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Morphology, Architecture and Growth of a Clonal Palm, Acoelorrhaphe wrightii

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MORPHOLOGY, ARCHITECTURE AND GROWTH OF A CLONAL PALM, *ACOELORRHAPHE WRIGHTII*

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by

Sara Melissa Edelman

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To: Dean Michael R. Heithaus
College of Arts, Sciences and Education

This dissertation, written by Sara Melissa Edelman, and entitled Morphology, Architecture and Growth of a Clonal Palm, *Acoelorrhaphe wrightii*, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this dissertation and recommend that it be approved.

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The dissertation of Sara Melissa Edelman is approved.

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Florida International University, 2017

DEDICATION

I dedicate this dissertation to my two biggest inspirations and mentors: Dr. Richard Campbell and Pamela Schlactman. You both sparked my passion of plants and gave me the courage to follow my dream to study them.

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ABSTRACT OF THE DISSERTATION

MORPHOLOGY, ARCHITECTURE AND GROWTH OF A CLONAL PALM, *ACOELORRHAPHE WRIGHTII*

by

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Professor Jennifer H. Richards, Major Professor

Palms provide valuable commercial resources in the tropics and are dominant species in tropical lowland forests. While general biology of palms is well studied, there are gaps in the literature on palm growth through life stages and in response to environmental conditions. Literature gaps on palm growth could be caused by the slow growth of palms; it is difficult to monitor morphology and architecture for the periods of time necessary to capture changes. *Acoelorrhaphe wrightii* is a threatened palm native to southern Florida with an unusual adult architecture. The purpose of this dissertation was to study growth *A. wrightii* throughout its life stages and in response to changes in environmental conditions. In order to do study growth, I first had to understand the evolutionary history and types of vegetative branching in palms to identify vegetative branching possibilities in *A. wrightii*. I described branching types for 1903 species from all 181 genera using literature reviews and hands-on analysis. I then studied adult morphology and architecture in a common garden setting by monitoring leaf morphology, ramet growth and architecture of *A. wrightii* in two gardens in Miami, FL, over a two year period. I tested the effects of water and light on germination and growth of juvenile plants

in a mesocosm where water and light were manipulated, following growth for a year. Finally, I compared leaf morphology and architecture of adult individuals in four populations in Belize and Florida. I found five branching types were present in the palms: lateral axillary branching, shoot apical division, false vivipary, abaxial branching and leaf-opposed branching. In the garden, *Acoelorrhaphe wrightii* displayed two types of lateral axillary branching: basal suckering and rhizomatous branching. The two branching types produced tiers in adult clones, which were used to model architecture. Ramets had an establishment period and growth varied seasonally in establishing and established phases. Low water levels and full sun yielded greater germination of *A. wrighti* and produced juveniles with a greater number of leaves, more root mass and more branches. Variability between populations and environmental conditions was observed in adult individuals in the field but differences were minimal.

TABLE OF CONTENTS

LIST OF TABLES

TABLE PAGE

CHAPTER IV

LIST OF FIGURES

FIGURE PAGE

CHAPTER I

CHAPTER II

CHAPTER IV

LIST OF ABBREVIATIONS AND ACRONYMS

ARE	Arecoideae
CAL	Calamoideae
CER	Ceroxyloideae
CH	Coastal Highway
COR	Coryphoideae
FL	Southern Everglades
FTBG	Fairchild Tropical Botanic Garden
LM	Leaf mass
LMF	Leaf mass fraction
MB	Monkey Bay Wildlife Sanctuary
MBC	Montgomery Botanical Center
NH	Northwestern Highway
NYP	Nypoideae
RM	Root mass
RMF	Root mass fraction
SM	Stem mass
SMF	Stem mass fraction
Surv.	Survivorship
TM	Total mass
Veg. reprod.	Vegetative reproduction

INTRODUCTION

Palms are an important plant family economically and ecologically, providing valuable commercial resources in the tropics and subtropics and being dominant species in tropical lowland forests. (Svenning et al., 2008; Stiegel et al., 2011). Coconuts, dates, and acaí are palm fruits enjoyed worldwide, and palm oil and rattan support million dollar industries that provide income to local communities in the tropics (Balick, 1990). Palms are known for their iconic growth form, with an erect, solitary trunk topped by a crown of plicate leaves. While the solitary habit is more widely recognized, many palm species are multi-stemmed. These clumping palms branch vegetatively to produce multi-stemmed clones. The multi-stemmed habit differs from how dicots and gymnosperms produce branches, because palms lack secondary growth, which is what thickens trunks and branches of dicot and gymnosperm trees.

While general biology and ecology of palms is well studied, there are gaps in the literature on the architecture and effects of environment on growth and morphology of juvenile and adult palms (Tomlinson, 1990). Literature gaps could be caused by the slow growth of palms; it is difficult to monitor morphology and architecture for the time necessary to capture changes in growth. In particular, morphology and architecture of clonal growth is not well-described in palm literature. Clonal palms are particularly interesting because they reproduce asexually, forming clumps where each new shoot is a clone of the initial shoot. For many clumping palms, both asexual and sexual reproduction increase with increased genet size (Souza, Martins, & Bernacci, 2003; Thompson, 2002; Thompson & Eckert, 2004). Thus, the life history of clonal palms differs from that of solitary palms.

Despite its common occurrence, vegetative branching in the palms has not been thoroughly investigated. The types of vegetative branching in palms have not been clearly described and quantified, and, therefore, the evolution of branching types in the palms cannot be understood. A better understanding of how palms branch vegetatively and the evolutionary history of branching types are essential to understand how palms create clonal clumps.

Palms can be very sensitive to minor changes in landscape elevation and topography, and these environmental changes can greatly influence morphology, architecture and growth (Vormisto et al., 2004; Avalos et al., 2005; Roncal, 2006; Sylvester & Avalos, 2013). A variety of environmental variables can influence leaf size, leaf production and overall architecture of a palm. The effect of environment on palm growth is particularly interesting because palm growth is uninterrupted—that is, the growth of each palm stem is continuous (Tomlinson, 1990). However, the rate of growth may change depending on day length, moisture, temperature, or other environmental variables (Tomlinson, 1990).

Acoelorrhaphe wrightii is a clonal palm native to the Florida Everglades. The natural range of *A. wrightii* is southern Florida, Mexico, Belize, Costa Rica, Guatemala, Honduras, Nicaragua, Cuba and Colombia (Wendland, 1879). The southern Everglades population is threatened (Ward et al., 2003), and seedling recruitment and juvenile individuals are not readily observed (personal observation). It is possible that human manipulation of hydroperiod and water level is impacting *A. wrightii* populations, since these changes have been shown to impact germination, growth, morphology and architecture of other Florida plants (Davis & Ogden, 1994; Newman et al., 1996). Analysis of morphological and architectural plasticity of *A.wrightii* and their response to

environmental vaiables that influence growth at different life stages will show how *A. wrightii* could be impacted by human modifications to the environment. The purpose of my dissertation was to create a conceptual model for branching in palms in order to place branching in clonal palms in an appropriate phylogenetic context, to describe in detail the morphology and architecture of *A. wrightii*, one clonal palm, and to understand how morphology and architecture are affected by age and environmental variation.

In order to study the morphological and architectural plasticity of *A. wrightii*, I first analyzed, described, and classified branching types throughout the palms, determined the distribution of branching types in the family, and placed branching in a phylogenetic context. This research is presented in Chapter I. After surveying branching in all genera and 1903 species using literature reports and observations of living specimens, I defined all vegetative branching types present in the palms and classified the observed species into the different types. The distribution of branching types throughout the family and subfamilies were analyzed using phylogenic trees, and a hypothesis for the ancestral branching type was developed.

In Chapter II, I focused on the morphology and architecture of *A. wrightii*, using a common garden approach by following growth of the species in two gardens in Miami, FL. Leaf morphology, adult architecture and growth variables were monitored over a two-year time period in order to understand the general morphology and growth of *A. wrightii*.

In Chapter III, I studied germination and juvenile morphology and architecture in mesocosms where shade and water depth were experimentally manipulated. Germination in different water depths was monitored for a year. In order to better understand the effect of environmental variables on juvenile growth of *A. wrightii*,

juvenile plants were grown in different water and light conditions. Leaf production, vegetative branching, and stem growth were measured on these plants over one year

Finally, in Chapter IV, in order to determine the environmental range and plasticity of the species, I analyzed the morphology, architecture and population structure of four wild populations of *A. wrightii.* The data from the chapter will help environmental managers make decisions to support growth of this threatened Florida native plant.

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CHAPTER I

DISTRIBUTION OF VEGETATIVE BRANCHING IN THE PALMS (ARECACEAE)

ABSTRACT:

Vegetative branching is common in the palms (Arecaceae). However, current branching terms to describe vegetative branching diversity are not consistent and do not cover the full range of branching. In this study, (1) vegetative branching types in the palms were identified and defined and (2) the phylogenetic distribution of palm branching types were described.

Vegetative branching terms were defined through a review of the literature and branching types were described from these reviews and field observations. Five branching types were found: lateral axillary branching, shoot apical division, false vivipary, abaxial branching and leaf-opposed branching. In total, 1903 species representing all 181 genera were included. The numbers of species with each branching type were counted to determine the most abundant branching type. Ancestral branching was predicted using the most parsimonious approach in the program Mesquite.

Most species exhibited no vegetative branching (1043 species, 55% observed species). Lateral axillary was the most common branching type, described in 646 species (34% observed species). Lateral axillary branching and shoot apical division were identified as the earliest-evolved branching types. The present study suggests that branching types have different evolutionary histories, and it is likely that the solitary habit is more common now than when palms initially diverged from commelinid relatives.

Keywords: Arecaceae; branching; commelinid monocots; monocotyledons; Palmae; palm phylogeny; vegetative anatomy; vegetative propagation

INTRODUCTION:

Branching is the outgrowth or division of a meristem and results in a new axis. Plants can branch sexually, producing an axis used for sexual reproduction, or vegetatively, producing a separate and genetically identical vegetative axis (Doust & Doust, 1988). The vast majority of plants display some form of vegetative branching, which results in a great diversity in plant form and architecture (Bell & Tomlinson, 1980). Plants branch vegetatively in three ways: axillary (occurring in the leaf axils), apically (at the apex of the shoot), or adventitiously (in neither of the previous two locations) (Halle et al., 1978). Axillary branching, the most common type of branching in plants, has two forms that account for much of architectural diversity displayed in plants: long and short shoots. Short shoots are specialized units, usually producing photosynthetic or reproductive structures or spines that bear no lateral branches (Halle et al., 1978). Long shoots grow, add height, and can proliferate to produce additional lateral axillary branches that become either long or short shoots.

Vegetative branching is common in the monocots, where it is used as a mechanism to increase in size, since most monocots lack secondary growth (Halle et al., 1978). The three main terms used to describe branching in the monocots are (1) axillary, (2) dichotomous, and (3) adventitious branching (Tomlinson, 1973). However, these terms are not consistently used in descriptions of monocot branching diversity.

While similar vegetative branching types exist in the palms (Arecaceae Bercht. & J.Presl) and their monocot relatives, the terminology to describe these types is not uniform and many terms have been applied to the same branching type (Tomlinson, 1961; Tomlinson, 1971; Fisher, 1973; Fisher & Tomlinson, 1973; Fisher, 1974; Fisher et al., 1989; Mendoza & Franco, 1998; Fisher & Zona, 2006). Detailed descriptions are

often not assimilated or are greatly simplified in the popular palm literature (Tomlinson, 1973; Dransfield et al., 2008). Consequently, the current branching vocabulary for palms does not consistently and accurately describe the diversity of vegetative branching in the family.

The three vegetative branching types commonly described in palms are similar to the branching types used for the monocots (Tomlinson, 1990), axillary branching, apical dichotomous branching, and non-axillary branching, but different types of these have been recognized depending on origin instead of variation in outgrowth. Axillary branching, the most commonly described, is used to describe the formation of a primordial bud in the leaf axil at the base of orthotropic (vertical) shoots. If axillay branches grow erect immediately, they create branch types called basal suckers. If the basal sucker grows horizontally before turning to grow erect, it forms a rhizome (Tomlinson, 1990). Rhizomatous branching is occasionally classified as its own, unique branching type.

Apical dichotomous branching occurs when the apical meristem of the stem bifurcates, creating two apical meristems. In palms, species differ in whether the meristem splits into two even (isotomous) or uneven (anisotomous) parts (Tomlinson & Moore, 1966; Gola, 2014). In palm literature, the term dichotomy has been used incorrectly to imply equality of outgrowth (Tomlinson, 1990).

Non-axillary branching describes a branch that does not arise in the leaf axil (Tomlinson, 1973). The term, however, does not further differentiate among locations of the branch (non-apical portions of the stem, lamina or inflorescence), which can differ among taxa.

In addition to being poorly described and classified, the frequency and distribution of branching types in palm subfamilies and genera have not been examined from a

phylogenetic perspective. Understanding the relationship between phylogeny and branching type will increase our understanding of the evolution and ecology of vegetative branching in the palms and will provide a framework for understanding branching in all monocots. The purpose of this study was to (1) identify, define and classify the types of vegetative branching in the palm family Arecaceae and (2) describe the phylogenetic distribution of these branching types in palms.

