowers are at anthesis, between 10-50 staphylinids typically are present at a pistillate inflorescence. They alight on rachillae and as they explore the inflorescence may walk over the stigmas or simply move in the spaces between flowers. A staphylinid often remains at an inflorescence for up to 10 minutes, and are likely attracted to the flowers by the emitted fragrance. They tend to visit pistillate inflorescences in large numbers (up to 40 have been found at an inflorescences during peak flowering hours), however after the first two to three days of anthesis they are less commonly encountered.

Crab spiders also arrive within a day after the flowers begin to open. They visit in low numbers, typically no more than three on a large inflorescence at any one time. Similarly, sweat bees are visitors during the first 4-5 days after petals part. They do not visit in the high numbers observed at staminate inflorescences, yet at least one bee may be found at any time during the peak visitation hours (with a maximum of four).

Figure 4.17
Visitors to pistillate *C. tepejilote*. **A.** Thrips are the most numerous of visitors and occur in abundance during early anthesis. **B.** The male thrips stand at a short distance from one another creating a distinctive pattern. **C**. Thrips continue to visit as stigmas become brown and lose receptivity. **D.** Staphylinid beetle (arrow) visiting the pistillate flowers.

Sweat bees investigate stigma lobes and gather stigmatic exudates, visiting a number of flowers and often several rachillae.

Other less common visitors, which were observed during the 2nd to 5th days after flowers began to open, include pollen beetles, ants, flies and wasps. Although numerous species of beetles visited staminate inflorescences, only staphylinid and pollen beetles were collected at pistillate inflorescences. No more than three (and often none) pollen beetles visited a particular pistillate inflorescence over its period of flowering. They usually only examined a few flowers, probably collecting sugary stigmatic exudates, before leaving. Flies and wasps did visit and investigate stigmas, however their appearance was rare. Finally, from the early morning in late afternoon throughout anthesis, up to three ants at a time may be observed on an inflorescence, marching along rachillae and collecting nectar.

4.3.5.9. Summary of Species Descriptions

To summarize, the four *Chamaedorea* species involved in this study exhibit a variety of floral characteristics. These findings are intriguing, not just because the palms were demonstrated to be entomophilous, but also because they are all pollinated by the same species of thrips. Although each species offers attractants and rewards that correspond with thrips' preferences (e.g., brood site, pollen, venue for mating aggregations), the four *Chamaedorea* species exhibit a variety of floral characteristics.

The only species with bright orange petals at anthesis is *C. ernesti-augustii*. All of the other species have greenish-yellow to yellow flowers, therefore the floral display from *C. ernesti-augustii* is much more visible and attractive. The flowers also have much thicker petals than those found in the staminate flowers of other species. Additionally, this is the only species with sticky pollen.

The pistillate flowers of *C. ernesti-augustii* are the same orange color as the staminate when they are receptive. Of the four species, this is the only one that has spicate pistillate inflorescences, therefore it produces relatively few pistillate flowers compared to the other species. However the pistillate flowers have thick, fleshy petals similar to those of staminate flowers, and provide a medium in which thrips may lay eggs. Moreover, this species produces the only pistillate flowers that insects must enter (or put some body part inside of) in order to make contact with the stigmas. The morphology of these pistillate flowers, which are cup-shaped, is likely to prevent air-borne pollen from reaching the stigmas. Therefore, it is posited that *C. ernesti-augustii* may be completely pollinated by thrips. If this is indeed the case, then the added rewards of more floral tissue for consumption, as well as pistillate flowers in which female thrips are able to oviposit, may reinforce the concept of insect pollination in this species.

The next two species, *C. oblongata* and *C. neurochlamys* are quite similar in morphology, so alike in fact that they often cannot be distinguished without the aid of flowers. Even the inflorescences are comparable. The staminate rachillae are pendulous, emit a strong fragrance at anthesis, and produce large quantities of dry, powdery pollen. Their petals are thick and change color from green to yellow as anthesis nears. However, there are also obvious differences, primarily in the morphology of staminate flowers. The staminate flowers of *C. oblongata* are open, with free petals and highly exposed interiors and anthers. Conversely, the staminate flowers of *C. neurochlamys* open only by lateral slits, such that an enclosed floral chamber is created. Both of these species are used by thrips for oviposition. The eggs are laid in flowers shortly after the petals begin to open and prior to anther dehiscence. During this period, the flowers of *C. oblongata* are relatively closed, and they do not open completely until pollen is released and the petals begin to dry.

Additionally, both *C. oblongata* and *C. neurochlamys* have pistillate rachillae that are relatively stiff. The receptive flowers are fragrant, with prominent stigmas that protrude past the thick, yellow petals at anthesis. For both species the constraints of their pistillate floral morphology (petals appressed to underlying stigmas) does not allow insects to enter the flowers. Pollen is brushed across stigmas as visitors move from flower to flower, and wind-borne pollen may also adhere to the exposed stigmas.

Finally, the most distinct staminate inflorescences produced by any of the species are those of *C. tepejilote*. In fact, morphology of displayed by this species' staminate inflorescences is akin to that of several beetle pollinated palms (Listabarth, 1994, 1996; Bernal & Ervik, 1996, Henderson et al., 2000a). The rachillae do not emerge from the inflorescence bract gradually as in the other species studied; instead the bract splits longitudinally to release all of the rachillae over an eight to ten hour period. The bract remains vertically oriented, while the rachillae become pendulous. Within 24 hours the closely-packed flowers open, change from green to pale yellow, and begin to emit a strong fragrance. Characteristics that are associated with beetle pollination include the erect inflorescence bract, the closely spaced flowers, and the musty odor (Henderson, 1986, 2002). The creamy white interior of the bract is posited to serve as a visual signal (a signpost) for pollinators. It is therefore not surprising that staphylinid beetles, along with thrips, are the most abundant visitors and likely pollinators for this species. In many ways, the pistillate inflorescences of *C. tepejilote* are equivalent to those of *C. oblongata* and *C. neurochlamys*. The rachillae are perpendicular to the rachis, and relatively straight. They also produce similar flowers, with large, exposed stigmas. The main difference here is that the pistillate inflorescences of *C. tepejilote* are larger, as are the flowers themselves, than those of the other species. Thus, as would be expected, they are the species on which thrips mating aggregations are the largest.

In sum, each of the sympatric species in this study displays slightly to highly different floral characteristics when compared with the other species. Nonetheless, all of the flowers provide the elements necessary to support thrips' mating and oviposition. Also, mating aggregations of male thrips occur on pistillate inflorescences of all four species. Thus, the floral characters and their effect on pollinator behavior play a role in maintaining the dependent mutualism between thrips and *Chamaedorea* species.

4.3.6. Thrips' Identity and Sex

All of the thrips collected from *Chamaedorea* inflorescences were identified as *Brooksithrips chamaedoreae* Retana & Mound, by Dr. Laurence Mound (Figure 4.18). Both the genus and species of this thrips were first described in 2005 from specimens collected in Belize during the field research described here, and by an entomologist in Costa Rica (Retana-Salazar & Mound, 2005).

Dr. Laurence Mound also determined the sex of visitors collected at staminate and pistillate inflorescences of all four study species (Table 4.5). Although these differences were not significant for all cases (Table 4.6), they do demonstrate highly skewed sex ratios among visiting thrips. More female thrips than male thrips visited staminate

