PHENOLOGY OF PALM TREES IN THE CHOCÓ RAINFOREST

AN HONORS THESIS

SUBMITTED ON THE 13TH DAY OF MAY, 2022

TO THE DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS

OF THE HONORS PROGRAM

OF NEWCOMB-TULANE COLLEGE

TULANE UNIVERSITY

FOR THE DEGREE OF

BACHELOR OF SCIENCES

WITH HONORS IN ENVIRONMENTAL BIOLOGY

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ABSTRACT

Palms are one of the most abundant life forms found in tropical rainforests, and their fruits and flowers are a significant food source for many animals, particularly insects. Arborescent palms provide food to indigenous people, birds, mammals, and insects in western Amazonia; therefore, understanding patterns of fruit production has both ecological and social implications. Observations and studies have led tropical ecologists to consider the temporal pattern of flowering as the result of coevolution with pollinators, seed predators, and most recently, climatic patterns. Climatic patterns are the focus of palm phenology research, however, subsequent studies have demonstrated the large variety and still widely unknown patterns of tropical plant phenology. Through analyzing fruiting and flowering data of 438 different palm trees from 15 different species from December 2020 to November 2021, a group of researchers found interesting patterns in phenology. We found that fruiting and flowering phenology, on average, differ in their degree of seasonality at the community level. Specifically, flowering production tends to be more seasonal than fruit production, with a greater average proportion of individual species bearing flowers between January and July. In contrast, the average proportion of individuals bearing mature fruits among species remained relatively constant throughout the year. There is a wide range of phenological patterns represented among species with some showing distinct population peaks sequentially repeated across all while others showing a high proportion of individuals within certain phenophases all year. Overall, this research creates a basis of phenological patterns for fifteen different species representing the important flowering and fruiting plants of the Chocó Rainforest at the community level.

ACKNOWLEDGMENTS

I am extremely grateful for my thesis advisor, Dr. Jordan Karubian, who provided me with this opportunity to work within my dream tropical ecosystem and further my career as an ecologist. I want to thank Tulane University, namely Newcomb Institute and Newcomb Tulane College for providing the financial support needed to complete this project. I am extremely grateful to my thesis readers, Dr. Sunshine Van Bael and Dr. Nicole Katin for introducing me to these topics and for their support both in and out of the classroom. I want to thank Tadeo Ramirez Parada for leading my data analysis and aiding in my understanding of phenological data. Most importantly, none of this research would have been possible without the local researchers at FCAT station, namely Domingo Cabrera Gomez who spent every day with me in June and July collecting data throughout the Chocó Rainforest. I would like to thank my family and friends for their constant love and support. None of this work would have been possible without the help of all the amazing scientists I have mentioned, the FCAT station, and many others who supported me during my most academically challenging endeavor yet.

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CHAPTER 1: INTRODUCTION

Palms are one of the most abundant life forms found in tropical rainforest, and their fruits and flowers create large sources of food for many animals and insects (Kahn and de Granville 1992, Henderson et al. 2000a). Arborescent palms provide food to indigenous people, birds, mammals, and insects in western Amazonia (Peres 1994). Plant and animal species have coevolved with palm species in which unique timing behaviors parallel each other in accordance with temperature precipitation, and sun light variations that are controlled by climatic conditions (Inouye and Iller 2020, Liang 2019). For example, continuous flowering in *O. batuaua* in the Brazilian Amazon was pivotal in providing its pollinator, the beetle *Phyllotrops sp*., with continuous food supply representing a symbiotic relationship (Henderson et al. 2000b). Several palm species have extended ripe fruiting periods that do not coincide with most fleshly fruits which indicates that frugivores are able to resort to palms during times of scarcity. The mesocarp of palm fruits are sources of energy rich nutrients with year-round productivity which makes palms a keystone resource in Amazonian terra firme forests (Peres 1994).