MATERIALS AND METHODS:

Basic vegetative branching terms were defined through a review of the literature. Vegetative branching terms used in the literature or derived from observations are defined in table 1 with synonyms. Species were recognized following the accepted species in the Kew World Checklist of Palms on February 5, 2016 (Goverts et al., 2011). Branching type(s) of species were described from literature reviews of journal articles and books describing branching patterns and from analysis of living specimens in the palm collections at Fairchild Tropical Botanic Garden and Montgomery Botanical Center (Coral Gables, FL, USA) (table 2). In total, 181 genera (out of 181 genera in the family, 100% genus coverage), comprising 1903 species (out of 2501 species in the family, 76% species coverage), were sampled (table 2). Each branching type was defined by (1) branching meristem (axillary, apical, non-axillary); and, if non-axillary, (2) location of branch (inflorescence, leaf base or stem). Using these criteria, five branching types in the palms were identified, which are distinguished from the solitary phenotype that had no vegetative branching. The five branching types were: lateral axillary branching, shoot apical division, false vivipary, abaxial branching and leaf-opposed branching. Lateral axillary branching was defined as vegetative outgrowth of an axillary meristem on the vegetative shoot (stem) (Fig. 1B). Many species display lateral axillary branching but could also not branch, presenting a solitary stem; these species were classified as

having lateral axillary branching. Shoot apical division was defined as the division of the apical meristem into two equal or unequal meristems (Fig. 1C). False vivipary was defined as adventitious vegetative outgrowth of buds in the apical bracts of inflorescence that eventually rooted in the soil and produced vegetative shoots (Fig. 1D). Abaxial branching was defined as the vegetative outgrowth of an adventitious meristem located on the abaxial surface of the leaf at the base of the leaf sheath (Fig. 1E). Leaf- opposed branching was defined as the vegetative outgrowth of an adventitious meristem borne on the stem, opposite the lamina and petiole and enclosed within the edges of the leaf sheath (Fig. 1F). Branching type combinations can also occur, and two branching combinations are present in the palms: shoot apical dichotomy + lateral axillary branching and false vivipary + lateral axillary branching.

The terms shoot apical division and false vivipary needed additional clarification because terms were not clearly defined in previous literature. Branching type names were assigned using the uniqueness and priority principles of botanical nomenclature (Greuter et al., 1999). The term dichotomy was not used because it has been defined multiple ways and the evidence for whether shoot apical division results from an equal apical division was often lacking. Most commonly, dichotomy implies equal division of the shoot apical meristem (Tomlinson, 1990), but the term has also been defined as (1) two independently functioning axes (Gola, 2014), or (2) two more or less equal axes (Harris & Harris, 2013). Thus, the term has been used to describe both a developmental process (equal division of the shoot apex) and the result of branch outgrowth. Since there was discrepancy among definitions and usage of dichotomy, the term apical division was used to describe any division of the apical meristem (uniqueness principle). The term false vivipary was selected because it was first published in the grass literature

to describe a phenomenon similar to what was found in the palms (priority principle) (Van der Pijl, 1982; Bell 2008).

The numbers of species, genera and subfamilies with each branching type were counted to determine the most abundant branching type and combination found at each taxonomic level. To determine the relationship between subfamily size and branching types, the number of solitary species in each subfamily and the number of branching types in each subfamily were counted and compared to the number of species in each subfamily. Comparisons between number of solitary species and total number of species among subfamilies were made using contingency tables and chi-squared tests in R (R studio team, 2015); expected values were obtained by multiplying the sample size of the subfamily by the sample proportion of solitary species in the palms (0.55). Comparisons between number of branching types and total number of species among subfamilies were made using contingency tables and chi-squared tests in R (R studio team, 2015); expected values was the average number of branching types exhibited in the subfamilies (3 types).

Mapping the phylogenetic distribution of vegetative branching types:

Subfamily-level and genus-level phylogenies were used to examine the phylogenetic distribution of branching types. The phylogeny from Baker et al. (2009) was selected for character mapping because it had the most recent genus-level phylogeny. Adjustments were made for new and deleted taxa (Dransfield, 2008; Baker & Bacon, 2011; Bernal & Galeano, 2013; Baker et al., 2015; Noblick & Meerow, 2015). Branching types were used for character mapping, since the specific branching type was the character that was retained or lost. The software Mesquite (Madison & Madison, 2016), a software package used by evolutionary biologists to analyze comparative data, was

used to map vegetative branching onto the published cladograms. The ancestral branching types were determined using the most parsimonious tree in Mesquite. A subfamily level cladogram was analyzed to predict the ancestral branching type for the family. Cladograms for Arecoideae, Calamoideae and Coryphoideae were analyzed to predict the ancestral branching type for each of these three subfamilies. A cladogram for Ceroxlyloideae was not included because this subfamily had no vegetative branching except for a single species, *Ravenea deliculata* Rakotoarin. A cladogram for Nypoideae was not included because it is monospecific (*Nypa fruticans* Wurmb).

RESULTS**:**

There were five vegetative branching types recognized in this study: lateral axillary branching, shoot apical division, false vivipary, abaxial branching and leaf-opposed branching. A dichotomous key was created to facilitate understanding and recognition of each branching type (Table 3). Some species displayed more than one branching types, referred to as branching combinations. Two branching combinations were also observed: shoot apical division + lateral axillary; and false vivipary + lateral axillary. Most commonly, species exhibited no vegetative branching; four subfamilies, 147 genera (81% of genera), and 1043 species (55% of observed species) did not branch vegetatively (Table 2, Fig. 2). Some species were found with a branching type or as a solitary individual (175 species, 9% of observed species).

1) Lateral axillary branching was the most widely distributed vegetative branching type in the palms; it was described in four subfamilies, 61 genera (34% of genera), and 646 species (34% of observed species) (Table 2). Four forms of lateral axillary branching were identified: basal suckering, rhizomatous branching, aerial suckering and relocated axillary branching. Basal suckering was defined as lateral axillary branching

where the branches grew orthotropically (vertically) immediately and were restricted to the base of the parent shoot. Basal suckering was the most common form of lateral axillary branching, found in at least 600 palm species. Basal suckers may be produced throughout the life of an individual or basal suckers may be produced only during certain times. For example, *Plectocomia* Mart. & Blume species (15 species) and two *Licuala* Thunb. species (*L*. *celebica* Miq. and *L. gracilis* Blume) produced basal suckers after a period of dormancy, usually after death of the parent shoot (Tomlinson, 1990). *Phoenix* L. species produced basal suckers until they were sexually reproductive and then stopped producing basal suckers (Tisserat & DeMason, 1985).

Rhizomatous branching was defined as lateral axillary branching where branches were restricted to the base of the stem but grew plagiotropically (horizontally) for some time before growing orthotropically (vertically). At least 33 species exhibited rhizomatous branching. Rhizomatous branching was found in combination with basal suckering in two species (*Acoelorrhaphe wrightii* H.Wendl. ex Becc. and *Cyrtostachys renda* Blume).

Aerial suckering was defined as basal suckering that was not restricted to the base of the stem and also occurred on the aerial portions of the stem. *Wendlandiella gracilis sub. Polyclada* Dammer, *Linospadix apetiolatus* Dowe & A.K.Irvine*, Hyospathe elegans* hort ex Hook. f.*,* and *Geonoma baculifera* Kunth exhibited aerial suckering (Tomlinson, 1990; Chazdon, 1991). In this study, aerial suckering was placed within lateral axillary branching because the branching mechanism for aerial suckering was developmentally the same as the branching mechanism for lateral axillary branching and species with aerial lateral axillary branching have basal suckering as well.

Displaced lateral axillary branching, found in *Korthalsia* Blume, was defined as vegetative axillary meristems that were initiated in the axil of the first or second leaf

primordium and then were displaced during development on to the internode above or onto the base of the leaf above. The displaced lateral axillary branching type was placed within lateral axillary branching because the branching mechanism was lateral axillary and the transition out of the axil occurred after initiation of the meristem (Fisher & Dransfield, 1979).

2) Shoot apical division was distributed throughout the palms, having been described in four subfamilies, seven genera (3% of genera), and 21 species (1% of observed species) (Table 2, Fig. 2). Three forms of shoot apical division were identified: isotomy, anisotomy and *Nannorrhops* branching.

Isotomy, which is equal apical division followed by equal growth, has been studied anatomically in three palm genera and eight species: *Hyphaene* Gaertn. (*H. compressa* H.Wendl, *H. coriacea* Gaertn., *H. dichotoma* (J.White Dubl. Ex Nimmo) Furtado, *H. reptans* Becc., and *H. thebaica* Mart., *Nypa fruticans* Wurmb. and *Manicaria saccifera* Gaertn. (Gola et al., 2014). Leaf arrangement and equal forking in divided crowns of mature plants suggest isotomy, but anatomical study of shoot apical development is needed for confirmation of other species (Fisher, personal correspondence).

Anisotomy, which is unequal division followed by differential growth, was exhibited by *Eugeissona* Griff. (*E. ambigua* Becc., *E. brachystachys* Ridl., *E. insignis* Becc., *E. minor* Becc., *E. triste* Griff., and *E. utilis* Becc.). Anisotomous division was so unequal in *Eugeissona* species that the division appeared to be lateral axillary branching on non-basal portions of the stem (Fisher et al., 1989). Apical division in palms has been reported to range from equal (isotomous) to unequal (aniosotomous) division. In *Chamaedorea cataractarum* Mart., the anisotomous division of the apical meristem

occurred very early in development, and as the stems matured, the division appeared to be equal (Fisher, 1973). Only developmental studies showed that the division did not initiate equally.

Nannorrhops branching, which has not previously been recognized as a distinct branching type, was defined as equal apical division with branch-pair differentiation. For example, in *Nannorrhops ritchiana* H.Wendl., the apical meristem divides into one fertile and one vegetative branch.

3) False vivipary has been described in two subfamilies, three genera (1 % of genera), and ten species (0.5% of observed species) (Table 2, Fig. 2): *Calamus* Auct. ex. L. (C*. castaeneus* Griff., *C. dianbaiensis* C.F.Wei, *C. gamblei* Becc., *C. ingens* (J.Dransf.) W.J.Baker, *C. kampucheaensis* A.J.Hend. & Hourt, *C. nematospadix* Becc., and *C. pygmaeus* Becc.) *Salacca* Reinw. *(S. flabellata* Furtado, and *S. wallichiana* Mart.) and *Socratea salazarii* H.E.Moore (Fisher & Mogea, 1980; Baker et al., 2000; Pintaud & Millan, 2004; Rupert et al., 2012). In each account of false vivipary, different terms were used to describe the phenomenon (Fisher & Mogea, 1980; Baker et al., 2000; Pintaud & Millan, 2004; Rupert et al., 2012). The architectures of the palms with false vivipary were different, yet the branching of the inflorescence was the same--vegetative shoots formed at the apex of the inflorescence. If the shoot reached the ground, it rooted and a shoot grew upward. *Calamus gamblei*, *C. pygmaeus* and *C. nematospadix* are all climbing rattans (Dransfield, 1992), *Socratea salazarii* is an erect and usually solitary palm (Pintaud, 2004), while *Salacca flabellata* is an acaulesent palm (Furtado, 1949).

4) Abaxial branching was described in one subfamily (Arecoideae), two genera (2% of genera), and seven species (0.3 % of observed species) (Table 2, Fig. 2). In abaxial branching, a vegetative branch originating on the abaxial surface of the leaf

sheath occurred on the basal and intermediate internodes of orthotropic stems in *Oncosperma* Blume species and *Dypsis lutescens* (H.Wendl.) Beentje & J. Dransf. Species with abaxial branching usually do not display lateral axillary branching.

5. Leaf-opposed branching was described in one subfamily (Calamoideae), two genera (1% of genera), and seven species (0.3% of observed species). Leaf opposed branching occurred on basal internodes and on aerial internodes of the stem, as in the liana *Myrialepis paradoxa* (Kurz.) J. Dransf. Axillary branching, leaf opposed branching and abaxial branching are distinct types of stem nodal meristems based on location and position of the branching meristem (Fig. 2). In axillary branching, the meristem is located in the axil of the leaf. In abaxial branching, the vegetative branching meristem is located on the abaxial surface of the leaf sheath. In leaf-opposed branching, the branching meristem is borne on the stem, enclosed by the edges of the leaf sheath and opposite to the lamina and petiole.

Individuals within a species sometimes displayed more than one branching type at a time, here called branching combinations. The two branching combinations were shoot apical division + lateral axillary and false vivipary + lateral axillary branching. Shoot apical division + lateral axillary branching was exhibited by one species of *Basselinia* Vieill. (Arecoideae), all 27 species of *Korthalsia* Blume (Calamoideae), two species of *Hyphaene* (Coryphoideae) and monospecific *Nannorrhops ritchiana* (Coryphoideae). False vivipary + lateral axillary branching was exhibited by five species of *Calamus* (Calamoideae), and *Socratea salazarii* (Arecoideae) (Table 2).

Distribution of branching types within the family:

At the subfamily level, lateral axillary branching and shoot apical division were predicted as the ancestral vegetative branching types (Fig. 4). The solitary state (no

vegetative branching) was also an ancestral state. False vivipary evolved a minimum of two times: once in the Calamoideae and once in the Arecoideae (Fig. 4A, 4C). Abaxial branching evolved a minimum of two times in the Arecoideae (*Oncosperma* and *Dypsis*) (Fig. 4C). Leaf-opposed branching evolved two times in the Calamoideae, in *Myrialepis* Becc*.* and in *Calamus* (Fig. 4A).