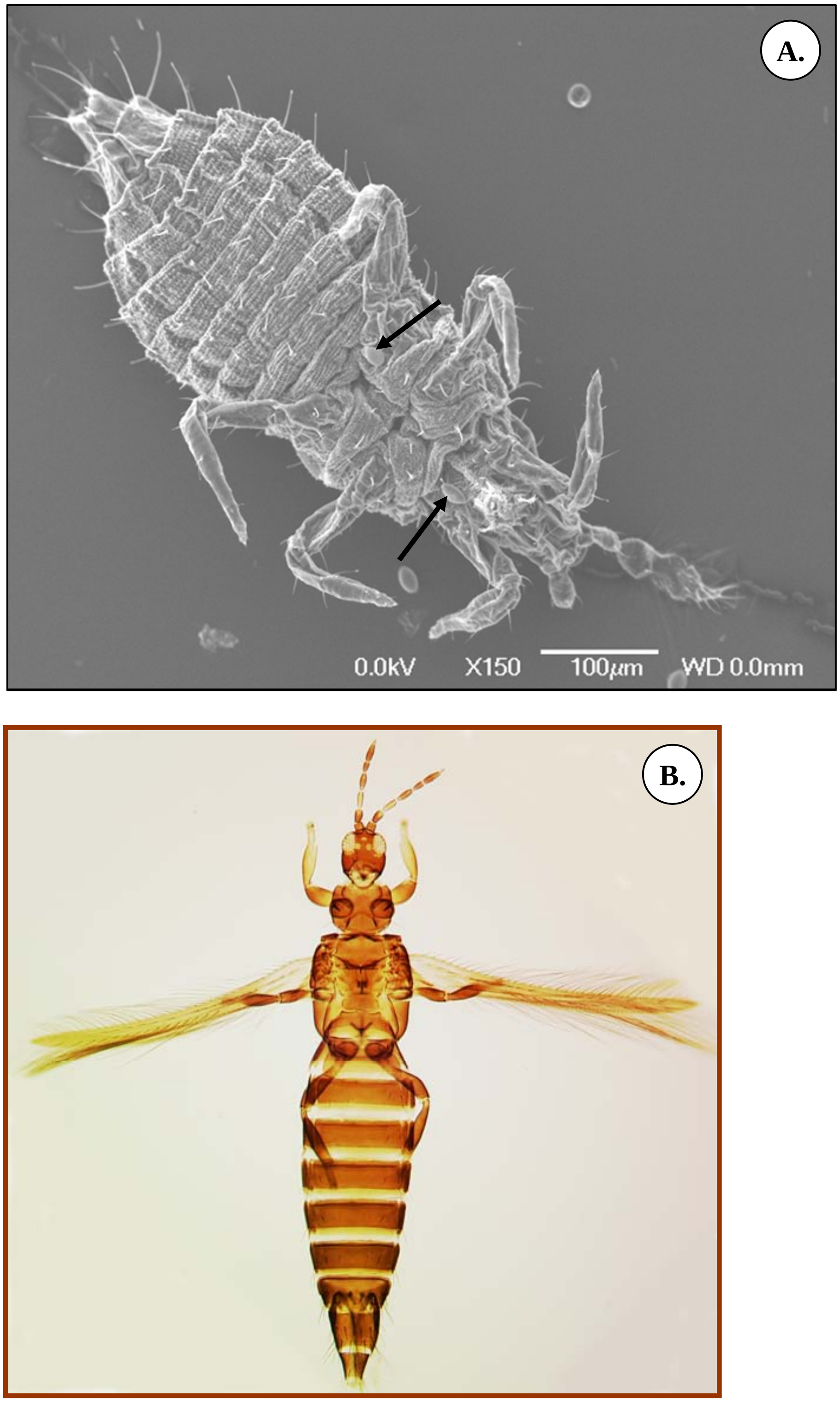


Figure 4.18
A. Scanning electron micrograph of *Brooksithrips chamaedoreae.* Arrows denote pollen grains adhered to the underside of the insect.
B. *Brooksithrips chamaedoreae* Retana & Mound. Photo by L. Mound.

Table 4.5 Number of male and female thrips in samples of visitors collected from staminate and pistillate *Chamaedorea* inflorescences at Las Cuevas Research Station, Belize. All samples sexed by Dr. Lawrence Mound, CSIRO.

	Thrips from Staminate Flowers			Thrips from Pistillate Flowers		
Species	**Sample**	**Male Thrips**	**Female Thrips**	**Sample**	**Male Thrips**	**Female Thrips**
C. ernesti-augustii	A	26	50	A	5	3
	B	30	70	B	100	12
	C	0	11	C	10	3
	D	7	4	D	40	2
	E	4	37	E	55	50
C. oblongata	A	4	22	A	11	0
	B	5	3	B	22	2
	C	2	10	C	20	8
	D	12	47	D	12	0
	E	0	11	E	5	1
C. neurochlamys	A	10	80	A	23	15
	B	6	4	B	2	1
	C	50	80	C	7	1
	D	12	30	D	1	0
	E	9	40	E	15	2
C. tepejilote	A	1	15	A	136	2
	B	8	24	B	8	1
	C	20	30	C	30	1
	D	0	4	D	4	2
	E	80	220	E	5	0

Table 4.6 Results of t-tests for differences in the number of male and female thrips in samples of visitors collected from staminate and pistillate *Chamaedorea* inflorescences at Las Cuevas Research Station, Belize. All samples sexed by Dr. Lawrence Mound, CSIRO. Non-significant values (p > .05) are denoted in table as n.s.

Taxon/Sex	t	df	Significance
C. ernesti-augustii			
Pistillate	1.435	8	n.s.
Staminate	-1.411	8	n.s.
C. oblongata			
Pistillate	3.415	8	n.s.
Staminate	-1.752	8	n.s.
C. neurochlamys			
Pistillate	1.153	8	n.s.
Staminate	-1.740	6	n.s.
C. tepejilote			
Pistillate	1.399	4	n.s.
Staminate	-0.851	8	n.s.

inflorescences of each study species. Also, greater numbers of male thrips were captured at pistillate inflorescences than were female thrips for all species.

4.3.7. Sticky Traps

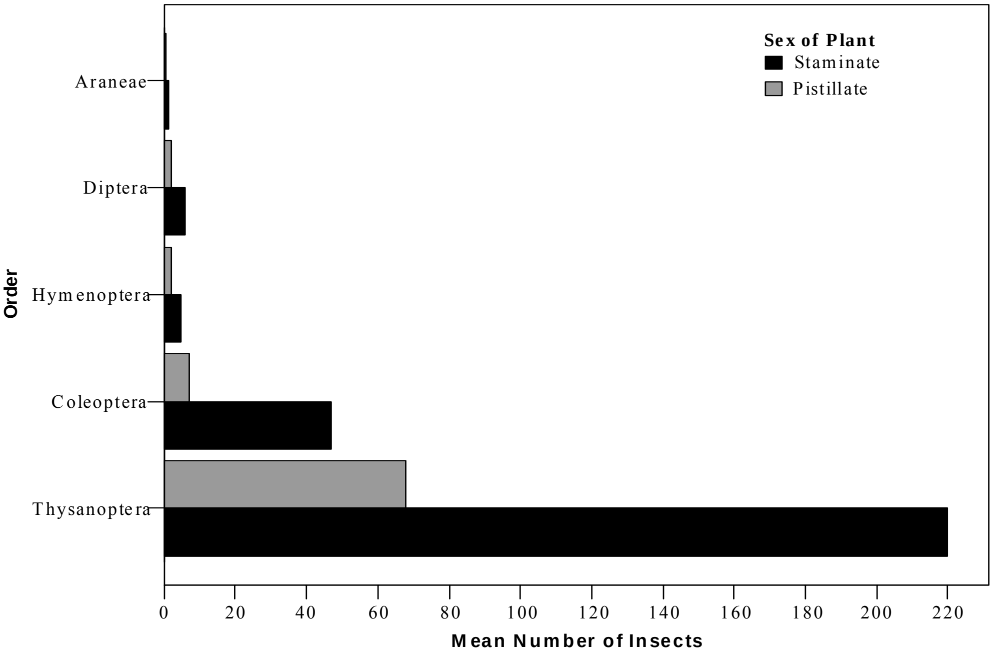
The sticky traps placed near staminate and pistillate individuals from each of the four study species were examined and all visitors identified to order. Using the dissecting microscope available at the field laboratory, pollen surrounding thrips' bodies was able to be observed, as it had been dislodged and trapped in the viscous coating after the insects landed (Terry et al., 2005). This confirms the fact that many of thrips captured on the traps were carrying pollen. The pollen grains observed here were not counted, due to the equipment available in the field laboratory.

The majority of visitors recorded during field observation periods were represented on the sticky traps and in comparable numbers (Figure 4.19). For example, the majority of insects on sticky traps were thrips (80.42%) (Table 4.7), and this percentage is in agreement with the relative abundance of thrips during observation periods.

Table 4.7 Mean number of visitors per order captured on sticky traps near staminate and pistillate individuals of *Chamaedorea* spp. (n = 16, 2 traps per sex for each species). Standard deviation and range also are indicated for each order.

Sex of Focal Palm	Thysanoptera	Coleoptera	Diptera	Hymenoptera	Araneae
Staminate	219.87 ± 73.91 (99 – 378)	46.81 ± 60.40 (4 - 233)	5.81 ± 4.60 (1 – 18)	4.56 ± 3.84 (1 - 14)	1.25 ± 1.06 (0 - 3)
Pistillate	67.75 ± 57.22 (9 – 237)	7.12 ± 11.05 (0 – 27)	2.0 ± 1.26 (0 – 4)	2.0 ± 1.78 (0 – 7)	0.43 ± 0.51 (0 - 3)

Figure 4.19 Mean number of visitors per order captured on sticky traps near staminate and pistillate individuals of *Chamaedorea* spp. (N = 16, two traps per sex for each species).



4.3.8. Air-Borne Pollen

As no compound microscope was available for use in the field laboratory, and the slides became moldy within a week, it was not possible to determine the identity of pollen adhered to the slide traps. It was feasible, however, to determine if wind-borne pollen was collected on the slides. For each of the species, as well as near both sexes of each species, the exposed slide traps were found to have collected pollen. Although pollen amounts were not quantified due to reasons described above, I was able to make general conclusions about the quantity of pollen collected by different traps.

In all cases, the abundance of pollen was higher for the slides near staminate individuals than for the slide traps near pistillate individuals. Another factor that was found to affect the amount of pollen collected was plant density. That is, how close was the focal palm to other palms. For individuals that were in close proximity (< 1 meter) to other individuals (n = 14), more pollen adhered to the slides than for those that were more isolated (n = 4). The issue of palm density affected the difference in pollen collected on slides placed at three and five meter intervals from the plants in the same manner resulting in less pollen. Again, the palms that were clumped collected noticeably higher pollen loads, than did those that were more remote. Still, it was obvious, even with the available equipment that the amount of pollen collected decreased with distance from the focal plant. However, in one case, this was not the case, as the more distant slide traps were located in the immediate vicinity of a flowering male and thus collected high amounts of pollen.

Finally, it is important to note that the slides placed inside of eight (2 per species) small mesh treatment bags did capture pollen. As above, the pollen amounts appeared to be higher when staminate individuals were in close proximity (< 1 meter) and lower when they were further away (> 2 meters). These results are relevant, as they demonstrate that the small mesh treatment, while permitting entry to only the smallest insects, also allows pollen to enter.

4.3.9. Thrips' Pollen Loads

Of the 40 thrips collected, two of those from staminate inflorescences carried no pollen, while six of those from pistillate inflorescences were not transporting pollen. For thrips captured at staminate inflorescences, an average of 73.27 pollen grains per thrips (SD = 62.48, range 0-212, n = 20) was found adhering to the specimens (Table 4.8). A mean pollen load of 21.42 pollen grains per thrips (SD = 21.18, range 0-88, n = 20) was calculated for individuals trapped at pistillate inflorescences. The majority of thrips carried pollen on various portions of their bodies including the pollen carried on their fringed wings, as well as on the legs, thorax, setae, and abdomen.