Phenology provides vital knowledge into the "interdependence of biosphere and atmosphere within specific spatial, temporal, and ecological contexts" since it is composed through biological and meteorological cycles (Liang 2019, 1). Phenology, the timing of recurring biological events, is tied to agriculture, horticulture, forestry, climatology, ecology, biology, meteorology, and geography (Leith 1974, Liang 2019). An understanding of phenology is pivotal to complete a full analysis and management of an ecosystem and its ecological services (Leith 1974).

Observed relationship between flowering peaks and pollinator activity (Henderson et al. 2000) led tropical ecologists to consider the temporal pattern of flowering as the result of coevolution with pollinators and seed predators. Palm flowering peaks coincide with periods of high pollinator activity, and different, overlapping flowering periods among various palm species reduce competition for pollinators and provide a continuous source of nectar. However, Borchert (1983) argues that staggered flowering depends on a palm's vegetative development which is determined by environmental constraints and not biotic actions related to pollinators. Borchert concluded that the temporal correlation between insects and flowering is more likely to result from insect lifestyles adapting to seasonal palm development. Augspurger (1983) hypothesized that pollination of an individual's flower may be influenced by a shrub's flower production referencing his earlier study which displayed that mass flowering by a shrub increased attraction of social bees. Augspurger (1983) drew various conclusions regarding the effects to population synchrony, referencing Borchert, and stating that synchrony and flowering are a result of various, complex dynamics that ecologists must continue to study to further understand.

Recent studies of palm phenology in tropical forests have focused on and analyzed climatic factors. Leaf phenology of tropical forests is unique compared to other biomes. Reich (1995) found that tree development is continuous in aseasonal lowland tropical rain forest and becomes episodic in response to increasing annual drought in tropical dry forests. This is vastly different from the temperature-related periodicity of temperate forests. Therefore, foliar development in tropical rain forests is controlled by internal factors rather than environmental, while tropical forests with annual dry seasons display responsive seasonality of leaf development. Reich (1995) concluded that "tropical forest phenology appears to be controlled by physiological processes and not direct environmental cues or thermo-periodic sensitivity" (172). Overall, recent findings have corroborated that climatic patterns are the determining factors of phenology.

Subsequent studies have demonstrated the large variety and still widely unknown patterns of tropical plant phenology. One pattern that has been repeatedly observed and studied is the continuous flowering or fruiting of palms in wet tropical forests (Rojas-Robles & Stiles, 2009). *O. bataua,* an abundant palm in the Amazon rainforest, has been the focus of recent studies due to its irregularity in phenology and importance as a resource to the human and animal communities in the Amazon. Most studies of *O. bataua* have observed a "lack of synchrony among the individuals of the population" while noting that "reproductive individuals are continuously present" (Henderson et al. 2000a, b; Miller 2002; Peres 1994). Rojas Robles and Stiles (2009) came to the hypothesis that the variation of productivity among the *O. bataua* may reflect genetic differences.

The most recent research regarding phenology of palm trees focuses on the *O. bataua* population found in the Chocó rainforest. As evidenced by Peres (1994) *O. bataua* is a keystone species of the Chocó rainforest due to its hyperdominance with large fruit and flower crops along with an extremely long flowering/fruiting presence that sustains a large variety of pollinators and frugivore (Ramirez-Parada et al. 2020). Ramirez-Parada et al (2020) examined the different resource related variables that could potentially impact the phenology variation found at a population and individual level. Climate variation proved to affect reproductive patterns through affecting resource supply. Anomalously warm conditions due to El Niño were connected to the higher inflorescence initiation in the study population (Ramirez-Parada et al. 2020). However, the production of infructescence was found to suppress increases in inflorescence leading to the belief that infructescence influence individual level phenological behavior by acting as a resource sink. Therefore, the overall analyses found that the weak reproductive synchrony among *Oenocarpus bataua* is a product of resource dynamics as resource sinks among individuals intervene with ENSO-induced climate anomalies that influence population level phenology (Ramirez-Parada et al. 2020).