The subfamilies had different relationships between size (species count) and number of branching types (Fig. 5A, X^2 test comparing number of branching types to genus size by subfamily $p<0.01$). The subfamilies also had different relationships between size and number of solitary species (Fig. 5B, X^2 test comparing number of solitary species to genus size by subfamily, $p<0.01$) The Calamoideae subfamily had a disproportionately large number of branching types and a disproportionately low number of solitary species for its size (Fig. 5A, Fig. 5B).

The Calamoideae, the most basal and second largest subfamily (659 species), exhibited four branching types and both branching combinations and was the most diverse in vegetative branching types (Table 2). On average number, one branching type was exhibited in a genus. With three branching types, *Calamus* exhibited the most branching types in Calamoideae . The ancestral branching type of Calamoideae was predicted to be lateral axillary branching (Fig. 4A). In the Calamoideae, more species had vegetative branching (341 species, 86% of observed Calamoideae species) than the solitary habit (58 species, 15% of observed species). Lateral axillary branching evolved a minimum of one time in the Calamoideae. In five genera, all species had lateral axillary branching; these genera were *Laccosperma* G. Mann & H.Wendl*.* (six species), *Eremospatha* Mann & H.Wendl*.* (11 species), *Oncocalamus* Mann & H.Wendl*.* (five species), *Mauritiella* Burret (four species), *Plectocomia* Mart. & Blume (15 species), and

Plectocomiopsis Becc. (six species). Ten species in two genera in the Calamoideae displayed false vivipary: *Calamus* (eight) and *Salacca* (two). Shoot apical division evolved at least two separate times in the Calamoideae; species of *Eugeissona* and *Korthalsia* exhibited shoot apical anisotomy. Leaf-opposed branching, described only in the Calamoideae, was the least common branching type in the Calamoideae; *Myrialepis* (one species) and *Calamus* (seven species) were the only two genera with leaf-opposed branching. In Calamoideae, 15% of observed species did not display any branching, and two genera, *Mauritia* L.f. (two species) and *Pigafetta* (Blume) Becc. (two species) exhibited no branching:.

The majority of the Coryphoideae, the third largest subfamily (492 species), were solitary, exhibiting no vegetative branching (39 genera/283 species, 74% of observed Coryphoideae species). Members of Coryphoideae displayed lateral axillary branching (16 genera /79 species, 20% of observed Coryphoideae species) and shoot apical division (three species of *Hyphaene*, 0.7% of observed Coryphoideae species), as well as one branching combination, shoot apical division + lateral axillary (two species of Hyphaene and *Nannorrhops ritchiana*) (Table 2). The ancestral branching type of the Coryphoideae was lateral axillary branching (Fig. 4B). Based on size, the Coryphoideae exhibited fewer branching types, given the number of species (Fig. 5A). The genus *Hyphaene* (eight species) exhibited the most branching types and combinations in the Coryphoideae (two types – lateral axillary and shoot apical division and one branching combination (shoot apical division + lateral axillary)). All species in subtribe Rhapidinae, except for *Trachycarpus* H.Wendl., exhibited lateral axillary branching: *Chamaerops* L. (one species), *Rhapidophyllum* H.Wendl. & Drude (one species), *Maxburretia* Furtado (three species), *Rhapis* L.f. (ten species) and *Guihaia* J.Dransf., S.K.Lee & F.N.Wei (two species). The subtribe Rhapidinae was the only clade greater than genus-level in the

Coryphoideae where lateral axillary branching was retained throughout all species of the clade. Lateral axillary branching evolved at least 12 times and shoot apical division evolved at least two times in Coryphoideae. There were no species in the Coryphoideae that displayed false vivipary, abaxial branching or leaf-opposed branching.

The Arecoideae, the largest subfamily (1376 species), exhibited four branching types and two branching combinations (Table 2). The majority of the Arecoideae exhibited no branching (59%, 657 observed species). *Dypsis* Noronha ex Mart. exhibited three branching types, which was the most branching types for the Arecoideae. The ancestral branching type of the Arecoideae palms was lateral axillary (Fig. 4C). Five genera in Arecoideae had no solitary species (i.e., all species exhibited vegetative branching): *Iriartella* H.Wendl. (two species), *Wettinia* Poepp. ex Endl. (21 species), *Jubaeopsis* Becc. (one species), *Podococcus* Mann & H.Wendl. (two species) and *Sclerosperma* G.Mann & H.Wendl. (three species). Shoot apical division evolved at least four times, occurring in *Allagoptera*, *Basselinia*, *Dypsis*, and *Manicaria*. However, shoot apical division was not easily observed in these genera. In *Basselinia*, *Dypsis* and *Manicaria*, shoot apical division occurs early in development of the stem (Moore, 1982; Fisher & Zona, 2006). *Allagoptera* Nees is a creeping palm and apical division occurs low to the ground. While shoot apical division was not as obvious as in *Hyphaene* (Coryphoideae), morphological signs of apical division (forking) are still present and observable in *Allagoptera*. False vivipary evolved once in *Socratea salazarii*. Abaxial branching evolved twice, occurring in *Dypsis lutescens* and *Oncosperma*.

The Ceroxyloideae, the fourth largest subfamily (47 species), had one species that branched vegetatively. The ancestral state of Ceroxyloideae was no branching; 99% of species exhibited no branching. *Ravenea deliculata,* from the largest genus in

Ceroxyloideae (*Ravenea,* 21 species), displayed lateral axillary branching both basally and aerially (Rakotoarinivo, 2008). On the basis of size, the Ceroxyloid palms exhibited fewer branching types and combinations than expected (Fig. 5A).

Nypoideae, the smallest subfamily (one species, *Nypa fruticans*), exhibited one branching type (shoot apical division), and the ancestral branching type was shoot apical division.

In the palm family, most genera displayed either no branching (147 genera, 81% of genera) or lateral axillary branching (61 genera, 34% of genera). There were only 15 genera (9% of genera) and 67 species (3% of observed species) that displayed branching types other than lateral axillary branching. In Calamoideae, four genera had non-axillary vegetative branching: *Calamus* (leaf-opposed, false vivipary + lateral axillary), *Korthalsia* (shoot apical division + lateral axillary), *Myrialepis* (leaf-opposed), and *Eugeissona* (shoot apical division). In Coryphoideae, two genera displayed non-axillary vegetative branching: *Hyphaene* (shoot apical division or shoot apical division + lateral axillary), and *Nannorrhops* (shoot apical division + lateral axillary). In Arecoideae eight genera displayed non-axillary branching: *Allagoptera* (shoot apical division), *Basselinia* (shoot apical division+ lateral axillary), *Chamaedorea* (shoot apical division), *Dypsis* (shoot apical division or false vivipary), *Manicaria* (shoot apical division), *Oncosperma* (abaxial), *Socratea* (false vivipary + lateral axillary), and *Syagrus* (shoot apical division).

Only six genera displayed two or more branching types. Genera with two branching types were *Basselinia* (14 species, Arecoideae), *Chamaedorea* (106 species, Arecoideae), *Syagrus* Mart. (58 species, Arecoideae) and *Hyphaene* (eight species, Coryphoideae). *Calamus* exhibited three branching types (498 species, Calamoideae),

and *Dypsis* exhibited three branching types (162 species, Arecoideae). The genera that displayed two or more branching types came from different sized genera but were disproportionately from Arecoideae. Multiple branching types occurred in one genus from Calamoideae, one from Coryphoideae and four from Arecoideae.

DISCUSSION**:**

Results from the current study suggest that lateral axillary branching is the ancestral branching type and that branching evolved before palm divergence from immediate ancestors. Monocots evolved in the mid/late Jurassic period about 160 million years ago. (Wikstrom et al., 2001). Recent evidence suggests palms diverged in the Turonian, about 90 million years ago (Harley, 2006). Newer findings demonstrate that palms diverged much earlier than commelinid relatives (Barrett, 2016). At some point between monocot evolution and evolution of the present palm species, a diversity of branching types evolved in the palms.

While fossilized remains of palms are distributed throughout the fossil record, stems are less commonly found as fossils and multiple-stemmed fossils are missing from the literature entirely (Erwin & Stockeny, 1994; Harley, 2006). There is a form genus for palms with rhizomatous stems, *Rhizopalmoxylon* (*Palmoxylon* is the form genus for petrified wood) and there is apparently no literature on its architecture, specifically, whether there are multiple stems per individual (Harley, 2006). *Nypa fruticans*, a multi-stemmed palm once widespread in many continents, has fossilized pollen, fruit, and leaves but no stem fossils (Gee, 2001; Mehrotra et al., 2002). It is difficult to determine when branching evolved in *Nypa*, and in palms in general, without any branching or architectural information from fossils.

While the fossil record does not distinguish the ancestral branching type, it is possible to predict evolutionary trajectories for each branching type. Because of the prevalence of lateral axillary branching in commelinid relatives, as well as in the palm family, lateral axillary branching may have been present before the divergence of palms. Lateral axillary branching is a common branching type in Poaceae Barnhart (Holtuum, 1995; Ward & Leyser, 2004; Steen & Leyser, 2005; Doust, 2007), Cyperaceae Juss. (Rodigues & Maranho-Estelita, 2009), Zingiberaceae Martinov (Bell, 1979) and Dasypogonaceae Dum. (Clifford et al., 1998); Dasypogonaceae is sister to the palms. Therefore, lateral axillary branching may share a common evolutionary history throughout the commelinid relatives.

While the results from the present study suggest that shoot apical division is an ancestral branching type, shoot apical division in the commelinids is described only in *Strelitzia* Banks (Strelitziaceae) (Fisher, 1976). Also, shoot apical division is not nearly as widespread through the palm family as lateral axillary branching. It is likely that shoot apical division evolved after the divergence of palms.

Results from this study suggest that the remaining branching types, false vivipary, abaxial branching and leaf-opposed branching, probably evolved after the divergence of palms. False vivipary and leaf-opposed branching are found in commelinid relatives. False vivipary is common in the Poaceae (*Chlorophytum comosum* (Thunb.) Jacques, *Deschampsia alpina* (L.) Roem. & Schult., *Festuca ovina var. vivipara* L., *Dactylis glomerata* L., *Poa* x *jemtlandica* K.Richt.), as well as the Zingiberales (Costaceae Nakai and Marantaceae R.Br.). In Costaceae (Zingiberales) and Marantaceae (Zingiberales), bulbils are produced in the axils of inflorescence bracts (Jenik, 1994), a branching type closely related to false vivipary. Leaf-opposed branching

is found in *Musa* L. (Fisher, 1973). However, the presence of these branching types in commelinid relatives does not mean that the ancestral palm could display the branching types. Results from this study suggest that false vivipary and leaf-opposed branching evolved later in palm evolutionary history. Results suggest that the false vivipary and leaf-opposed branching displayed by the palms and their commelinid relatives is an example of homoplasy, and distinct evolutionary histories led to similar branching types. Abaxial branching, however, has been described only in the palms and may be a branching type unique to the family.

The evolutionary history of branching types may not be easily determined because the evolution (and loss) of branching types in the palms is continuous and occurred at different speeds among subfamilies (Faurby et al., 2016). The different evolutionary trajectories of vegetative branching in subfamilies Calmoideae and Arecoideae exemplify that evolution (and loss) of branching types is continuous and occurred at different speeds. In Calamoideae, most commonly an entire genus shares a branching type. Branching types in Calamoideae do not appear to be changing at the species level. Alternatively, in Arecoideae, species within a genus may not share a common branching type. In the Arecoideae, the genera are mostly solitary but have a few branching species. There are two distinct trajectories that could lead to a primarily solitary genus with a few branching species in Arecoideae. Either the ancestor to the genus did not branch and the ability to branch is re-evolving in a few species, or the ancestor did branch and the extant species have lost the ability to branch. Evolution of branching in palms may be influenced by differences in the ecology of different taxa.

Ecology of branching in palms

Regardless of evolutionary history, vegetative branching is less common in palms than in their commelinid relatives (Tomlinson, 1973). Like most monocots, including their commelinid relatives, palms do not produce secondary xylem (wood) from a vascular cambium, which limits their ability to make large trees. One of the main differences between palms and their close relatives, however, is their large, strong, woody trunks. Palms form a woody trunk through cell thickening and lignification on the surface layers of the cells in the outer cortex. It is possible that the lignification of the surface of the palm stem prevents activation and growth of dormant axillary buds. The lignified stem may have imprisoned the buds and the ability to branch via axillary buds was lost over evolutionary time. Lignified stems (woody trunks) presumably have been selected because they increase fitness and the chance of survival (Schluter, 2001). Vegetative branching may be less common in the palms because there was a selection for palms with thicker, taller and faster-growing trunks rather than thinner trunks that can branch (Henderson, 2002a).