4.3.10. Pollination System

Results of the experimental bagging treatments are summarized in Table 4.9. All of the individuals tested for apomixis (the closed bag treatment) failed to set seed, and therefore were not included in the post hoc analyses. Although the lack of apomixis was expected, a portion of these results may be due to the microhabitat within the pollination bags; relatively hot and humid in comparison to natural conditions. Nonetheless, the total exclusion experiments demonstrate that apomixis does not occur in *C. ernesti-augustii*, *C. oblongata*, *C. neurochlamys*, or *C. tepejilote*.

For all four species, the control treatment plants consistently produced the highest fruit set (Figures 4.20-4.23). Under natural pollination conditions, an average of 26.64% to 48.26% of the flowers produced fruit, dependant on species. When the largest pollination vectors, such as bees, were excluded and smaller pollinators, as well as wind-borne pollen were allowed entry to the inflorescence (the large mesh treatment; 1 mm /1000 μm per aperture), the second highest fruit set (22.04%-36.22%) occurred for

Table 4.8 Average pollen loads of thrips collected at staminate and pistillate *Chamaedorea* spp. inflorescences (N = 40, five per sex for each species).

Sex of Focal Inflorescence	Sum	Mean ± SD	Range	# Thrips with No Pollen
Pistillate	857	21.42 ± 21.18	0 - 88	6 of 20
Staminate	2931	73.27 ± 62.48	0 – 212	2 of 20

Table 4.9 Percentage fruit set in *Chamaedorea* species under the indicated bagging treatments. Closed bag = exclusion of wind and visitor carried pollen; Mesh, large = 1 mm/ 1000 µm per aperture; Mesh, small = 0.1 mm/100 µm per aperture; Open bag = exclusion of wind and large visitor carried pollen; Control = untreated.

Species / Treatment	Mean Fruit Set	SD	Range	N
C. ernesti-augustii				
Closed bag	0.00%	0.00%	NA	10
Mesh, large	33.10%	11.87%	13.66% - 51.84%	22
Mesh, small	25.67%	13.57%	9.00% - 50.00%	13
Open bag	29.19%	11.44%	13.55% - 47.22%	17
Control	46.96%	16.63%	23.53% - 75.59%	22
C. oblongata				
Closed bag	0.00%	0.00%	NA	10
Mesh, Large	36.06%	12.36%	19.87% - 67.65%	14
Mesh, Small	31.82%	12.83%	14.88% - 61.09%	15
Open Bag	43.73%	16.62%	16.66% - 75.00%	14
Control	48.26%	22.25%	14.42% - 94.60%	16
C. neurochlamys				
Closed bag	0.00%	0.00%	NA	10
Mesh, Large	22.04%	8.29%	11.00% - 32.40%	10
Mesh, Small	19.68%	5.58%	12.40% - 33.00%	12
Open Bag	18.68%	6.36%	11.44% - 33.40%	13
Control `	26.64%	8.67%	12.70% - 40.78%	14
C. tepejilote				
Closed Bag	0.00%	0.00%	NA	10
Mesh, Large	36.22%	10.72%	19.40% - 54.85%	12
Mesh, Small	32.69%	7.31%	23.60% - 49.80%	10
Open Bag	35.22%	12.17%	19.75% - 62.78%	13
Control	40.34%	8.11%	26.45% - 55.00%	13

the species *C. ernesti-augustii*, *C. neurochlamys*, and *C. tepejilote*. However, for *C. oblongata*, inflorescences subjected to the open bag treatment experienced the second highest fruit set (43.73%) in relation to controls. The exclusion of all but the smallest insects and air-borne pollen with the small mesh treatment (0.1 mm/100 µm per aperture) resulted in the lowest fruit set (25.67%-32.69%) for *C. ernesti-augustii*, *C. neurochlamys*, and *C. tepejilote*, while in the species *C. neurochlamys*, the open bag treatment produced the lowest fruit set (18.68%).

The open bag treatment, which was designed to exclude wind-borne pollen, yet allows insect access, produced mixed results. For *C. ernesti-augustii*, and *C. tepejilote*, the fruit set was only higher than that of the small mesh treatment (29.19% and 35.22%, respectively). Conversely, for *C. oblongata*, the open bag treatment produced a higher fruit set (43.73%) than either the large mesh or small mesh treatments. As mentioned above, unlike its sympatric relatives, the final species *C. neurochlamys*, produced its lowest number of fruit (18.68%) under the open bag treatment.

Kruskal-Wallis tests (Table 4.10) determined that the fruit set among control inflorescences was significantly higher than that of flowers subjected to the experimental treatments for both *C. ernesti-augustii* (H (3) = 16.54, $p < .001$) and *C. oblongata* (H (3) = 8.45, $p < .05$). On the other hand, no statistically significantly differences were found between control and treatment inflorescences for either *C. neurochlamys* (H (3) = 6.7, *ns*) or *C. tepejilote* (H (3) = 4.86, *ns*).

Non-parametric Mann-Whitney post hoc tests were conducted for the two species that were found to have significant differences (Table 4.11). As three comparisons were conducted, a Bonferroni correction of $p < 0.0167$ ($p = 0.05/3$) was used. For the first of these species, *C. ernesti-augustii*, the tests determined that more of the treatments for this species were significantly different than those of *C. oblongata*; in fact, all three treatments were significant. The large mesh treatment was found to be significantly different from the control (U = 137, p < .0167, r = -.286), as was the small mesh treatment (U = 46, p < .001, r = -.385), and the open bag treatment (U = 155, p < .001, r = -.373). Conversely, for the species *C. oblongata*, a single treatment was found to be significant, the small mesh treatment (U = 55, p < .0167, r = -.334).

Table 4.10 Results of Kruskal-Wallis analyses testing for differences in fruit set among bagging treatments for each *Chamaedorea* species. Significant values (*p* < .05) are denoted in table with an asterisk (*).

Species	H	df	*p*
C. ernesti-augustii	16.54	3	.001*
C. oblongata	8.45	3	.038*
C. neurochlamys	6.70	3	.082
C. tepejilote	4.86	3	.182

4.4. Discussion

4.4.1. *Chamaedorea* Pollination by Thrips

The study described here, including the species *Chamaedorea ernesti-augustii*, *C. oblongata*, *C. neurochlamys*, and *C. tepejilote*, is only the fourth study of pollination biology known for this genus, and the first to report entomophily. Previous studies of *Chamaedorea* pollination (Listabarth, 1992a; Otero-Arnaiz & Oyama, 2001; Berry & Gorchov, 2004) concluded that the main pollen vector was wind. However, this study produced results that clearly demonstrate thrips are the primary pollination vector for the

Table 4.11 Results of Mann-Whitney post hoc tests for differences in fruit set among bagging treatments for each *Chamaedorea* species. Significant values (Bonferroni correction of $p = 0.05/3 < 0.0167$) are denoted in table with an asterisk (*). No post hoc tests were conducted for fruit set values of *C. neurochlamys* or *C. tepejilote*, because both had non-significant results for the Kruskal-Wallis test.

Species/Test	U	Significance
C. ernesti-augustii		
Test 1: Large Mesh compared to Control (no mesh)	137.0	.014*
Test 2: Small Mesh compared to Control (no mesh)	46.0	.001*
Test 3: Open Bag compared to Control (no mesh)	155.0	.001*
C. oblongata		
Test 1: Large Mesh compared to Control (no mesh)	72.5	.101
Test 2: Small Mesh compared to Control (no mesh)	55.0	.010*
Test 3: Open Bag compared to Control (no mesh)	103.0	.708

four *Chamaedorea* species investigated. Several pieces of evidence support the role of thrips as pollinators including visitor observations, thrips' abundance, pollen loads, and behavior, and the results of the exclusion experiments.

Field observations of floral visitors demonstrate that the most abundant visitor to both staminate and pistillate inflorescences of all four study species is thrips. These results are corroborated by the counts of insects collected with sticky traps, where thrips constituted over 80% of the captured insects. Although some of the other visitors to staminate inflorescences, such as bees, ants, and spiders, also were found to visit pistillate inflorescences, they did not do so in the numbers necessary for pollination, nor do they exhibit behavior indicative of pollinators (e.g. contact with receptive stigmas).

The contribution that thrips make to *Chamaedorea* pollination cannot be determined based only on their high abundance at inflorescences. They also must carry pollen on their bodies and behave in a way that allows the pollen to be carried to a receptive stigma. The first criterion was met by quantification of pollen loads from thrips collected at staminate and pistillate inflorescences, 73.27 grains per thrips and 21.42 grains per thrips, respectively. These counts confirm that thrips do indeed transport pollen between individuals. The pollen loads recorded here are comparable to those found in other studies where thrips were reported as the primary pollen vectors (Mound & Terry, 2001; Sakai, 2001; Terry, 2001; Moog et al., 2002; Terry et al., 2005).

Although the number of pollen grains carried by a single thrips is certainly sufficient to effect pollination, it is likely that thrips transport pollen from more than one *Chamaedorea* species at a time. Nonetheless, the densities of visiting thrips are high enough for these tiny insects to be effective pollinators (Mound & Terry, 2001). It is important to note that the differences in pollen load between thrips from staminate and pistillate inflorescences, as well as the large range of carried pollen, was expected. One reason is because thrips regularly groom their bodies, thereby removing some pollen (Lewis, 1973; Kirk, 1996; Williams et al., 2001), a behavior that was observed during the course of this study. Other factors that may reduce pollen loads include the stage at which staminate flowers are visited (dehisced, non-dehisced, after most of the pollen has been shed), previous visitation to pistillate flowers, which would result in the deposition of some portion of the pollen load to the stigmas, and the distance between staminate and pistillate individuals (Terry et al., 2005). The further the distance between sexes, the more likely that pollen will be dislodged from thrips during flight.