Phenological events have been recorded for centuries with earliest literature dating to 234 BCE; however, the importance of recording phenology at the community level is relatively new within scientific literature (Inuoye and Iller 2020, Liang 2019). What are the fruiting and flowering patterns of the main fruiting palms and trees in the Chocó Rainforest? Do palm trees spread out their fruiting at different times to reduce competition or do they all fruit at the same time? I have two predictions which oppose each other. I predict that palm species produce fruit asynchronously to avoid competition with each other for seed dispersal agents. Alternatively, it may be that they fruit synchronously as they respond to the same environmental cues, like rainfall and sunlight. The study subjects of this paper include fifteen important fruiting and flowering species of the Chocó Rainforest in Northwest Ecuador. The results of this data will enhance current understandings of the timing and extent of fruit production by the approximately fifteen species of palm and other major fruiting and flowering trees of the Chocó Rainforest.

CHAPTER 2: METHODS

Research was conducted at the Fundación para la Conservación de los Andes Tropicales, a 1500 acres reserve of the Chocó Rainforest in Northwest Ecuador. Rainfall is seasonal with a 5-month dry season between July and November when there is consistent cloud cover and low precipitation (Ramirez-Parada et al 2020). Through literature review alongside consultations with local forest dwellers, fifteen different species of trees were identified as the main flowering and fruiting trees of the region. A relatively small area was used to complete intensive studies on the phenophases of the entire ecosystem. (Leith 1974). In September 2020, local researchers placed metal tree tags on 450 different trees with around equal amounts of each species which included twelve palms and three other species of trees including *Prestoea decurrens, Desmoncus cirrhiferus, Synechanthus warscewiczianus, Astrocaryum chambria, Otoba gordoniifolia, Iriatea deltoidea, Virola dixonii, Bactris gasipaes, Wettina equalis, Bactris setulosa, Ficus sp., Coussapoa sp., Phytelephas aequatorialis, Socratea exorrhiza, and Oenocarpus bataua*. Starting in September 2020 and continuing to present day, local researchers recorded data on sex, buttons (live, pierced, dry), inflorescence, flowers, green fruit bunches, mature fruit bunches, dry bunches, green fruits, and mature fruits for each individual every month.

Inflorescence refers to the flowering stem and branch of a palm tree. For most species, after fertilization, each flower develops into a drupe. The drupe expands and merges into the fleshy fruit called a syncarp. Buttons refer to the growth sprout of inflorescence. By counting the number of buttons and inflorescence over the past year, we were able to map out the phenology of this community. This past summer, using a

GPS unit and guidance from a local researcher, I collected data on the exact distribution of palm trees and used binoculars to make clear observations on the state of the palm trees and the surrounding biodiversity. Domingo Cabrera Gomez, a researcher at FCAT, and I completed data collection during June and July while a group of local researchers continues to collect data. Although there were 450 individuals tagged, the analyzed data includes a sample size of 438 individuals as twelve individuals either fell or were cut down over the past year.

Due to technological and human error, there were not complete data collections for November 2020, December 2021, and January 2022, so the graphs depict reproductive stages from December 2020 to November 2021. We calculated the proportion of trees in each phenophases every month between December 2020 and November 2021. One graph includes the twelve palm species in which the percentage of individuals within each species that have unopened fruit, flowers, green fruits, and fruits are visualized. Another graph depicts the percentage of individuals with flowers and fruits to visualize palms and hardwoods together. A third graph was made showing the average percentage of individuals that bore mature flowers and fruits each month among species to assess the degree of seasonality of flower and fruit production at the community level. All data manipulation, visualization, and analysis for this study were carried out using R version 3.6.1 (R Core Development Team, 2018).

CHAPTER 3: RESULTS

Phenological Patterns

Desmoncus cirrhiferus, Bactris gasipaes, Bactris setulosa, Virola dixonii have distinct population peaks sequentially repeated across all phenophases (Figure 1 and Figure 2). *Synechanthus warscewiczianus, Iriartea deltoidea, Phytelephas equatorialis,* and *Coussapoa sp. Otoba gordoniifolia* all have a high proportion of individuals within certain phenophases all year (Figure 1 and Figure 2). Certain species displayed a continuously high proportion of individuals in some phenophases, but distinct, sequential seasonal peaks in others.