It is important to note that all palms, even solitary palms, branch sexually. All palms have meristems that produce inflorescences. Similar branching types exist in vegetative and sexual branching in the palms. The most common type of sexual branching is axillary, exhibited by the vast majority of palms, where an inflorescence is produced from a bud in the leaf axil (Dransfield et al., 2008). In sexual branches, there is variation in types of displaced axillary branching that results in different branching patterns (Fisher & Maidman, 1999). In *Salacca* and *Kerriodoxa* J.Dransf., the sexual bud is borne in the leaf axil but may be captured by the subtending developing leaf and the bud emerges through a slit on the abaxial side of the leaf sheath (Fisher & Mogea,

1980). In a few genera in the Calamoideae (*Korthalsia*, *Calamus*, *Myrialepis*, *Plectocomia* and *Plectocomiopsis*) the bud is displaced longitudinally and is adnate to the internode and leaf sheath above the node of origin (Fisher & Dransfield, 1977; Fisher, 1980). In sexual apical branching, the apical meristem aborts vegetatively and produces a large inflorescence (i.e., *Corypha* L. and *Tahina* J.Dransf. & Rakotoarin.) (Dransfield et al., 2008). False vivipary is a convergence between asexual and sexual branching and is both sexual and vegetative. Abaxial and leaf-opposed sexual branching types have not been recorded in the palms.

While sexual branching is more common in the palms than vegetative branching, there are ecological benefits of vegetative branching. First, branching could increase net primary productivity for the individual genet. When the palm branches vegetatively, it produces more crowns with more leaves, and the increase in leaves could increase photosynthetic potential (Duncan, 1971). Since not all leaves are photosynethically equivalent, having multiple crowns would increase photosynthesis. In palms like *Serenoa* Hook.f., *Allagoptera* and *Nypa*, a creeping habit allows the stem to produce more roots (Tomlison, 1990; Fisher, 1999). The creeping habit can support a greater photosynthetic potential. However, if the branching type is shoot apical division and the habit is erect (as in *Hyphaene dichotoma*), the trunk may be unable to support more crowns physically and physiologically.

Another ecological consequence of branching is that having multiple stems increases chances of an individual's survival in unstable environments, such as understories of rainforests and coastal strands (Tomlinson, 1990). Certain species of *Chamaedorea* Willd. and *Geonoma* Willd. live in unstable environments in the understory of rainforests where falling debris poses a threat to their survival (Bullock,

1980; Clark & Clark, 1989; Chazdon, 1992; James, 2013;) A solitary palm only has one apical meristem and damage to the apical meristem results in death of the plant. In a multiple-stemmed palm, a genet can survive after damage to a single apical meristem. Thus, having multiple stems increases their chance of surviving a fallen branch or trunk of a large upper canopy tree, exemplified by *Geonoma baculifera* and *Hyospathe*. These species are clumping palms that grow in the understory of rainforests. However, if damage occurs on an apical meristem (at the apex of the stem), aerial axillary buds grow to produce plantlets. The stem eventually falls and the plantlets root into the ground, producing new ramets.

Nypa and *Allagoptera* also colonize environments where water level and substrate are unstable. *Nypa fruticans* colonizes coastal strands where water level is in constant flux and muddy banks are unstable (Tomlinson, 1990). *Allogoptera* colonizes sandy beaches and dunes, where water level changes daily and dunes are likely to change shape (Dransfield et al., 2008). For *Nypa* and *Allogoptera*, branching is by shoot apical division, which allows them to form large monotypic stands. If damage occurs to a stem, such as meristem or stem rot from prolonged flooding, many other apical meristems exist that will survive and continue branching. *Nypa* and *Allagoptera* may also help stabilize these unstable environments.

While vegetative branching is a survival method, as in *Chamaedorea*, *Geonoma*, *Hyospathe* Mart., *Nypa* and *Allagoptera*, it is also a mechanism for reproduction (Mogie, 1992). In unstable environments, such as flood plains, coastal strands and habitats with frequent fire and droughts, seed germination and establishment can be difficult. The ability of an individual to branch vegetatively and reproduce asexually ensures continued reproduction of the species into the next generation.

The Calamoideae epitomize the ecological benefit gained from vegetative branching. They are an interesting group because most species exhibit vegetative branching and climb prolifically. A major innovation in the Calamoideae was their liana habit (Gianoli, 2004; Couvreur et al., 2013). These palms climb, branch and dominate the canopy of Asian rainforests (Dransfield, 1992; Dransfield, 1997; Dransfield et al., 2008). Vegetative branching, therefore, allows the Calamoideae to climb through and explore the canopy prolifically. These palms climb, branch and colonize the canopy more efficiently than unbranched palms. Vegetative branching allows the Calamoideae to exploit the canopy habitat; at the same time, the liana habit means that they plants do not invest in large woody trunks.

The Calamoideae also contain the greatest number of species that branch through false vivipary. False vivipary is interesting ecologically because it is only successful if the inflorescence is able to root in the forest floor, presumably when the crown is close to the ground (Bell, 1980). In grasses displaying false vivipary, the inflorescence is never more than a few centimeters from the ground and the plantlet can easily reach the soil to root. In palms, false vivipary occurs on both erect (*Socratea*), climbing (*Calamus*) and acaulescent (*Salacca*) stems and is successful in all of these habits (Fisher & Mogea, 1980; Dransfield, 1992; Dransfield, 1997; Baker et al., 2000; Pintaud & Millan, 2004; Rupert et al., 2012). For all species that exhibit false vivpary, successful rooting of the false viviparous shoot has been described for stems near the soil, but the exact heights have not been recorded. There are at least four possible relationships between stem height and successful false vivipary. First, there could be no relationship; false viviparous shoots could form at any height in the canopy and successfully root in the soil. No relationship between height of the shoot and successfully rooting is the least likely of the scenarios, since the viviparous shoot may

have a very long distance to travel to reach to soil. Second, the false viviarpous shoots could form at any height in the canopy but may not successfully root above a certain stem height (critical height). Alternatively, false vivipary may only occur on stems below a critical height and stems of *Calamus* and *Socratea* may stop producing false viviparous inflorescences once they reach a certain height. The fourth possibility is that the viviparous shoot could abscise and fall to the forest floor. More studies on the morphology and ecology of false vivipary in the palms are needed in order to determine which mechanism occurs in which species.

This study of vegetative branching in palms demonstrates that diverse branching types exist in the Arecaceae. The distribution of shoot apical division, false vivipary, abaxial branching and leaf-opposed branching within the palm family and subfamilies gives insights into palm evolutionary history and ecological constraints. This study highlights how the simplification of vegetative branching in the palm literature has inhibited our understanding of basic palm evolution and ecology.

TABLES:

Table 1: Definitions of branching terms used in this study with synonyms, reference and palm example.

Term (synonym(s))	Reference(s)	Definition	Palm example
Lateral axillary branch	Tomlinson, 1990	Branch originates in the axil of the leaf	*Serenoa repens*
Basal sucker	Tomlinson, 1990	Lateral axillary branch immediately grows upward, limited to basal internodes	*Pytchosperma macarthurii*
Aerial lateral axillary branch	Tomlinson, 1990	Lateral axillary branch is not limited to basal internodes	*Geonoma baculifera*, *Hyospathe elegans*
Dormant basal suckers	Tomlinson, 1990	Basal sucker outgrowth is dormant until death of parent stem	*Plectomia spp.*
Rhizomatous branch	Zimmerman & Tomlinson, 1967	Vegetative outgrowth of axillary meristem at base of stem where monopodial or sympodial units form a plagiotropic rhizome	*Rhapis excelsa*
Sympodial rhizomatous branch	Zimmerman & Tomlinson, 1967	Vegetative outgrowth of axillary meristem at base of stem where sympodial units form a plagiotropic rhizome	*Rhapis exelsa*
Monopodial rhizomatous branch	Bell & Tomlison, 1980	Vegetative outgrowth of axillary meristem at base of stem where monopodial units form a plagiotropic rhizome	No palm example
Apical branch	Tomlinson, 1990	Branch originates in the apical meristem, most commonly as a	*Hyphaene thebaica*

		division of the apical meristem	
Apical division	Gola, 2014	More or less equal division of apical meristem, resulting in two independent functioning axes	*Hyphaene coriaceae*
Apical isotomy	Gola, 2014	Equal division apical meristem that results in two independent functioning axes of similar size and morphology	*Nypa fruticans*
Apical anisotomy	Gola, 2014	Unequal division apical meristem that results in two independent functioning axes of different size and morphology	*Eugeissona tristis*
Nannorhops branching	* new term	Equal division apical meristem that results in two independent functioning axes of different size and morphology	*Nannorhops richiana*
Adventitious bud/branching	Fisher, 1973	Meristem not in typical position	*Socratea salazarii*
False vivipary (prolification, vegetative transformation of inflorescence, broadly as proliferation (sensu latu)	Fisher & Dransfield, 1977; Bell & Bryan, 2008	Adventitious vegetative outgrowth at the shoot apex of the inflorescence, growing independently of inflorescence axis	*Calamus castaneus*
Proliferation (sensu stricto)	Bell & Bryan, 2008	Adventitious meristem originates from vegetative material, usually leaves	No palm example

Abaxial branch	Fisher, 1973, Fisher et al., 1989;	Vegetative branch meristem borne on the abaxial surface of leaf, on the base of the leaf sheath	*Dypsis lutescens*
Leaf-opposed branch	Fisher & Dransfield, 1979; Tillich, 1998	Vegetative branch meristem borne on the stem opposite of leaf and enclosed in the leaf sheath	*Myrialepis*

Table 2: Palm subfamilies and their species counts for the four branching types and their combinations; species only assigned to one combination. References for sub-families can be found in the individual sub-family tables.

Subfamily	Species count	Number of spcies that exhibit…							
		No branching	Lateral axillary	Shoot apical dichotomy	Shoot apical dichotomy with lateral axillary	False vivipary	False vivipary with lateral axillary	Abaxial	Leaf-opposed
Arecoideae	1112/1376	657	423	13	1		1	7	
Calamoideae	395/659	58	292	6	28	2	2		7
Ceroxyloideae	47/47	46	1						
Coryphoideae	381/492	283	92	3	3				
Nypoideae	1/1			1					
Arecaceae	**(1903/2501)**	**1043**	**646**	**21**	**31**	**2**	**3**	**7**	7

Table 3: Key to major branching types in the palms; palms branching types were distinguished by location of the meristem.

If there are more than one crowns: meristem used for branching (a) axillary, (b) apical, (c), adventitious (atypical position)

a. Axillary: ……(1) Lateral axillary branching

b. Apical: ……..(2) Shoot apical division

c. Adventitious: bud borne on (a) inflorescence, (b) leaf sheath, (c) stem

a. Inflorescence…….(3) False vivipary

b. Leaf sheath, base…….……...…….(4) Abaxial

c. Stem, enclosed in leaf sheath…….……...….(5) Leaf-opposed

FIGURES**:**

Fig. 1: Vegetative branching types in the palms (arrows indicate vegetative branch): A. No branching type (*Hyophorbe laugenicaulis*) or solitary; B. Lateral axillary branching (*Rhapis mulifida*); C. shoot apical division (*Hyphaene dichotoma*); D. false vivipary (*Socratea salazarii*); D. abaxial branching (*Dypsis lutescens*); and E. leaf-opposed branching (*Myrialepis paradoxa*). Arrow points to branch.

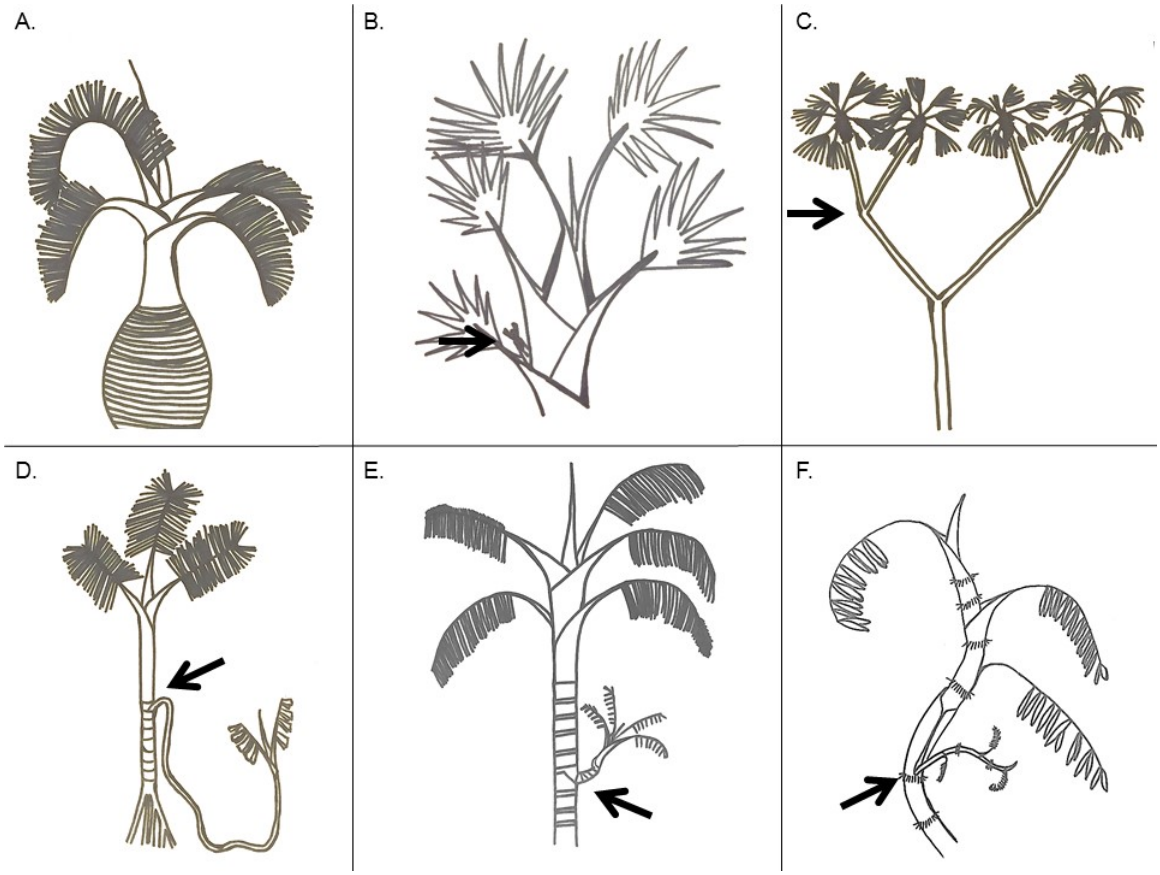


Fig. 2: Plan view of a palm leaf with locations of the three distinct types of stem nodal branching; the stem is not drawn but the encircling leaf base is shown. (A) Axillary branching--the meristem arises in the axil of the leaf; (B) Abaxial branching--the meristem is located on the base of the leaf sheath, on the abaxial surface of the leaf; and (C) Leaf-opposed branching--the meristem is borne on the stem of the palm, enclosed by the outer edges of the leaf sheath and opposite to the lamina and petiole.