In terms of behavior that might enact pollination, thrips are very small relative to *Chamaedorea* flowers, and therefore must enter the flowers to obtain rewards such as pollen and nectar. In this manner, they collect pollen on their bodies, or their activity deposits pollen on stigmas. The only other insects that exhibit behavior indicative of pollinators are staphylinid beetles, which carry pollen between the staminate and pistillate inflorescences of only one species, *C. tepejilote*, yet in smaller quantities than do thrips. During daylight hours, thrips are readily observed moving between flowers, as well between staminate and pistillate individuals. Little activity transpires at night, when thrips remain inside flowers. The highest thrips activity occurs when light intensity is high, sunlight is available, and the temperature is above 21º C (Lewis, 1973). These constraints are due to the fact that thrips are unable to take-off from an inflorescence if conditions are too cold or rainy and will not take flight in low light. This also explains why flight between inflorescences, as well as movement between flowers of an inflorescence, abates approximately one to two hours prior to sunset.

4.4.2. Experimental Bagging Treatments

Another line of evidence supporting thrips pollination is the results of the experimental bagging treatments. The tests for apomixis demonstrate that when no insects or wind-borne pollen have access to pistillate inflorescences, no fruit are set. Therefore, a pollen vector is necessary in order to enact fertilization in the *Chamaedorea* species studied. These results are equivalent to those of many other palm pollination studies, where no apomixis was reported (Búrquez et al., 1987; Anderson et al., 1988; Otero-Arnaiz & Oyama, 2001; Voeks, 2002).

The highest fruit set was found in the naturally-pollinated control inflorescences for all species. For the large mesh treatment, in three of the four species studied, the fruit set was lower than of the open, control inflorescences. However, these differences were small, between 4.12% and 13.86%, demonstrating that the large mesh treatment had less of an impact on fruit set and thus on the access of pollen vectors to pistillate inflorescences, than did the other experimental treatments.

However, based on the Mann-Whitney tests, the difference between control and large mesh fruit set was significant in *C. ernesti-augustii*. It is possible that the small number of flowers produced by this species, an average of 44.44 compared to an average of 443.93 flowers for pistillate inflorescences of the other study species (see Table 3.3), inflated results such that the impact was statistically higher for *C. ernesti-augustii*. Nonetheless, by excluding all pollen vectors except small insects and wind-borne pollen, the large mesh treatment effectively reduced the pool of potential pollen vectors to these two choices.

Likewise, the lowest fruit set relative to natural pollination was found in those inflorescences bagged with small mesh, for three of the four study species. The reason that the open bag treatment yielded less fruit than did the small mesh in *C. neurochlamys* remains unknown. The fact that the fruit set was far lower in the small mesh treatment than in the control is intriguing, as I had expected these two values to be fairly similar. Still, it is likely that the bags prevented some amount of wind-borne pollen from entering by covering a large portion of the surface area. Also, it is apparent that the mesh used in this treatment, as well as that used in the large mesh treatment, deterred thrips' visitation to some degree. Even so, thrips were observed on bagged inflorescences of both treatments during anthesis. I suspect that the mesh material may diminish the visual impact of the floral display, and it may also have an odor that affects thrips' attraction to inflorescences. This is supported by the fact that in two of the species, *C. ernesti-augustii* and *C. oblongata*, the difference between control and small mesh was statistically significant. Yet, despite the presence of these issues, the results of the small mesh treatment demonstrate that that the only possible pollen vectors are thrips and wind-borne pollen.

The open bag treatment, which was designed to exclude air-borne pollen, but allow thrips to enter, yielded similar results to that of the small mesh treatment for three of the species (excepting *C. oblongata* for which it inexplicably produced a higher fruit set than the large mesh treatment). These results were expected, as I assume that only a small amount of pollen is delivered to the flowers via wind, and thrips are the primary pollinators. Even though thrips were observed to visit the open bagged inflorescences, the number of visitors was lower than anticipated, probably because some thrips were deterred by the sight and smell of the plastic exclusion bags, as well as the very high humidity created by the enclosures. Also, of all the experimental treatments tested, the open bag was the most likely to disrupt the dispersion of fragrance from pistillate flowers, thereby attracting fewer visitors. As with the large mesh treatment, the fruit set for the open bagged inflorescences was not significantly different from that of the controls in all species except *C. ernesti-augustii*. These results, along with those of the other experimental treatments, support the probability that thrips are the main pollen vector for the four studied species of *Chamaedorea*.

4.4.3. Why do Thrips Visit Pistillate Inflorescences?

Based on the evidence presented thus far, one might suspect that thrips are attracted to pistillate inflorescences because they mimic the staminate inflorescences. I have reported that pistillate inflorescences produce flowers similar in color to staminate flowers when at anthesis, and they emit a fragrance that is similar to that released by staminate flowers, albeit not as strong. Also, pistillate flowers offer a sugary stigmatic exudate as a reward. Still, it is unlikely that these relatively weak rewards would entice thrips to leave staminate inflorescences in order to visit pistillate inflorescences, and potentially result in pollination. Therefore, with thrips demonstrated to be the primary pollinators of these *Chamaedorea* taxa, the question of why they visit pistillate inflorescences must be asked.

The reasons for thrips visitation to staminate inflorescences are obvious. With more than twice as many flowers as the pistillate inflorescences, the inflorescences produced by staminate individuals exhibit highly visible floral displays. They also emit strong fragrances that attract numerous visitors, including large numbers of thrips. Once at an inflorescence, the staminate flowers provide a number of rewards including nectar from the pistillode, copious pollen, and fleshy petals on which to feed. Pollen is an important source of protein for thrips. These insects have mouthparts characterized as piercing and sucking, which they use to extract the contents of pollen grains (Kirk, 1984). Pollen's significance to thrips stems from the fact that it provides the necessary nutritious for mating, and it may actually by required by female thrips to achieve the energy needed for oviposition (Lewis, 1973; Mound, pers. comm.).

In addition to pollen, staminate flowers of all the species have a very different structure than the pistillate flowers (except for those of *C. ernesti-augustii*), which allow them to provide a highly attractive reward, brood sites. The bases of their thick petals create enclosed floral chambers, exactly the type of area that thrips prefer as a brood site. The oviposition of thrips eggs in staminate *Chamaedorea* flowers was observed directly in the laboratory, and it is further supported by the fact that toward the end of the floral life cycle, large quantities of thrips larvae may be seen emerging from the drying staminate flowers and covering the rachillae. The flowers also provide pollen and floral tissues that sustain the developing larvae.

As a bonus, this floral structure entices thrips to remain inside the staminate flowers overnight, by offering food and shelter during the hours when the light intensity is low and thrips do not fly (Lewis, 1973). Evidence of damage on petals of flowers at late anthesis suggests herbivory by thrips, however it is not known how much of the observed damage results from the insertion of eggs and subsequent feeding of hatched larvae on floral tissue, and how much is due to the actions of adult thrips or other insects. Although both male and female thrips were collected from staminate inflorescences, it is likely that male thrips visit the flowers for food and possibly mating opportunities, but do not remain at inflorescences as long as females. This is supported by the skewed sex distribution found on staminate inflorescences, where female thrips heavily outnumber the males. As the female thrips utilize the flowers not only for food, but also as a location in which to lay their eggs, they would be expected to occur in higher numbers on staminate inflorescences. Thus, with all of the rewards offered by staminate flowers, it appears implausible that either male or female thrips would leave them to visit pistillate inflorescences, yet they do. Is it possible that the mimicry of staminate flowers is so well enacted by pistillate flowers that they are able to lure thrips to them?

Actually, the situation found in *Chamaedorea* is far more complex than that of classic ‘deceit’ pollination system, also termed Batesian mimicry, whereby pistillate flowers produce cues that mimic those of males, yet do not provide a reward (Dafni, 1984; Proctor et al., 1996). As stated above, the pistillate flowers of the studied *Chamaedorea* species do produce stigmatic exudates, which are consumed by visiting insects. By virtue of this reward alone, the issue of deceit pollination can be dispelled. However, in light of the data collected during this research on other rewards, the production of nectar may be viewed only as a secondary reward.

One of the most significant outcomes of the research presented here is the observation that thrips visit pistillate inflorescences in large numbers, although not as large as the numbers that visit staminate inflorescences. This observation is especially interesting, because the three previous studies of *Chamaedorea* pollination reported low to no visitation of pistillate flowers by thrips (Listabarth, 1992a; Otero-Arnaíz and Oyama, 2001; Berry and Gorchov, 2004). In fact, during the peak hours of insect visitation, I observed thrips not only swarming over staminate inflorescences, but also aggregating on pistillate inflorescences. The most visible case of this phenomenon was observed in the species, *C. tepejilote*, where the thrips stand a few centimeters apart from one another, and remain on pistillate inflorescence in this manner for hours. A clue as to why thrips exhibit this behavior is provided by the sex ratios of male to female thrips. On pistillate inflorescences, the majority of thrips are male, not female as found on staminate inflorescences. I suggest that these aggregations of males offer the main reward for visiting pistillate inflorescences, that of mating opportunities.

While the use of inflorescences or flowers as thrips' mating sites has been recognized (Kirk, 1985, 1996; Kiers, 2000), researchers have only recently begun to study the intricacies of this behavior (Zerega et al., 2004; Webster et al., 2006). Aggregations of males are described for several thrips species, and they tend to occur near areas housing large numbers of female thrips (Terry & Gardner, 1989; Terry, 1997; Mound & Jackman, 1998; Terry et al., 2005). Additionally, these males engaged in these clusters release a pheromone from a series of sternal glandular areas. Through controlled laboratory experiments, Webster et al. (2006) established that these glandular areas emit a chemical that is attractive to female thrips. Additionally, this odor, which the authors termed an "aggregation pheromone," is released in larger quantities during times of peak mating activity, which correspond with the hours during which thrips are most active (e.g. mid-morning) (Webster et al., 2006). The thrips involved in pollinating the *Chamaedorea* species in this study, *Brooksithrips chamaedoreae*, are confirmed to bear a number of these sternal glands (Retana-Salazar & Mound, 2005). It is likely that they gather in large groups in order to more effectively attract female thrips through collective pheromone emission. The results of this study, along with current research on thrips' pheromones, suggest that the aggregated male thrips observed on pistillate *Chamaedorea* inflorescences are releasing a chemical from their sternal glands that functions to attract females to these inflorescences for the purpose of mating (Kirk & Hamilton, 2004). Although thrips do occur in abundance on staminate inflorescences, it is difficult to determine if the thrips on staminate rachillae are aggregations for mating or simply a result of the large quantity of thrips that visit in order to feed on pollen. Based on their morphology, pistillate inflorescences do provide a more open and less crowded venue for mating to occur. Still, it can be assumed that some degree of mating transpires, as both male and female thrips are found on staminate inflorescences, albeit male thrips are present in much lower numbers.