Over 85% of *S. warscewiczianus* individuals were observed bearing immature inflorescences throughout the year, but open flowers, green fruits, and mature fruits were observed during a shorter period and in succession between January and August. The proportion of immature inflorescences did not decrease as the number of developed inflorescences increased. Over 85% of *Iriartea deltoidea* individuals were observed bearing immature inflorescences throughout the year, while over 60% of individuals were bearing green fruits throughout the year. *Iriartea deltoidia* was observed to have a constant production of unopened flowers and very concentrated and overlapping periods of mature flowers and fruits (Figure 1). *Socratea exorrhiza* had a high percentage of individuals with green fruits throughout the year, but a very distinct short period of flowers from February to June (Figure 1).

Degrees of Seasonality

On average, fruiting and flowering phenology differ in their degree of seasonality at the community level for the subset of the community these species represent. (Figure 3). Flowering production tends to be more seasonal than fruit production with a greater average proportion of individuals bearing flowers between January and July among species (Figure 3). In contrast, the average proportion of individuals bearing mature fruits among species remained relatively constant throughout the year (Figure 3). Variability among species in the percentage of individuals bearing flowers and fruits was highest between February and August for both flowering and fruiting (Figure 3).

CHAPTER 4: DISCUSSION

Palms are essential centers of ecosystems by playing a role in every layer of tropical ecosystems from shrubbery, understory, canopy, and lianas (Eiserhardt et a 2011). The data does provide a preliminary snapshot of the fruiting and flowering patterns of fifteen keystone tree species of the Chocó Rainforest. There is extremely varied phenological phases; however, there are two main patterns noticed. The species either have distinct peaks within phenophases or individuals have constant phenophases throughout the year. This data indicates possible inquiries into the evolution of these species and their abiotic determinants. The data does not provide sufficient information to suggest these species are fruiting asynchronously to avoid competition with each other for seed dispersal agents. Current research along with my results indicate that palms are responding to environmental cues like precipitation patterns and sunlight. Within tropical ecosystems, annual climatic variations strongly influence phenological patterns (De Steven 1987, Reich 1995, Ramirez-Parada et al 2020).

In regard to degrees of seasonality, results suggest that flowering patterns are more responsive to abiotic factors such as precipitation since flowering was significantly more seasonal. Average individual’s flowering was lowest during the dry season which is July to November which suggests that rainfall is determining flowering patterns in this region. *Iriartea deltoidea’s* varied phenophases suggest that while individuals are always producing flowers, there seems to be an abiotic cue that controls when flowers open. According to the data, flowers open from February to July which further supports the determinant of rainfall for flowering. *S. exorrhiza, D. cirrifeus, S. warscewiczianus, W. equalis* also display this fruiting pattern suggesting the same abiotic response to precipitation. *A chambria, B. setulosa, and Coussapoa sp* evidenced an opposite flowering pattern in which June to November is the main flowering phenophase. These species range from understory to canopy, so the reasoning for this phenological difference is unclear but may suggest a difference in reproductive structures among these species.

It is important to note that certain species' phenology within this study cannot be characterized within twelve months of data. Brokamp et al. (2014) found that the total duration from formation of the inflorescence bud to the mature infructescence of *Phyletelphas aequatorilis* was about 2.6 years to 3.5 years and Ramirez-Parada et al (2020) found that *Oenocarpus bataua* is also supra-annual and completed a full development cycle in around 2.3 years. This data is meant to serve as preliminary information and a snapshot into the phenological patterns and degrees of seasonality. However, there did seem to be a delineation between canopy and understory species' development time. Nearly all the understory species have a "fast" rate of fruit development whereas most of the canopy species appear to have a "slow" rate of development. However, *Astrocaryum chambria*, a canopy palm, took less than 12 months to complete a phenological cycle and *Phytelphas aequatorialis*, an understory palm, indicates that a full phenological cycle takes more than 12 months. The main difference between the canopy and understory is the amount of sunlight received so it could suggest that lack of sunlight leads to a faster phenological cycle, but the literature to support this claim is lacking. Ramirez-Parada et al (2020) found the opposite trend in which access to sunlight influences photosynthetic rates and carbohydrate production and enhances various components of plant reproduction, including reproductive frequency and crop sizes. Since palm phenology has an intense variety of phenological patterns, the reasons for these patterns are still highly questionable. However, through the collection of further data, species' phenological patterns will be better understood.