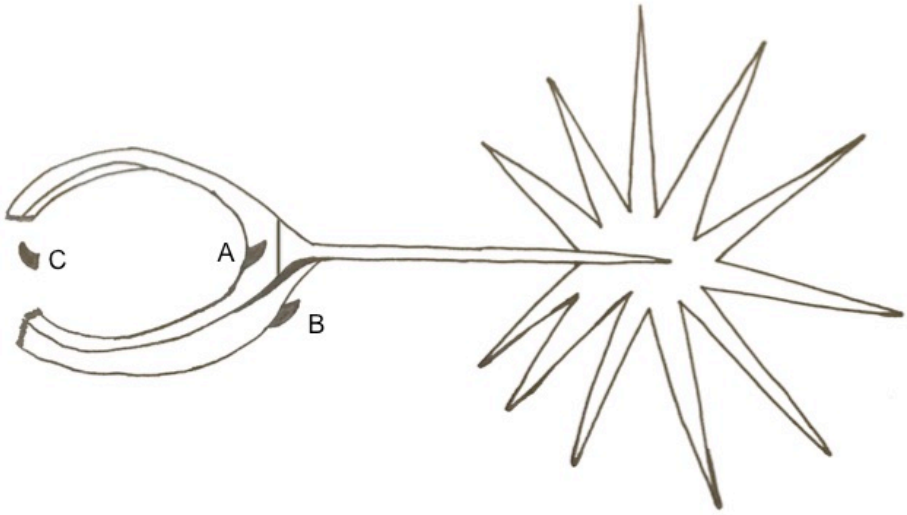


Fig 3: Distribution of branching types in the palm family (Arecaceae) on a sub-family level cladogram (A. key to branching types; B. sub-family cladogram)

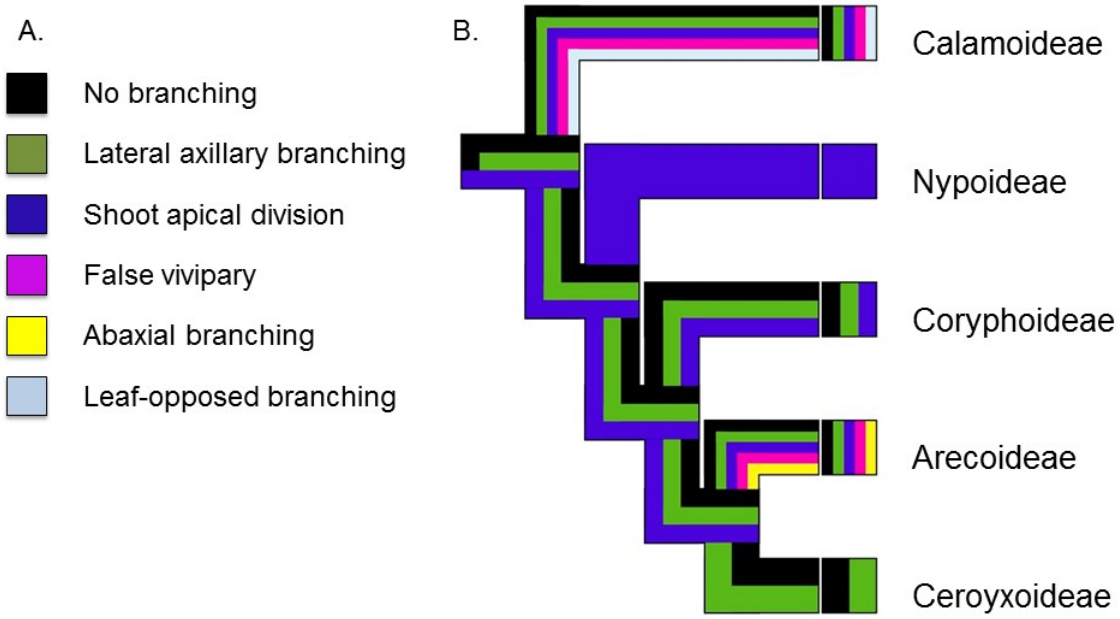


Fig 4: Distribution of branching types in the Calamoideae on a genus level cladogram. Key the same as Fig. 2.

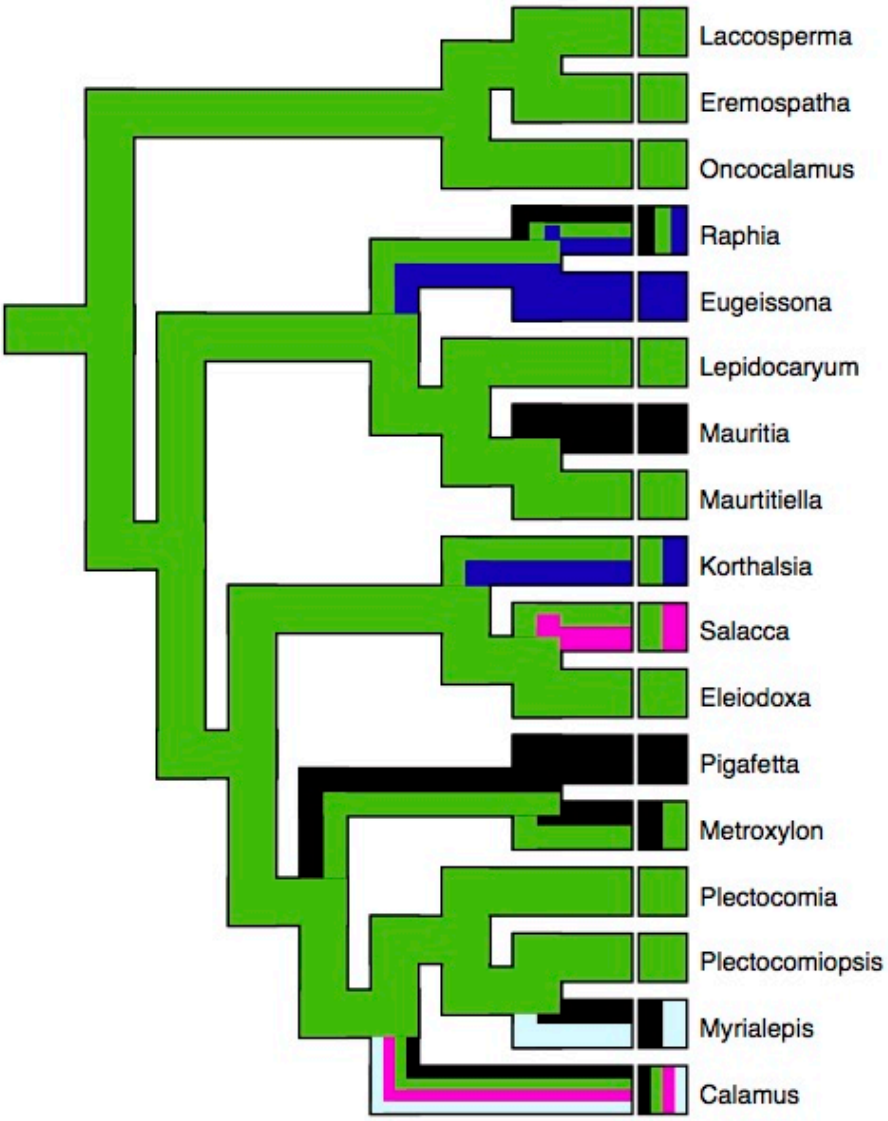


Fig. 5**:** Distribution of branching types in the Calamoideae on a genus level cladogram.