4.4.4. Mutualism Between Thrips and *Chamaedorea*

When the life cycle of the pollinating thrips, *Brooksithrips chamaedoreae*, is examined in the context of the reproductive activities of the *Chamaedorea* species involved in this study, it becomes clear that these thrips and *Chamaedorea* are involved in a highly specialized dependent mutualism. Based on my observations, the life cycle of *Brooksithrips chamaedoreae* occurs as follows. Adult female thrips lay eggs inside of staminate *Chamaedorea* flowers and, after hatching; the larvae feed on the drying flowers and rachillae. Next, larvae probably pass through at least one more larval stage before they either drop to ground of their own accord, or fall with the senescing flowers (Lewis, 1973). There is probably one generation each year. The thrips remain in the soil, usually within the top 30 cm (Lewis, 1973; Kirk, 1996), for the duration of the rainy season. Pupae are cued to complete their development and become adult thrips by the rising temperature and reduction of rain that signals the beginning of the warm, dry season. The adult thrips emerge from the soil, where they have spent the cool and rainy ‘winter’ months and seek out *Chamaedorea* flowers. Due to the clustered distribution of the palms, as well as the fact that the larvae fall to the ground under their parent plants, *Chamaedorea* flowers tend to be located easily. Also, the phenology of these

Chamaedorea species is such that they flower soon after the rainy season ends. Thus, the flowers become available at approximate the same time as the adult thrips are emerging.

Male thrips visit staminate inflorescences primarily for pollen and other nutritional rewards, while they visit pistillate inflorescences primarily to entice females for mating activity. On the other hand, female thrips visit staminate inflorescences for both nutritional rewards, specifically pollen, and to utilize staminate flowers as a brood site. Female thrips are attracted to pistillate inflorescences primarily by the male-produced sex pheromone during the peak hours of activity for mating opportunities, rather than by the fragrance produced by the pistillate inflorescence. As pollen has been cited as a food that provides the necessary energy for thrips mating, the majority of the thrips arriving at the pistillate inflorescences of *Chamaedorea* for copulation may have previously visited staminate flowers and therefore be carrying *Chamaedorea* pollen.

It is important to note that female thrips must oviposit in staminate flowers that have not yet undergone anthesis, because the hatching of eggs and development of larvae to a stage where they are able to leave the inflorescence and pupate requires approximately eight days, and the flowers are at anthesis only for four to six days (Kirk, 1996). Therefore, eggs must be laid prior to anthesis to ensure the proper amount of development time. This requirement is not problematic for thrips, as they tend to oviposit in small, closed locations, where their bodies are in maximum contact with the surrounding floral tissues (Lewis, 1973; Terry, 2001). The opening flowers of *Chamaedorea* provide enclosed floral chambers, which thrips utilize as areas in which to lay their eggs (Lewis, 1973; Kirk, 1985). Also, by entering the flowers and ovipositing prior to anthesis, thrips allow their eggs the time necessary for development. Therefore, the timing of oviposition and the timing of floral development and anthesis are closely linked.

4.4.5. Conclusions

In sum, the results of pollination observations and experiments for *Chamaedorea ernesti-augustii*, *C. oblongata*, *C. neurochlamys*, and *C. tepejilote* demonstrate that insects, specifically insects of the thrips species, *Brooksithrips chamaedoreae*, are likely to be the primary pollen vectors. This thrips pollinates all four study species and is engaged in a mutualism with the palms whereby the thrips is dependant upon *Chamaedorea* flowers for reproduction and the *Chamaedorea* is dependant on the thrips as their most effective pollinator. As the palms flower relatively synchronously, both pollinator identity and flowering phenology may be ruled out as mechanisms for reproductive isolation and an incompatibility system is posited. Although some wind-borne pollination is probable in those species with exposed stigmas (*C. oblongata*, *C. neurochlamys*, and *C. tepejilote*), wind is considered to be a secondary pollination vector based on the results of exclusion experiments.

Chapter 5

Discussion

5.1. Summary

This study concerns the reproductive biology of four sympatric palm species, *Chamaedorea ernesti-augustii*, *C. oblongata*, *C. neurochlamys*, and *C. tepejilote*, in Belize. The main questions addressed in this thesis were:

- What is the flowering phenology for each of the study species?
- What is the primary pollination vector for each of the study species?
- What differences exist between the study species with respect to floral morphology, insect visitation and behavior, and floral activity during anthesis?

Over a three-year period, a number of research activities were performed to answer these questions. By establishing a series of plots and following the *Chamaedorea* individuals located therein on a monthly basis for two years, flowering patterns were determined. Both field observations and experiments were utilized to examine the characteristics of pollination. Observations determined the identity of any insects that visited each sex of the four study species, the quantity of insects that visited, and their activities when at the inflorescences. Additionally, experiments in the field station's laboratory and *in situ* investigated such issues as the impact of excluding various pollen vectors, pollen loads, and the presence of air-borne pollen. The results of this research provided answers to the study questions, and also revealed the different factors and interactions that contribute to the complex pollination systems of these *Chamaedorea* species. The main conclusions are as follows: study species are pollinated by thrips, these thrips are engaged in a dependant mutualism with the palms, and this mutualism is supported by the flowering phenology of the *Chamaedorea* community. The following sections detail these findings and describe how different components of *Chamaedorea* reproductive ecology are related to function of the pollination system as a whole.

5.2. Thrips Pollination of *Chamaedorea*

Despite the conclusions of anemophily for other *Chamaedorea* species (Listabarth, 1992a; Otero-Arnaiz and Oyama, 2001; Berry and Gorchov, 2004), the research described here established that *C. ernesti-augustii*, *C. oblongata*, *C. neurochlamys*, and *C. tepejilote* are primarily entomophilous. To determine which of the observed floral visitors were the main pollen vectors, I employed Baker and Hurd's (1968) criteria for pollinators. For an insect to be an effective pollinator in a dioecious species, the criteria state that the insect must visit the inflorescences of both staminate and pistillate individuals, visit in sufficient numbers to enact pollination, transport pollen on their bodies, and behave in a manner that allows them to deposit pollen on receptive stigmas. Adhering to these requirements, I was able to eliminate all of the visitors to *Chamaedorea* individuals except for thrips and staphylinid beetles (although staphylinids only were indicated for *C. tepejilote*). Thrips were observed at staminate and pistillate inflorescences of all study species during anthesis, transported sufficient pollen loads, and their activities allowed them to contact stigmas, thereby enacting pollination. Additionally, bagging treatments designed to exclude different visitors confirmed that the only possible pollen vectors of these *Chamaedorea* species are thrips and wind-borne pollen. Further, the bagging experiments demonstrated that the contribution of wind is likely to be minimal.

Thus, thrips are determined to be the primary pollen vectors. Although thrips do visit pistillate inflorescences, they do so in smaller numbers than staminate inflorescences. This finding is especially intriguing, because the three previous studies of *Chamaedorea* pollination reported low to no visitation of pistillate flowers by thrips (Listabarth, 1992a; Otero-Arnaiz & Oyama, 2001; Berry & Gorchov, 2004). However, thrips were noted to be active and abundant visitors to staminate inflorescences by both Listabarth (1992a) and Otero-Arnaiz and Oyama (2001). Otero-Arnaiz and Oyama (2001) suggested that further investigation could provide evidence of thrips involvement in pollen release. Although they did not observe any insect visitors on pistillate inflorescences of *C. alternans*, the authors also stated that they only recorded diurnal visitors to flowering individuals every six days, and as thrips often visit pistillate flowers only for the first few days of anthesis, they may have been missed. Listabarth (1992a) presented detailed descriptions of thrips, floral development, and the behavior of thrips at staminate flowers. Although he concluded that *C. pinnatifrons* is anemophilous, Listabarth (1992a) did state that the activity of thrips in staminate flowers contributed to pollen release. However, the precise relationship between thrips and *C. pinnatifrons* was not demonstrated experimentally. In addition, Listabarth's hypothesis would have been strengthened if he had captured the thrips that visited pistillate inflorescences and examined them to determine if they were carrying *Chamaedorea* pollen. Finally, although Berry and Gorchov (2004) reported no visitors to pistillate flowers of *C. radicalis*, it is possible visits to pistillate inflorescences did occur and either were not noticed due to the small size of the visitors, or the numbers of visitors were so low that they were deemed insignificant as pollinators and therefore not mentioned in the literature.

The contradictions between the results of my study and those of other researchers who investigated *Chamaedorea* pollination systems may be due in part to differences in methodology. Although wind was reported as the only pollen vector, none of these studies included tests for wind-borne pollen (e.g. slide traps), which demonstrate if pollen is carried by wind, the amount of pollen that is wind-borne, and the degree to which pistillate plants at various distances from staminate ones are reached by air-borne pollen. More importantly, based on my field experiments and observations, I believe that the exclusion treatments used by Otero-Arnaiz and Oyama (2001) and Berry and Gorchov (2004) to exclude all possible visitors while allowing entry to wind-borne pollen, were not constructed with mesh of a sufficient size to exclude thrips. The researchers used mesh that measured 0.1 mm per aperture and 0.5 mm per aperture, respectively. In my experiments with a treatment bags constructed with a fine mesh of less than 0.1 mm per opening, all of the thrips that visited were able to enter the bags, move about, and oviposit in flowers. Although thrips tend to be approximately 1-2 mm in length, their body width is a very small fraction of their length, enabling them to enter even fine mesh in a headfirst manner with ease. Although it is possible that different species of thrips are present at the various study sites, the majority of thrips are of such a small size that they are able to move easily through all but the finest mesh.