Expansive phenological data collection and analysis are extremely important to understanding the effects of global climate change. Since temperature and rainfall influence reproductive timing, global climate change could drastically alter palm phenology (Cleland et al 2007). Phenology within tropical ecosystems is heavily affected by precipitation patterns. Research has indicated that the frequency and intensity of El Niño are expected to increase due to global climate change. Ramirez-Parada et al (2020) found the impact of global climate events, such as El Niño on palm phenology while Cleland et al (2007) found that global climatic events are already affecting Brazilian forest phenology. Research by Sherry et al (2007) demonstrated that global warming was related to accelerated development in early season species with delayed development in later active species which could result in new phenological niches that could increase non-native species dismantling ecosystems.

Palms provide one of the main economic services for the people of northwestern South America through production and commercial use (Brokamp et al., 2014). Many local communities and households entirely depend on palm-derived non-timber forest products (NTFPs) for their source of income (Brokamp et al., 2014, 262). For example, *P. aequatorialis*, otherwise known as vegetable ivory is the "second most important product from native palms in Ecuador, after palm hearts" (Brokamp et al., 2014). More species of palm are concentrated in Ecuador than across South America (Balsev 1987). Due to the intense diversity and availability of these palms, Ecuadorians have developed profound local knowledge regarding the palms and their uses including oils, edible fruits, fibers, thatch, construction material, tools for fishing and hunting, medicines, and cultural creations (Macía 2003). Not only is it central to various Ecuadorian communities' economics, spirituality, and life, but it also plays a central role in the ecosystem with squirrels, agoutis, deer, opossums, porcupines, and pacas feeding on its mesocarp (Barfod 1991). Bats, marsupials, and crabs are also documented to subsist and pollinate palm species. However, Henderson (1986) found that beetle pollination (cantharophily), bee pollination (melittophily), and fly pollination (myophily) are the main contributors in transferring pollen from anthers to stigma of palms. Considering the critical role these fifteen species play in the biotic system and ecosystem services, creating extensive sound phenological data will only increase the ability for scientists to conserve these species that is needed to sustain the natural ecosystem and economic services for the rainforest's human communities.

Data continues to be collected [for these study subjects] which will only increase the magnitude of knowledge and understanding of the phenological and seasonal patterns for these fifteen species, especially species that have phenological cycles that span larger than a year. Also, FCAT station has recently instituted a weather station that is directly tracking solar radiation and other climatic trends which will allow future research to look at abiotic control for the seasonal trends seen in the results. Precise climatic data will enhance the ability to interpret the abiotic mechanism behind phenology of these fifteen species. It would also prove valuable for future researchers to develop a methodology to track individual reproductive structures to further understand the morphological patterns of development more deeply. The phenological data collection of these fifteen species continues to grow and the wealth of knowledge grows with it to aid scientists in understanding the sporadic, cryptic patterns of the Chocó rainforest's most important species.

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Figure 1. Percent of palm trees bearing unopened flowers (red), flowers (green), green fruits (blue), and fruits (purple) from December 2020 to November 2021.