Key the same as Fig. 2

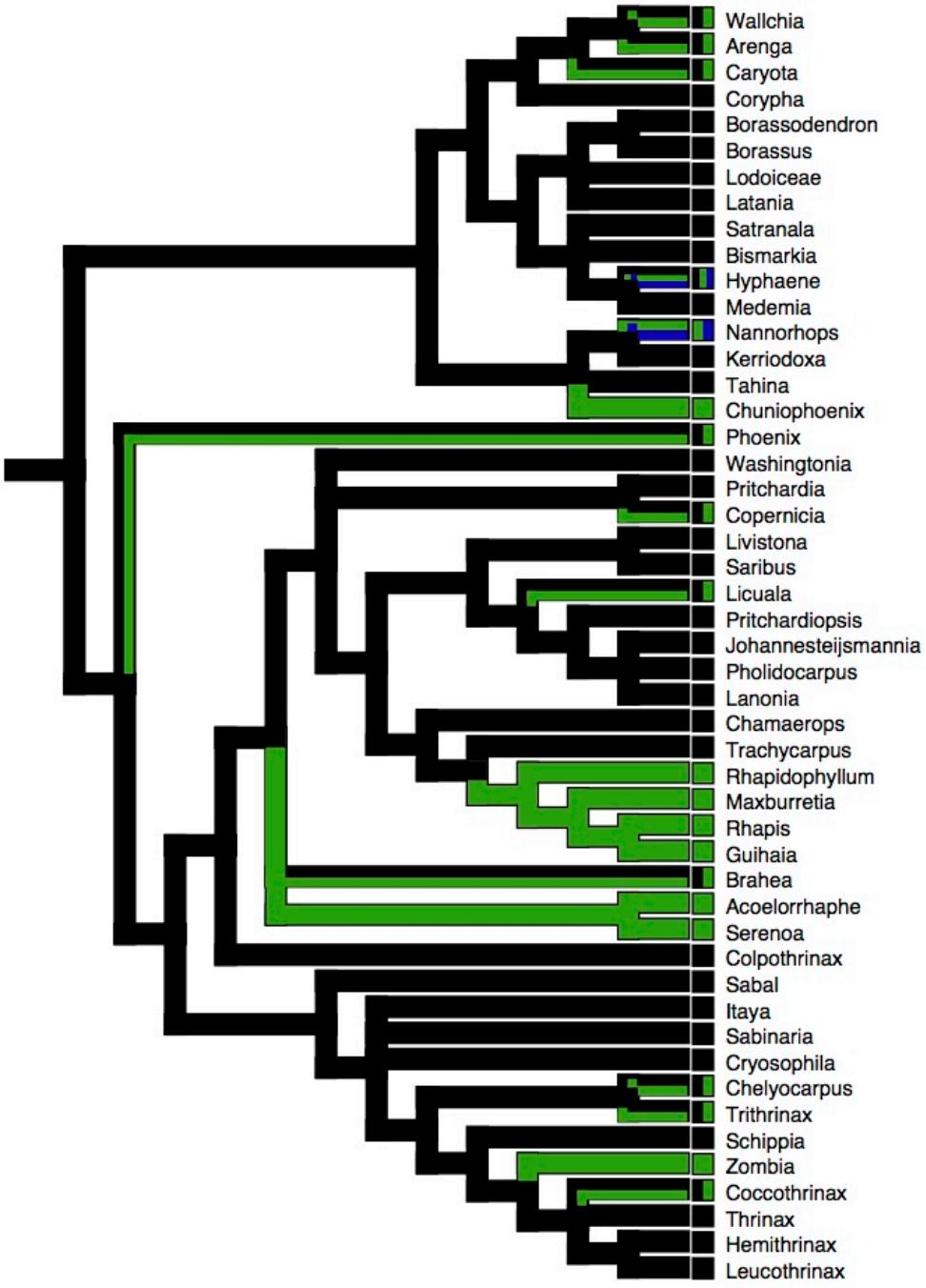
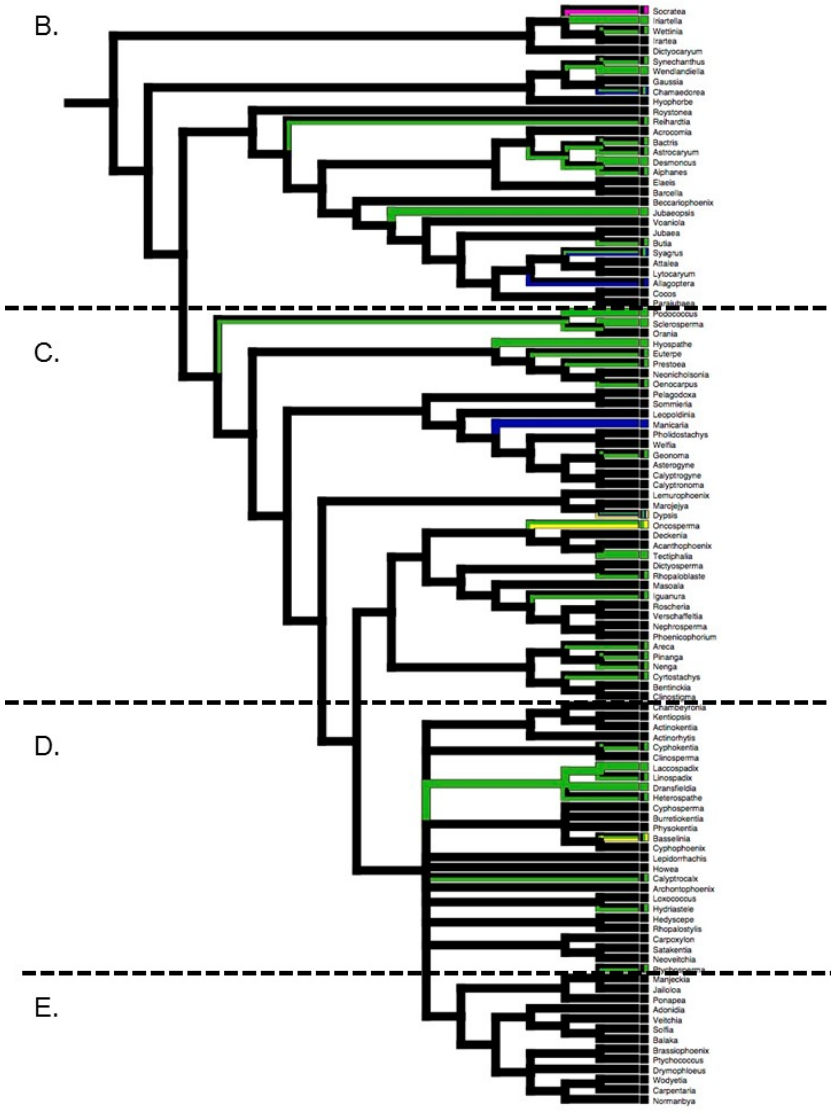
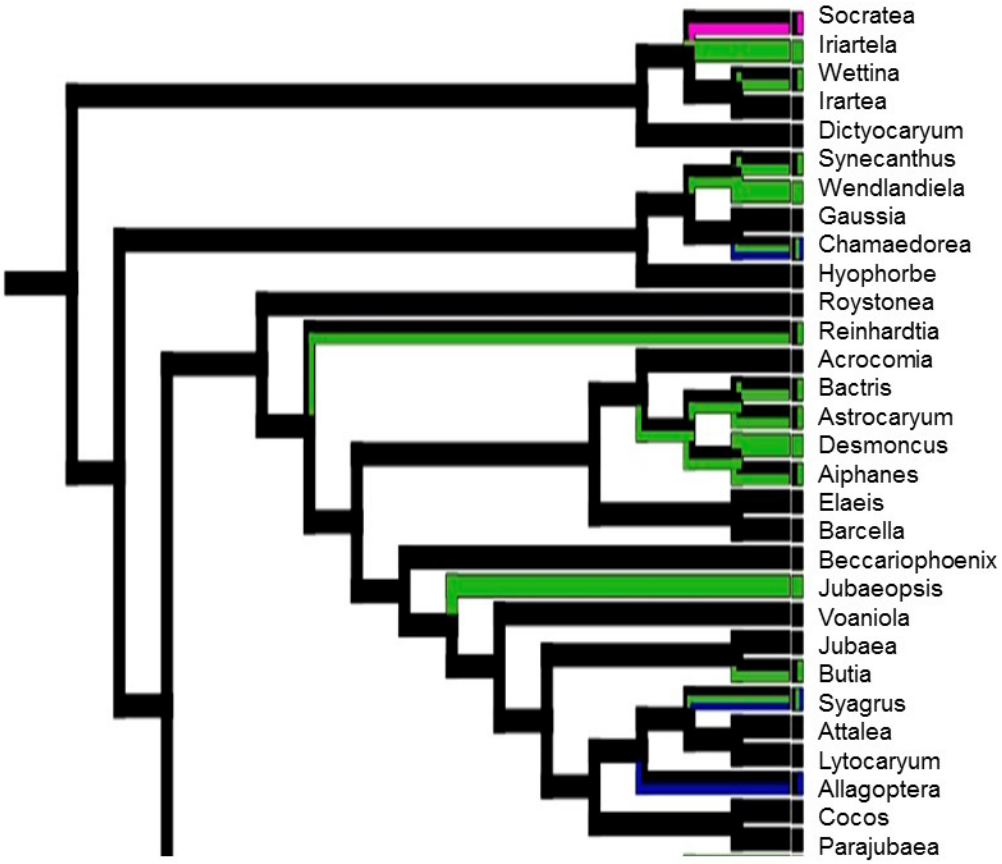


Fig. 6: Distribution of branching types in the Arecoideae on a genus level cladogram (A. entire cladogram showing further break down, B. *Socratea- Parajubaea* C. *Podococcus- Clinostigma* D. *Chambeyronia- Neoveitchia*, and E. *Ptychosperma- Normanbya*). Key the same as Fig. 2.

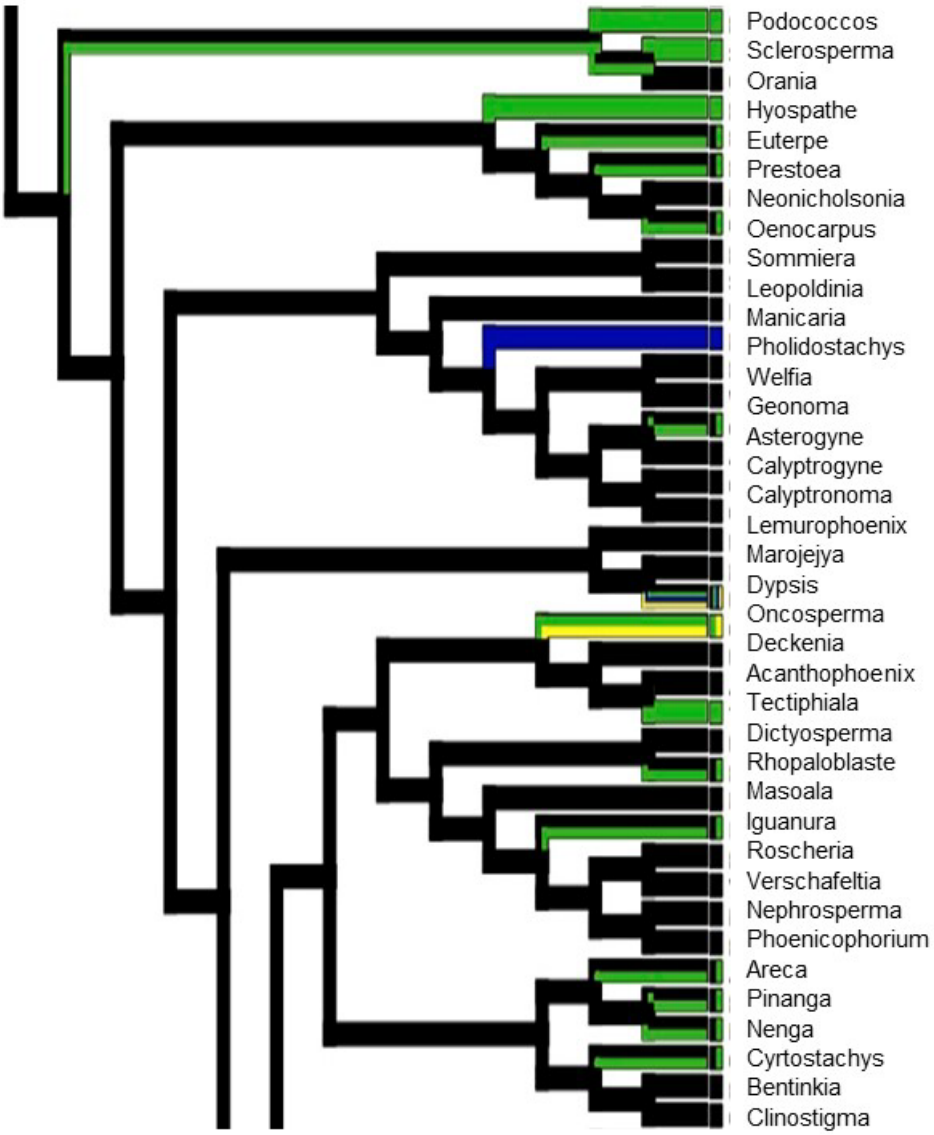
A.



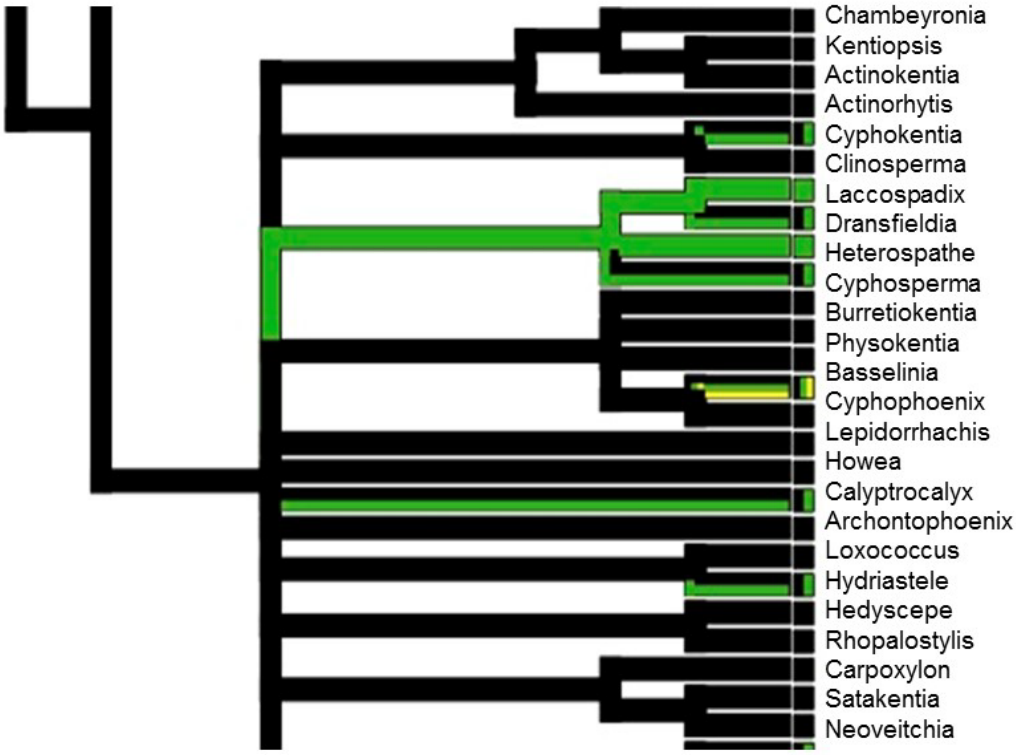
B.


Socratea
Iriartela
Wettina
Irartea
Dictyocaryum
Synecanthus
Wendlandiela
Gaussia
Chamaedorea
Hyophorbe
Roystonea
Reinhardtia
Acrocomia
Bactris
Astrocaryum
Desmoncus
Aiphanes
Elaeis
Barcella
Beccariophoenix
Jubaeopsis
Voaniola
Jubaea
Butia
Syagrus
Attalea
Lytocaryum
Allagoptera
Cocos
Parajubaea

C.


Podococcos
Sclerosperma
Orania
Hyospathe
Euterpe
Prestoea
Neonicholsonia
Oenocarpus
Sommiera
Leopoldinia
Manicaria
Pholidostachys
Welfia
Geonoma
Asterogyne
Calyptrogyne
Calyptronoma
Lemurophoenix
Marojejya
Dypsis
Oncosperma
Deckenia
Acanthophoenix
Tectiphiala
Dictyosperma
Rhopaloblaste
Masoala
Iguanura
Roscheria
Verschafeltia
Nephrosperma
Phoenicophorium
Areca
Pinanga
Nenga
Cyrtostachys
Bentinkia
Clinostigma

D.


Chambeyronia
Kentiopsis
Actinokentia
Actinorhytis
Cyphokentia
Clinosperma
Laccospadix
Dransfieldia
Heterospathe
Cyphosperma
Burretiokentia
Physokentia
Basselinia
Cyphophoenix
Lepidorrhachis
Howea
Calyptrocalyx
Archontophoenix
Loxococcus
Hydriastele
Hedyscepe
Rhopalostylis
Carpoxylon
Satakentia
Neoveitchia

E.