5.3. Thrips as Effective Pollinators

The conclusion that thrips pollinate the four *Chamaedorea* species studied here is significant, because it represents the first experimental evidence of insect pollination in this genus. These results also are unexpected, as thrips have achieved more renown for their destruction of plants than their pollination (Mound & Jackman, 1998). Thrips are tiny insects that belong to the order Thysanoptera, which can be translated as 'fringed wings.' Typically, adult thrips reach no more than 1-3 mm in length (although there are a few species that are significantly larger) (Kirk, 1996). Approximately 5,550 species of thrips currently have been described throughout the world, with roughly 40% of these classified as flower living (Mound, 2005). Thrips generally are regarded as plant predators, as some taxa are major crop pests, using their piercing-sucking mouthparts to feed upon, damage, and spread viruses to crops such as tomatoes and wheat (Lewis, 1973; Kirk, 1997). Many species subsist on plant tissues, including both vegetative and reproductive parts. Additionally, pollen is a primary component of many thrips' diets, as it is nutritious, containing lipids, proteins, starches, and vitamins (Kirk, 1984, 1996; Roulston & Cane, 2000). Other thrips feed on fungal hyphae, dead wood, and small insects such as mites (Lewis, 1973; Mound, 2005).

In terms of pollination, thrips have been disregarded for a number of reasons. According to Kirk (1997), this view stems from the fact they do not have many of the characteristics typically considered necessary for effective pollinators. First, due to their small size, thrips tend not to be considered in pollination experiments or are simply overlooked when observing plants for potential pollinators. Thrips characteristically occur as part of a larger guild, which includes Coleoptera, Hymenoptera, and Diptera

(Williams et al., 2001). As they tend to be the most inconspicuous of this visitation guild, thrips therefore are the most likely to be deemed ineffectual as pollinators.

In addition, thrips lack specialized organs for use in transporting pollen. Due to their size, the pollen loads carried by thrips are relatively small, a fact which might suggest that they would not be capable of carrying pollen in sufficient quantities to be effective pollinators (Appanah & Chan, 1981; Armstrong & Irvine, 1989). Finally, thrips generally are believed to be poor fliers, with little ability to direct their flight or landings, an important characteristic for any insect transporting pollen from anther to stigma (Kirk, 1997).

It has come to light in the past few decades that many of these assumptions are incorrect, and thrips do indeed play a role in the pollination of several plant species, both as primary and secondary components of pollination systems (Mound, 2005). Although small and relatively unspecialized for carrying pollen, thrips have been observed visiting and moving between plants in large numbers, thereby providing the potential for a great deal of pollen transfer (Kirk, 1988). They have been confirmed to travel distances of several meters, and have the ability to direct their flight to some degree and to land on inflorescences in a deliberate manner (Lewis, 1973; Mound, 2005).

As was observed in this study, a thrips may carry pollen on its thorax, abdomen, setae, and legs. In addition, large numbers of pollen grains easily adhere to the long fringed wings for which these insects are named. Although their pollen loads are low relative to larger insects, thrips do carry pollen loads sufficient to enact pollination, and subsequently, fruit set. In fact, the total amount of pollen transported between sexes is comparable to that of other known pollinators due to the vast numbers of thrips that visit inflorescences (Kirk, 1996; Mound & Terry, 2001; Terry, 2001).

Thrips have been reported as floral visitors for a number of taxa (Lewis, 1973; Norton, 1980; Kirk, 1984, 1985; Armstrong & Irvine, 1989; William et al., 2001; Datwyler & Weiblen, 2004), and many plants in tropical forests are inhabited by thrips (Sakai, 2001). Although evidence for their role in pollination was reported by Darwin (1876), who stated that transportation of pollen between sexes by thrips was a source of error in his experiments, only recently have these insects been considered as legitimate pollinators. A variety of families have been demonstrated as containing species pollinated by thrips including Annonaceae (Momose et al., 1998; Gottsberger, 1999; Silberbauer-Gottsberger et al., 2003), Castilleae (Zerenga et al., 2004), Dipterocarpaceae (Appanah & Chan, 1981), Euphorbiaceae (Moog et al., 2002)**,** Lauraceae (Norton, 1984), Monimiaceae (Williams et al., 2001), Moraceae (Sakai, 2001), Winteraceae (Pellmyr et al., 1990), and Zamiaceae (Mound & Terry, 2001; Terry, 2001; Terry et al., 2005).

Flowers pollinated by thrips tend have a number of characteristics in common, such as white or yellow petals, a discernable to strong fragrance, small, dry pollen that is easily dislodged from the anthers (Kirk, 1997; Williams, 2001). Plants that are thrips pollinated typically have flowers that are cup-shaped, or have petals that form an enclosed, protected area, which can serve as a brood site (Williams & Adam, 1994; Williams, 1995). Kirk (1997) and Williams (2001) have suggested that a thrips pollination syndrome exists, and these characters define plants that are ‘thripophilous.’ While many thrips pollinated flowers do indeed meet these criteria, there are many cases of flowers utilized by thrips for food and oviposition that do not. For example, Mound and Terry (2001) explain that thrips are associated with open and relatively exposed flowers of several families such as Myrtaceae and Rosaceae. Additionally, as thrips have only recently been as accepted as potential pollinators, much more research is needed to determine their floral preferences.

In the case of Arecaceae, a number of researchers have reported small flying insects as visitors to various palm species during anthesis. Several of these studies list thrips as visitors, while others simply state that small flying insects were observed. Still, it is possible that these unknown insects may include thrips. Taxa in which unidentified small flying insects or thrips were observed include *Acrocomia aculeata* (Scariot et al., 1991), *Attalea funifera* (Voeks, 2002), *Bactris* spp. (Listabarth, 1996; Henderson et al., 2000b), *Calamus* spp. (Bøgh, 1996), *Chamaedorea* spp. (Listabarth, 1992a; Otero-Arnaiz & Oyama, 2001), *Cocos nucifera* (Melendez-Ramírez et al., 2004), *Desmoncus* spp. (Listabarth, 1994), *Euterpe precatoria* (Küchmeister et al., 1997), *Geonoma* spp. (Listabarth, 1993), and *Hyospathe elegans* (Listabarth, 2001). In each of these studies, the insects in question were considered minor visitors and not concluded to be pollen vectors.

There is little mention of thrips as potential pollinators in the literature on palm reproductive biology. For example, in their discussion of oil palm plantations (*Elaeis guineensis*), Uhl & Dransfield (1987) state that thrips appears to be the primary pollinator of these palms in some natural populations. Also, Shatz (1990) states that the strong odor and abundance of insects, specifically thrips, during flowering may indicate that thrips play a role in the pollination of *Chamaedorea* species. Still, these conclusions are based on observations only and therefore require experimental evidence for confirmation.

Conversely, the study presented in this thesis describes the first experimental research to conclude that thrips do indeed serve as pollinators in the Arecaceae.

5.4. Thrips and their Relationship with *Chamaedorea*: A Nursery Pollination System

Based on the evidence presented here, the thrips *Brooksithrips chamaedoreae* not only pollinate the four sympatric species of *Chamaedorea* studied, but also they are engaged in a dependent mutualism with their hosts. A mutualism may be described as an association between individuals of different species that produces positive net results for both of the partners (Molles, 2005). A variety of mutualistic interactions have been defined, from obligate mutualisms, in which the partners are so dependent upon one another than they cannot survive in the absence of the relationship, to facultative mutualisms, in which the interspecific association is advantageous for each of the individuals, yet they retain the ability to survive without their mutualistic partner (Kephart et al., 2005).

Based on my research, the relationship between *Brooksithrips chamaedoreae* and the four *Chamaedorea* species studied may be summarized as follows (Fig. 5.1). Thrips are offered a variety of rewards by staminate and pistillate flowers. Staminate flowers attract the visitors with a strong fragrance, and provide the rewards of pollen, nectar, floral tissues, and enclosed areas for laying eggs, which are especially suited to thrips. Pistillate flowers, while emitting a fragrance similar to their staminate counterparts, offer a different reward in the form mating opportunities created by aggregations of male thrips along the rachillae of inflorescences. Some degree of mating may also occur at staminate inflorescences, however the observed aggregations of pheromone emitting male thrips thus far have only been observed at pistillate inflorescences.