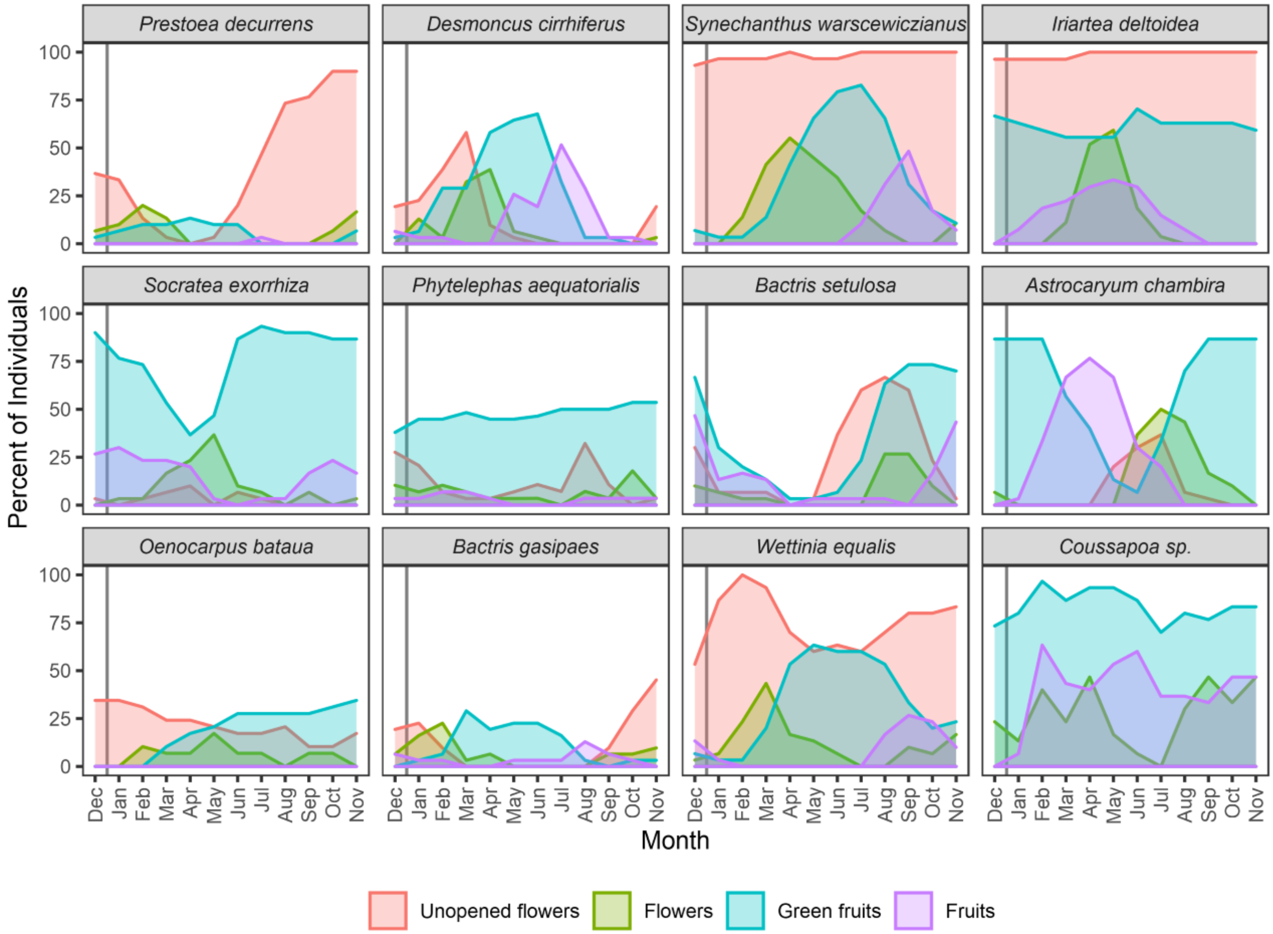

Figure 2**.** Percent of palm and hardwood individuals bearing fruits (red) and flowers (yellow) from December 2020 to November 2021.

Figure 3. Monthly series of the average percentage of individuals in phenophases among species. Vertical bars correspond to the standard deviation of the percentage of individuals seen in each phenophases that month among species.