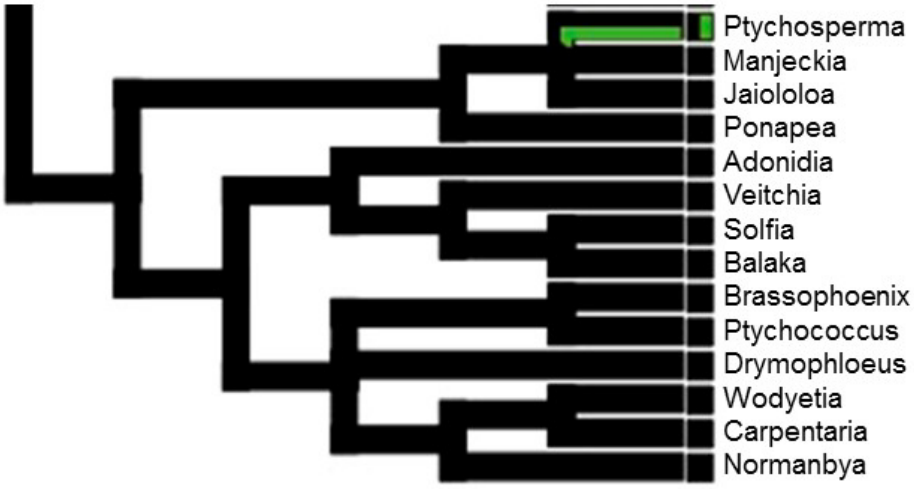
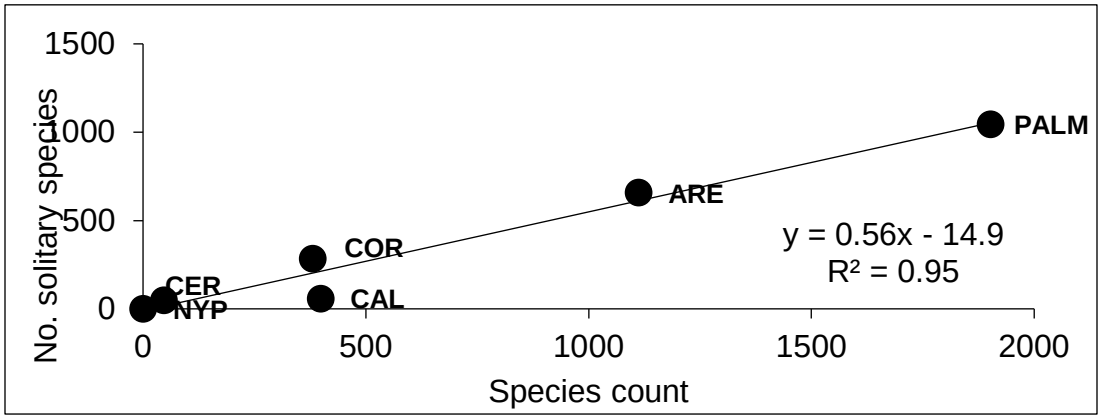
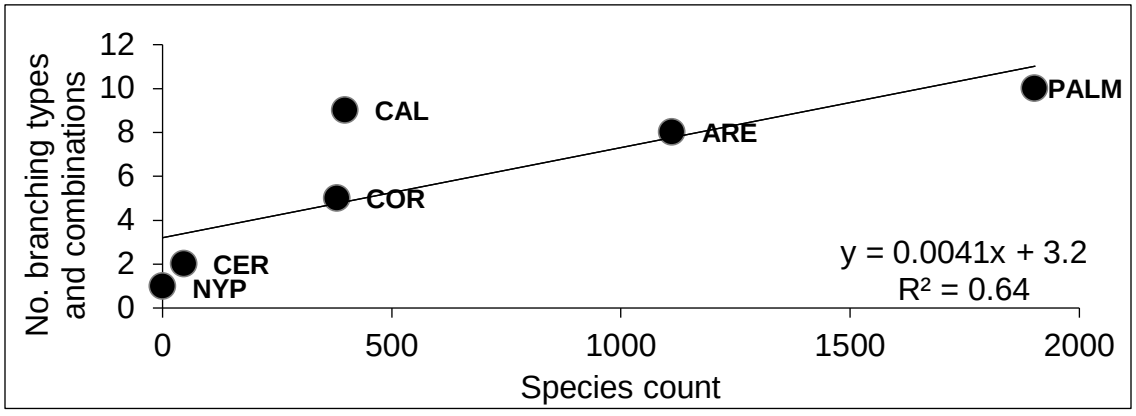

Ptychosperma
Manjeckia
Jaiololoa
Ponapea
Adonidia
Veitchia
Solfia
Balaka
Brassophoenix
Ptychococcus
Drymophloeus
Wodyetia
Carpentaria
Normanbya

Fig.7: A. Number of branching types and combinations in each subfamily and the entire family plotted with size of subfamily and family (species count) and B. number of solitary species in each sub family plotted against size of subfamily and family. (ARE= Arecoideae, CAL= Calamoideae, CER= Ceroxyloideae, COR= Coryphoideae, NYP=Nypoideae).

A.



B.



APPENDICES:

Appendix A: Genera, species counts for the four branching types and their combinations for subfamily Calamoideae with references.

A.		Number of species that exhibit…								
Genus	Species count	No branching	Lateral axillary	Shoot apical dichotomy	Shoot apical dichotomy with lateral axillary	False vivipary	False vivipary with lateral axillary	Abaxial	Leaf-opposed	References

Calamus	263/521	40	210				2		6	Beccari, 1902; Beccari, 1914; Dransfield, 1977; Dransfield, 1979; Fisher & Dransfield, 1979; Dransfield, 1982; Dransfield, 1984a; Kramadibrata, 1992; Dransfield, 1997; Dransfield, 2001; Renuka et al., 2001; Baker & Dransfield, 2002a; Baker & Dransfield, 2002b; Rustiami, 2002a; Rustiami, 2002b; Baker et al., 2003; Dransfield et al., 2005; Henderson, 2005; Baker & Dransfield; 2007; Henderson & Henderson, 2007; Henderson et al., 2008; Henderson, 2009; Sunderland, 2012; Henderson & Dung, 2013; Rustiami et al.

										2014; Baker et al., 2014
Eleiodoxa	1/1		1							Dransfield et al., 2008
Eremospatha	11/11		11							Dransfield et al., 2008
Eugeissona	6/6			6						Fisher et al., 1989;
Korthalsia	28/28				28*					Fisher & Dransfield, 1979
Laccosperma	6/6		6							Dransfield et al., 2008

Lepidocaryum	1/1		1							Dransfield et al., 2008
Mauritia	2/2	2								Dransfield et al., 2008
Mauritiella	4/4		4							Bernal & Galeano, 2001
Metroxylon	7/7	6	1							Barrau, 1959; McClatchey ,1998
Myrialepis	1/1								1	Dransfield,1982
Oncocalamus	5/5		5							Dransfield et al., 2008
Pigafetta	2/2	2								Dransfield et al., 2008
Plectocomia	15/15		15							Dransfield, 1982
Plectocomiopsis	6/6		6							Dransfield et al., 2008
Raphia	19/20	8	11							Russell, 1965; Fisher et al., 1989
Salacca	22/23		21			2				Fisher & Mogea, 1980
Calamoideae	**399/659**	**58**	**292**	**6**	**28**	**2**	**2**		**7**	

Appendix B: Genera, species counts for the four branching types and their combinations for subfamily Coryphoideae with references.

B.		Number of species that exhibit…								
Genus	Species count	No branching	Lateral axillary	Shoot apical dichotomy	Shoot apical dichotomy with lateral axillary	False vivipary	False vivipary with lateral axillary	Abaxial	Leaf-opposed	References
Acoelorrhaphe	1/1		1							Personal observation
Arenga	20/24	3	17							Dransfield et al., 2008; Jeanson & Guo, 2011
Bismarkia	1/1	1								Dransfield et al., 2008
Borassodendron	2/2	2								Dransfield et al., 2008
Borassus	5/5	5								Dransfield et al., 2008
Brahea	11/11	10	1							Dransfield et al., 2008

Caryota	14/14	11	3							Dransfield et al., 2008; Personal observation
Chamaerops	1/1	1								Dransfield et al., 2008; personal observation
Chelyocarpus	4/4	2	2							Kahn & Mejia,1988; Dransfield et al., 2008
Chuniophoenix	2/2		2							Dransfield et al., 2008; Personal observation
Coccothrinax	50/53	46	4							Henderson et al. 1997; Henderson, 2005; Moya, 1997b
Colpothrinax	3/3	3								Dransfield et al., 2008; Personal observation
Copernicia	22/22	21	1							Henderson et al., 1997; Moya, 1997a
Corypha	5/5	5								Dransfield et al., 2008; Personal observation

Cryosophila	10/10	10								Dransfield et al., 2008; Personal observation
Guihaia	2/2		2							Dransfield et al., 1985; Dransfield et al., 2008;
Hemithrinax	3/3	3								Dransfield et al., 2008
Hyphaene	7/8	2		3	2					Moore & Uhl, 1982; Valkenburg & Dransfield, 2004
Itaya	1/1	1								Dransfield et al., 2008; personal observation
Johannesteijsmannia	4/4	4								Dransfield et al., 2008
Kerriodoxa	1/1	1								Dransfield et al., 2008; Personal observation
Lanonia	8/8	1	7							Henderson & Bacon, 2011
Latania	3/3	3								Dransfield et al., 2008; Personal observation

Leucothrinax	1/1	1								Dransfield et al., 2008; Personal observation
Licuala	60/162	38	22							Henderson, 1997; Takenaka et al., 2001; Dransfield et al., 2008; Henderson et al., 2008;
Livistona	27/27	27								Dransfield et al., 2008; Dowe, 2009
Lodoicea	1/1	1								Dransfield et al., 2008
Maxburretia	2/3		2							Dransfield et al., 2008; Henderson, 2009
Medemia	1/1	1								Dransfield et al., 2008
Nannorhops	1/1				1					Tomlinson and Moore, 1968
Phoenix	13/13	6	7							Davis, 1950; Chevalier, 1952; Barrow, 1998; Dransfield et al., 2008
Pholidocarpus	6/6	6								Dransfield et al., 2008

Pritchardia	30/30	30								Dransfield et al., 2008; Personal observation
Pritchardiopsis	1/1	1								Dransfield et al., 2008
Rhapidophyllum	1/1		1							Dransfield et al., 2008; Personal observation
Rhapis	10/10		10							Dransfield et al., 2008; Personal observation
Sabal	14/14	14								Dransfield et al., 2008
Sabinaria	1/1	1								Dransfield et al., 2008
Saribus	1/1	1								Bacon & Baker, 2011
Satranala	1/1	1								Dransfield et al., 2008
Schippia	1/1	1								Dransfield et al., 2008
Serenoa	1/1		1							Fisher & Tomlinson, 193; Bennet & Hicklin, 1998; Abrahamson, 1999; Personal observation

Tahina	1/1	1								Dransfield et al., 2008
Thrinax	3/3	3								Dransfield et al., 2008
Trachycarpus	10/10	10								Dransfield et al., 2008
Trithrinax	3/3	2	1							Dransfield et al., 2008; Personal observation
Wallchia	8/8	1	7							Dransfield et al., 2008; Personal observation
Washingtonia	2/2	2								Henderson, 2007; Dransfield et al., 2008
Zombia	1/1		1							Dransfield et al., 2008; Personal observation
Coryphoideae	**381/492**	**283**	**92**	**3**	**3**					

Appendix C: Genera, species counts for the four branching types and their combinations for subfamily Ceroxyloideae with references.