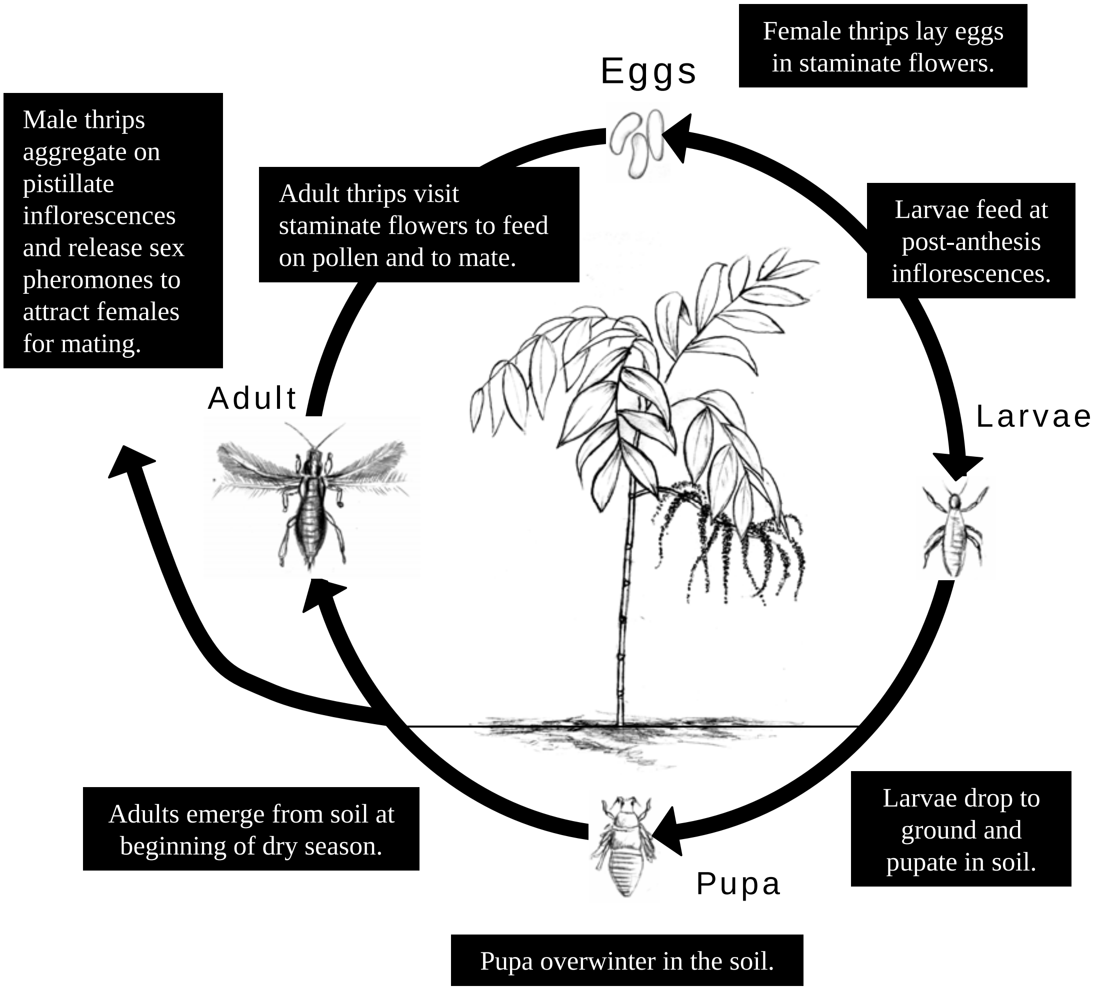


Figure 5.1
Proposed life cycle of *Brooksithrips chamaedoreae* in relation to *Chamaedorea* palms.

Therefore, thrips visit staminate plants to feed, as well as to oviposit, and in the process they collect pollen on their bodies. Thrips visit pistillate plants primarily for the mating opportunities, although some stigmatic exudates are also consumed. At pistillate inflorescences, thrips move across the rachillae assessing their potential mates or finding an unoccupied location from which to emit sex pheromones, and in doing so pollen may be deposited on the prominent stigmas. It is important to note that the pollen of more than one *Chamaedorea* species may be carried on each thrips, thus it is posited that a chemical mechanism is responsible for reproductive isolation in the study species.

The eggs laid in staminate flowers of all four study species, as well as the pistillate flowers of *C. ernesti-augustii*, eventually hatch and the larvae feed on pollen and floral tissues. Although these facts have been confirmed by the present research, the complete life cycle of *Brooksithrips chamaedoreae* needs further intensive study. However, the research presented here, as well as the taxonomic description of Retana-Salazar & Mound (2005), does provide evidence that thrips develop on *Chamaedorea* inflorescences throughout the floral life cycle. After flowering has ceased, the thrips drop to the soil to pupate, overwintering, that is spending the wet season, in the topsoil.

Emergence of adult thrips is triggered by the reduction or cessation of rains and the increasing soil temperatures. Thrips activity coincides with *Chamaedorea* flowering, as the highly synchronized flowering of these palms also exhibits a seasonal pattern. It should be noted that, as the availability of both adult thrips and *Chamaedorea* flowers is dependant on seasonality, the pollination cue therefore is abiotic. Thus, as thrips emerge from the soil, they are attracted to *Chamaedorea* that are in the correct developmental stage (e.g. nearing anthesis), and thereby repeat the entire process. In this manner, the thrips are provided with food and sites for reproduction, while the palms benefit from a dedicated group of insects that transport their pollen from staminate to pistillate flowers.

In this study, the *Chamaedorea* species and the pollinating thrips are engaged in a highly specialized relationship called a nursery pollination system (Dufäy & Anstett, 2003). A nursery pollination system is a mutualism in which an insect reproduces in or on the reproductive structures of their host plant. Many of these systems are known (see Dufaÿ & Anstett, 2003), and they typically entail a tradeoff between the advantages and disadvantages of supplying a breeding site for pollinators. The plant benefits by breeding insects that will disperse its pollen, and the insect benefits from availability of an egg-laying site and location for larval development.

Several researchers have identified nursery pollination systems between palms and their pollinators (Henderson, 1986; Anderson et al., 1988; Listabarth, 1994; Anstett, 1999; Henderson et al., 2000b; Consiglio & Bourne, 2001; Núñez et al., 2005). For example, Listabarth (1996) has described two species of *Bactris* in which the pollinators reproduce within the flowers of the plants they pollinate. The author explains that the palms maintain their pollinators by providing large number of flowers that serve as sites for mating activity, oviposition, and sustenance for the emerging larvae. In exchange, the insects carry pollen from inflorescences at male phase to those at female phase. Listabarth (1996) also discusses how these *Bactris* species, along with two species of the genus *Desmoncus* constitute a palm assemblage in which the members exhibit similar pollination systems and provide brood sites for their common pollinators. The beetles that are engaged in mutualism with these palms are supported throughout the flowering period by staggered flowering of the different taxa, as well as by multiple flowering episodes in a few species.

Similarly, Scariot et al. (1991) describe the relationship between pollinating beetles and *Acrocomia aculeata*. The principal pollinators are identified as three different genera of beetles. The authors state that the beetles arrive at female phase inflorescences, immediately after the rachises are released from the inflorescence bract. The female phase lasts for a single day, while it may take up to five days for the male phase to be completed. All three of the pollinating beetle species use the inflorescences as mating sites and a source of food, with two of these also ovipositing in the flowers. Hundreds of beetles may be observed moving between male phase inflorescences and female phase inflorescences at anthesis.

A more complex pollination system is reported by Bernal and Ervik (1996) for the dioecious palm, *Phytelephas seemannii*. The authors found that the palm is pollinated by several species of staphylinid beetles, which are involved in a nursery pollination mutualism with their host plant. Beetles are attracted to staminate inflorescences by the strong fragrance emitted shortly after bract opening, as well as by the rewards of mating opportunities and oviposition sites. Although beetles carrying pollen loads visit pistillate inflorescences, they do not remain long. They appear to be attracted to pistillate flowers by a fragrance that mimics the scent of staminate flowers. An especially interesting part of this nursery pollination system involves the activity of beetles when inside staminate flowers. The beetles create chambers in the fleshy receptacles in which they deposit groups of eggs. Then, they seal the egg chambers with clumps of pollen that subsequently will be fed on by the larvae after the eggs hatch. Bernal and Ervik (1996) suggest that the floral structure, specifically the fleshy tissue of the receptacle, is an adaptation to beetle oviposition activity, and therefore serves to promote the association between the plant and its pollinators.

It is important to note that nursery pollination systems, such as those described for these palms, may involve a high cost for the host plant. For dioecious species, the staminate plant must produce reproductive structures amenable to its pollinators, and often also must produce a quantity of pollen sufficient to both feed pollinators, as well as allow for pollination to occur. In those interactions where the insects lay eggs on the flowers of pistillate individuals, the cost for pollination services also includes the development of the larvae of the pollinators, which are sustained by seeds or various plant tissues. This is a big risk, as the plant must have enough flowers such they can both rear pollinators, and produce seeds. If the insects utilize too many flowers for their larvae, the plant may suffer lowered fruit set. Thus, while the plant rears its pollinators and ensures a supply of pollinators, it does so at the expense of some portion of its own offspring. Interactions where the insects develop in staminate flower therefore may be less risky.

This cost-benefit balance is likely to be the reason that one characteristic of nursery pollination systems in dioecious plants is that the pollinators almost always develop on the staminate individuals (Dufaÿ & Anstett, 2003). This is certainly the case for the *Chamaedorea* taxa in this study where, in three of the four species, thrips oviposit exclusively in the staminate inflorescences.

5.5. Support of the *Chamaedorea*-Thrips Mutualism: Floral Morphology

The morphology of staminate versus pistillate flowers in the *Chamaedorea* species studied contributes to the exclusive use of staminate flowers for oviposition in all but one of the species. In each of the taxa, the petals of staminate flowers (and the pistillate flowers of *C. ernesti-augustii*) create an enclosed floral chamber, in which thrips are able to lay their eggs. By contrast, these taxa have pistillate flowers where the petals are tightly appressed to the stigma and do not provide a space for thrips to enter the flowers (Hodel, 1992a; Williams et al., 2001). This morphological difference between staminate and pistillate flowers allows the thrips that serve as primary pollination vectors for these taxa to reproduce in the staminate inflorescences (Retana-Salazar & Mound, 2005).

Staminate inflorescences are able to support large populations of pollinators by providing them with numerous flowers in which to breed and oviposit, as well as pollen and tissue food rewards. This part of the nursery pollination system represents a high energetic cost for the staminate plants, as they produce a significantly larger number of flowers than do their pistillate counterparts. This is possible because the staminate flowers of all four study species are much more densely packed on the rachillae, and many more rachillae are produced in relation to pistillate inflorescences. The proliferation of staminate flowers also provides a large unit that is quite effective in attracting visitors. Thus, staminate *Chamaedorea* individuals provide their thrips partners with a large number of potential sites for ovipositing, and produce enough pollen to satiate pollinators, with ample pollen left for transport to pistillate flowers (Moog et al., 2002). Furthermore, the pistillate flowers of the species *C. ernesti-augustii* have a similar structure to those of the staminate flowers. Although there are significantly fewer pistillate flowers, they do provide some additional brood sites for use by thrips. Also, this added reward contributes to the attractiveness of the pistillate inflorescences and is important, as this *Chamaedorea* species receives little air-borne pollen due to the morphology of the pistillate flowers (stigmas are not exerted past petals, but completely contained inside them).

5.6. Support of the *Chamaedorea*-Thrips Mutualism: Flowering Phenology

Another feature of the *Chamaedorea* species studied that maintains the mutualism between these palms and their thrips pollinators is the synchronized pattern of flowering found for all species. In fact, flowering synchrony and high synchrony of initiation month have been observed for many thrips-pollinated plants. For example, in their article on thrips pollination of the dioecious plant *Macaranga hullettii* (Euphorbiaceae) in Southeast Asia, Moog et al. (2002), found highly synchronized staminate and pistillate flowering periods. In addition, they noted that staminate anthesis was preceded by an ‘open bud’ phase, during which the open, yet non-dehisced flowers, were visited by thrips for the purposes of breeding and oviposition. This phase of floral development effectively lengthens the amount of time available for thrips to build up the large populations associated with pollination.

Likewise, Sakai (2001) determined that a species of thrips breeds in the staminate inflorescences of *Castilla elastica* (Castilleae) and is the primary pollen vector for this species. Both staminate and pistillate inflorescences were found to flower during the same period. Terry (2001) confirmed a comparable pollination system in the cycad

Macrozamia communis (Zamiaceae), again with concurrent coning of male and female plants.

Perhaps the most widely quoted example of thrips in a nursery pollination system is that of the Dipterocarpaceae in Southeast Asia. The mast-flowering dipterocarps are pollinated by thrips, which reproduce in their flowers over a period of 2-3 weeks (Appanah & Chan, 1981). Thrips are especially important to the pollination of this community, as they are one of the few insects that have the ability to increase their numbers within short periods of time in order to accommodate the needs of mast-flowering taxa. In this case, the species of thrips that pollinate the study taxa produce several generations per year, effectively raising the number of pollinators available to the large tree community.

Although flowering of staminate and pistillate individuals is highly synchronized, the staminate flowers begin to open their petals and admit visitors prior to anther dehiscence. It is during this pre-anthesis open bud stage, which lasts from 2-4 days in the different species, that thrips enter the chambers formed by the petals and breed and oviposit (see also Moog et al., 2002). As thrips have a relatively short time of development, the ability of thrips to enter and breed in staminate inflorescences prior to stigma receptivity enhances the potential for rapid multiplication of the thrips population such that large numbers of potential pollinators are available to migrate to pistillate inflorescences. In this manner, the duration of floral access is increased in order to accommodate thrips behavior and increase oviposition. The high density of thrips attracted to staminate individuals presumably promotes the dispersal of thrips with pollen loads, leading to an increase in pollen dispersal. Accordingly, the high number of inflorescences associated with the synchronous flowering of sympatric species and the large number of flowers available at each staminate inflorescence, favors the mass production of potential pollen vectors.

It is interesting to note that plants that flowered during the earliest portion of the flowering season (approximately the first month) had lower seed set than later flowering individuals. This fact supports the hypothesis that large numbers of simultaneously produced inflorescences serve to ensure the pollination of these taxa. At the beginning of the flowering period, few pollinators have emerged and few inflorescences are available to attract them, thus the low fruit set. Therefore, as thrips emerge from the soil at the beginning of the dry season, the high seasonal regularity found in the study taxa serves to coordinate the plants' need for pollination vectors, with the pollinators' need for a brood site. In fact, the observed fruit set during this period may be primarily from the posited supplementary wind pollination.

In sum, the relatively synchronized flowering of the *Chamaedorea* community over a short period of time, as well as the seasonal regularity and duration of flowering, has implications for the pollination of these taxa. The phenological patterns facilitate pollination by providing many sites for breeding and oviposition at the time of year when adult thrips are most likely to be active, leading to an increase in potential pollen vectors, as well as a large floral display with which to attract the pollinators.

5.7. Support of the *Chamaedorea*-Thrips Mutualism: Spatial Distribution

The spatial distribution of *Chamaedorea* individuals also contributes to the specialized mutualistic relationship between these palms and their thrips pollinators. As described in Chapter 2, the sympatric *Chamaedorea* species studied exhibit a clumped distribution at the community level. The distance between *Chamaedorea* individuals in the study plots was found to be quite small, averaging 1.34 ± 1.04 meters. This is important, because the relatively synchronized flowering of staminate and pistillate individuals in all of the study species promotes the attraction of thrips to all species by contributing to the overall attractiveness and size of the floral display. The individual species in this *Chamaedorea* community also contribute to the maintenance of pollinators by collectively providing a high number of brood sites for adult thrips when they emerge from the soil. As a single thrips species *Brooksithrips chamaedoreae* is known to transport pollen for all four study species, the issue of competition between plants for pollen vectors must be addressed. However, each flower can only support a few larvae, therefore female thrips will move to other flowers and inflorescences, when the maximum capacity of oviposition is reached.

Additionally, neither the staminate nor pistillate plants were clumped or spatially segregated for any of the study species. Bawa and Opler (1977) suggest that levels of pollination are higher when the spatial distribution of different sexes is not segregated, as the short distances should promote the likelihood that pistillate stigmas will receive pollen. These un-segregated populations of staminate and pistillate plants also promote the nursery pollination system of *Chamaedorea* and thrips. This occurs, because if pistillate plants were too far away from staminate ones, it is possible that the sexual pheromone released by male thrips, which aggregate for mating on pistillate inflorescences, would not be as effective at attracting females. Finally, this random spatial distribution of staminate plants with respect to pistillate plants is advantageous by facilitating secondary wind pollination. When dioecious individuals of the opposite sex are located far apart, the possibility for air-borne pollen to be effectively transported between staminate and pistillate plants is low (Culley et al., 2002).

5.8. Research Implications

This study provides detailed information on the flowering phenology and pollination ecology of four sympatric *Chamaedorea* species. Although researchers have concluded that various *Chamaedorea* species are wind-pollinated (Listabarth, 1992a; Otero-Arnaiz & Oyama, 2001; Berry & Gorchov, 2004), *C. ernesti-augustii*, *C. oblongata*, *C. neurochlamys*, and *C. tepejilote* are pollinated primarily by a single thrips species, *Brooksithrips chamaedoreae*. As these taxa also have a synchronized flowering phenology, and hybrids have not been recorded in the wild (Hodel, 1992a), a chemical mechanism for reproductive isolation is posited. Additionally, a highly dependent nursery pollination mutualism was determined to exist between these palms and their thrips pollinators.

Foremost, these results demonstrate the complex nature of palm reproduction and the importance in assessing all of the components that might contribute to the pollination system. The conclusions highlight the need for several further lines of research. First, future studies regarding the pollination of palms, as well as of other groups of flowering plants, should investigate the possibility of thrips visitation and their potential importance as pollinators. Several plant families are currently being examined for possible thrips mutualisms including Zamiaceae (Terry et al., 2005) and Annonaceae (Zerenga et al., 2004). It is important that palm pollination biologists also take advantage of the recent evidence on pollination by thrips and integrate it into their research. Likewise, previous research where wind was determined to be the primary pollen vector should be reassessed to determine if thrips also are involved. In addition, more effective methods for assessing the relative contribution of thrips and wind need to be created. This thesis emphasized the difficulties involved in eliminating thrips from pollination experiments. It is therefore necessary to develop better techniques and materials that are easily implemented, and to disseminate them so that they can be utilized in future pollination studies.

Another avenue that warrants exploration is that of mutualisms between palms and their pollinators, specifically nursery pollination mutualisms. Several studies have reported dependent pollinator mutualisms for palms including *Attalea funifera* (Voeks, 2002), *Chamaerops humilis* (Anstett, 1999), and *Phytelephas seemannii* (Bernal & Ervik, 1996). However, a question that is seldom answered definitively is why the pollinators visit pistillate flowers or inflorescences. In each of the studies mentioned above, mimicry of staminate flowers or deceit pollination was suggested. Reexamination of these palms may determine that factors in addition to mimicry are involved in their pollination. One genus that might benefit from further investigation is *Bactris*. Henderson et al. (2000a) reported on the pollination of 10 sympatric species of *Bactris*. Although the authors did not conclude that pollination was the result of deceit on the part of pistillate flowers, they did concede that the reason for insect visits to stigmas remained unclear. Yet, Henderson et al. (2000a) also described another aspect of pollination, one that may shed light on the visitation question. They stated that beetles captured at pistillate flowers were predominately male. It is likely that *Bactris* exhibits a similar pollination system to that of *Chamaedorea*, and that this skewed sex ratio is due to the aggregating of pheromone-releasing male beetles attempting to attract mates. This example reinforces the significance of current reports on sexually attracting pheromones in many insects (Webster et al., 2006), and the necessity of investigating this phenomenon when studying palm reproduction.

Finally, in terms of *Chamaedorea* pollination, only a handful of species have been investigated. As populations of the highly commercial *Chamaedorea* species become degraded due to overexploitation, it is vital that more attention be placed on reforestation and plantation efforts. Detailed knowledge of the reproductive ecology for each species will be an essential part of any effective program to manage and cultivate these palms (Peters, 1994). Therefore, it is my hope that this thesis will lend to a better understanding of the complexities of *Chamaedorea* pollination, and motivate other researchers to implement studies into the reproduction of additional *Chamaedorea* species.

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