		Number of species that exhibit…								
C.	Species count	No branching	Lateral axillary	Shoot apical dichotomy	Shoot apical dichotomy with lateral axillary	False vivipary	False vivipary with lateral axillary	Abaxial	Leaf-opposed	References
Ammandra	1/1	1								Dransfield et al., 2008
Aphandra	1/1	1								Dransfield et al., 2008
Ceroxylon	12/12	12								Dransfield et al., 2008
Juania	1/1	1								Dransfield et al., 2008
Oraniopsis	1/1	1								Dransfield et al., 2008
Phytelephas	6/6	4	2							Dransfield et al., 2008

Pseudophoenix	4/4	4								Dransfield et al., 2008
Ravenea	21/21	20	1							Beentje, 1994a; Beentje, 1994b; Dransfield et al., 2008; Rakotoarinivo, 2008; Rakotoarinivo & Dransfield, 2010
Ceroxyloideae	**47/47**	**46**	**1**							

Appendix D: Genera, species counts for the four branching types and their combinations for subfamily Arecoideae with references (A. Acanthophoenix- Beccariophoenix, B. Bentinckia- Drymophloeus, C. Dypsis- Leopoldinia, D. Lepidorrhachis-Prestoea, E. Ptychococcus-Voaniola, F. Wallaceodoxa- Wodyetia

D.		Number of species that exhibit…								
Genus	Species count	No branching	Lateral axillary	Shoot apical dichotomy	Shoot apical dichotomy with lateral axillary	False vivipary	False vivipary with lateral axillary	Abaxial	Leaf-opposed	References
Acanthophoenix		3								Dransfield et al., 2008
Acrocomia	8/8	8								Dransfield et al., 2008
Actinokentia	2/2	2								Dransfield et al., 2008
Actinorhytis	1/1	1								Dransfield et al., 2008
Adonidia	1/1	1								Dransfield et al., 2008
Aiphanes	23/29	11	12							Borchsenius & Bernal, 1996;

										Henderson et al., 1997
Allagoptera	5/5	1		4						Tomlinson, 1967
Archontophoenix	6/6	6								Personal observation
Areca	37/46	24	13							Dransfield, 1984b; Henderson, 2009; Heatubun, 2011; Heatubun et al., 2012
Asterogyne	5/5	5								Henderson & Steyermark, 1986; deGranville & Henderson, 1988; Stauffer et al., 2003; Dransfield et al., 2008
Astrocaryum	32/38	24	8							Kahn & Millán, 1992; Henderson et al., 1997; Borchsenius et al., 1998; Kahn & de Granville,

										1998; Kahn, 2008
Attalea	66/66	66								Dransfield et al., 2008
Bactris	72/79	5	67							Tomlinson, 1990; Henderson et al., 1997; Henderson, 2000
Balaka	9/9	9								Dransfield et al., 2008
Barcella	1/1	1								Dransfield et al., 2008
Basselinia	14/14	10	3		1					Moore, 1984; Essig et al., 1999; Pintaud & Baker, 2008; Pintaud & Stauffer, 2015
Beccariophoenix	3/3	1								Dransfield et al., 2008
Bentinckia	2/2	2								Dransfield et al., 2008

Brassiophoenix	2/2	2								Dransfield et al., 2008
Burretiokentia	5/5	5								Dransfield et al., 2008
Butia	17/20	14	3							Gaiero et al., 2011
Calyptrocalx	21/26	12	9							Dowe & Ferrero, 2001
Calyptrogyne	10/17	10								Henderson et al., 1997; Dransfield et al., 2008
Calyptronoma	3/3	3								Dransfield et al., 2008
Carpentaria	1/1	1								Dransfield et al., 2008
Carpoxylon	1/1	1								Dransfield et al., 2008
Chamaedorea	91/104	73	17	1						Fisher, 1974; Hodel, 1992
Chambeyronia	2/2	2								Dransfield et al., 2008
Clinosperma	4/4	4								Dransfield et al., 2008

Clinostigma	11/11	11								Dransfield et al., 2008
Cocos	1/1	1								Dransfield et al., 2008
Cyphokentia	2/2	1	1							Moore & Uhl, 1984; Jaffré & Veillon, 1989
Cyphophoenix	4/4	4								Dransfield et al., 2008
Cyphosperma	5/5	5								Dransfield et al., 2008
Cyrtostachys	5/7	1	4							Dransfield, 1978; Heatubun et al., 2009
Deckenia	1/1	1								Dransfield et al., 2008
Desmoncus	24/24		24							Putz, 1990; Isnard et al., 2005; Tomlinson & Zimmerman, 2003
Dictyocaryum	3/3	3								Henderson, 1990; Dransfield et al., 2008

Dictyosperma	1/1	1								Dransfield et al., 2008
Dransfieldia	1/1		1							Baker et al., 2006
Drymophloeus	5/7	5								Zona, 1999
Dypsis	160/167	63	90	6				1		Dransfield & Beentje, 1995; Fisher and Maidman, 1999; Dransfield, 2003; Britt, 2005; Hodel et al., 2005; Rakoarinivo, 2010
Elaeis	2/2	2								Dransfield et al., 2008
Euterpe	7/7	1	6							Henderson & Galeano, 1996; Dransfield et al., 2008
Gaussia	5/5	5								Dransfield et al., 2008
Geonoma	39/68	14	25							Henderson, 1995; Henderson et al., 1997;

										Dransfield et al., 2008; Henderson, 2011a
Hedyscepe	1/1	1								Dransfield et al., 2008
Heterospathe	22/41	18	4							Fernando, 1990
Howea	2/2	2								Dransfield et al., 2008
Hydriastele	30/49	16	14							Baker & Dransfield, 2007
Hyophorbe	5/5	5								Dransfield et al., 2008
Hyospathe	2/5		2							Skov & Balslev, 1989; Borschsenius et al., 1998
Iguanura	25/33	15	10							Kiew, 1976; Henderson, 2009
Irartea	1/1	1								Dransfield et al., 2008
Iriartella	2/2		2							Dransfield et al., 2008

Jailoloa	1/1	1								Heatubun et al., 2014
Jubaea	1/1	1								Dransfield et al., 2008
Jubaeopsis	1/1		1							Dransfield, 1989
Kentiopsis	4/4	4								Dransfield et al., 2008
Laccospadix	1/1		1							Dowe, 2010
Lemurophoenix	1/1	1								Dransfield et al., 2008
Leopoldinia	2/2	2								Bernal & Galeano, 2001; Henderson, 2011
Lepidorrhachis	1/1	1								Dransfield et al., 2008
Linospadix	7/7	1	6							Dowe & Irvine, 1997; Dowe & Ferrero, 2001
Loxococcus	1/1	1								Dransfield et al., 2008
Lytocaryum	4/4	4								Dransfield et al., 2008

Manicaria	2/2	1		1						Bernal & Galeano, 2001; Fisher & Zona, 2006
Manjekia	1/1	1								Heatubun et al., 2014
Marojejya	2/2	2								Dransfield et al., 2008
Masoala	2/2	2								Dransfield et al., 2008
Nenga	4/5	1	3							Fernando, 1983; Henderson, 2009
Neonicholsonia	1/1	1								Henderson & Galeano, 1996; Dransfield et al., 2008
Neoveitchia	2/2	2								Dransfield et al., 2008
Nephrosperma	1/1	1								Dransfield et al., 2008
Normanbya	1/1	1								Dransfield et al., 2008
Oenocarpus	9/9	8	1							Bernal et al., 1991;

										Henderson et al., 1997; Dransfield et al., 2008
Oncosperma	6/6							6		Fisher et al., 1989; Fisher and Maidman, 1999
Orania	18/18	18								Dransfield et al., 2008
Parajubaea	3/3	3								Dransfield et al., 2008
Pelagodoxa	1/1	1								Dransfield et al., 2008
Phoenicophorium	1/1	1								Dransfield et al., 2008
Pholidostachys	4/8	4								Dransfield et al., 2008
Physokentia	7/7	7								Dransfield et al., 2008
Pinanga	60/139	12	48							Dransfield et al., 1978; Henderson, 2009

Podococcus	2/2		2							Bullock, 1980; Van Valkenburg et al., 2007
Ponapea	4/4	4								Dransfield et al., 2008
Prestoea	10/10	2	8							Henderson & deNevers, 1988; Henderson & Galeano, 1996
Ptychococcus	2/2	3								Dransfield et al., 2008
Ptychosperma	19/29	7	12							Essig, 1977; Essig, 1978; Dowe, 2001
Reihardtia	6/6	1	5							Henderson et al., 1997; Henderson, 2002b
Rhopaloblaste	6/6	5	1							Banka & Baker, 2004
Rhopalostylis	2/2	2								Dransfield et al., 2008
Roscheria	1/1	1								Dransfield et al., 2008

Roystonea	10/10	1								Dransfield et al., 2008
Satakentia	1/1	1								Dransfield et al., 2008
Sclerosperma	3/3		3							Van Valkenburg et al., 2007; van Valkenburg, et al., 2008
Socratea	5/5	4					1			Bernal-Gonzales & Henderson, 1986; Svenning & Balslev, 1998; Pintaud & Millan, 2004
Solfia	1/1	1								Dransfield et al., 2008
Sommieria	1/1	1								Dransfield et al., 2008
Syagrus	36/61	23	12	1						Henderson et al., 1995; Pinheiro et al., 1996; Noblick, 1996; Noblick, 2004; Noblick & Lorenzi, 2010; Noblick et al.,

										2014; Noblick & Meerow, 2015
Synechanthus	2/2	1	1							Dransfield et al., 2008
Tectiphiala	1/1		1							Moore, 1978
Veitchia	11/11	11								Dransfield et al., 2008
Verschaffeltia	1/1	1								Dransfield et al., 2008
Voaniola	1/1	1								Dransfield, 1989; Dransfield et al., 2008
Wallaceodoxa	1/1	1								Heatubun et al., 2014
Welfia	1/1	1								Dransfield et al., 2008
Wendlandiella	1/1		1							Dransfield et al., 2008
Wettinia	21/21	19	2							Henderson et al., 1997; Borchsenius et al.,1998
Wodyetia	1/1	1								Dransfield et al.2008

Arecoideae	**1112/1376**	**657**	**423**	**13**	**1**		**1**	**7**	**0**	

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CHAPTER II

MORPHOLOGY AND ARCHITECTURE OF THE THREATENED FLORIDA PALM *ACOELORRHAPHE WRIGHTII* (GRISEB. & H. WENDL.) H. WENDL. EX BECC.

ABSTRACT:

Palms are important economically and ecologically and have diverse architectures, but the morphology and architecture of rhizomatous multi-stemmed palms are poorly described. The purpose of this study was to describe growth, morphology and architecture of one such species, *Acoelorraphe wrightii,* in a common garden setting. The study was conducted at Fairchild Tropical Botanic Garden and Montgomery Botanical Center, Coral Gables, Florida, USA. Leaf morphology variables were measured on two or three ramets of 16 genets. Ramet growth rates were determined by recording leaf production and number of leaves present per ramet every three months for two years on two ramets of 38 genets. Genet circumference, diameter, and number of ramet tiers, and number of living ramets > 0.5 m, were measured on 41 genets. An exponential model was used to model asexual clonal architectural growth (number of ramets) using data collected on survivorship and reproduction rate of rhizomes and tier numbers as a proxy for time. Ramets have an establishment period from inception to 0.3 m ramet height. Plant growth varies seasonally in establishing and established phases, with greater leaf production in the warmer, wet season and less in the cooler, dry season. Clonal architecture can be modeled as the number of established ramets in a genet, using an exponential model that depends on number of ramet tiers, the rate of ramet production, and their survivorship. The *ex-situ* study provides an understanding of the architectural potential for *A. wrightii*, and highlights the importance of botanical gardens for research, especially on large, slow-growing species.

INTRODUCTION:

Palms are ecologically and economically important, particularly in the tropics. Their diversity in architecture helps them to grow and often dominate in a variety of tropical and subtropical ecosystems (Henderson, 2002). However, palms are rarely used in demographic and developmental studies because of their slow growth and large size. Thus, most demographic studies conducted on palms are restricted to species that are economically important or small (Bullock, 1980; De Steven, 1989; Clancy & Sullivan, 1990; Olmstead & Alvarez-Bullya, 1995; Barot et al., 2000; Escalante, Montaña, & Orellana, 2004; Rodríguez-Buriticá, Orjuela, & Galeano, 2005; Endress, Gorchov, & Berry, 2006; Portela, Bruna, & Santos, 2010). As a result, the diversity of palm morphology and architecture is not well understood.

The architecture of multi-stemmed individuals in particular is not well described, even though multi-stemmed species are present in almost every palm genus (Dransfield et al., 2008, Edelman, Chap. 1). There are two commonly-used architectural models that describe the multi-stemmed palm habit (Henderson, Galeano, & Bernal, 1995; Henderson, 2002; Dransfield et al., 2008): (1) the caespitose habit, which is created from basal node branching where new ramets immediately grow upward, producing closely-spaced vertical stems; and (2) the colonial habit, which is formed from horizontal elongation of the basal node branch before it grows upward, i.e., elongation of the branch produces a rhizome. While these models are useful, they do not encompass the diversity of architecture in clonal palms.

One way to understand plant architecture is to model it mathematically (Fisher & Honda, 1979). Exponential growth models are used in population ecology to model population growth of a single population and can be useful for predicting clonal growth

(Vandermeer, 2010). These types of models have not been used to model palm architecture but could be particularly useful for modeling growth in a clonal palm (Souza et al. 2003).

Acoelorrhaphe wrightii (Griseb. & H. Wendl.) H. Wendl. ex Becc., paurotis palm, is a clonal palm that grows in wetland habits along the coastal Caribbean basin (southern Florida; western Cuba; Caribbean coast from Mexico to northern Costa Rica; and Andros and New Providence Island in the Bahamas) (Henderson et al., 1995). It is economically important in Central America, where its stems are used for timber and its fruits for medicines, similar to the closely-related species, saw palmetto, *Serenoa repens* (Balick & Beck, 1990). *Acoelorrhaphe wrightii* is ecologically important because its round, raised clumps create habitat for terrestrial animals and plants in seasonally flooded marshes (Henderson et al., 1995). The species is at the northern end of its range in southern Florida, where it is native to the Everglades and is widely used horticulturally. In Florida it is listed as a state threatened species (USDA, 2015).

Acoelorrhaphe wrightii has a combination of basal node branching and rhizomatous growth that produces an unusual palm architecture (Edelman, Chap. 1). Despite morphological complexity and economic and ecological importance, no morphological or demographic studies have been conducted on it, and only a handful of horticultural studies have been published (Broschat, 2005; Broschat, 2011) . The goal of the present study, therefore, was to describe the morphology, growth and architecture of clonal *A. wrightii*, to determine the range of variation in these characteristics in a common-garden setting, and to explore the ability of an exponential model to describe *A. wrightii* whole plant architecture.

MATERIAL AND METHODS:

Study site and selection of individuals — The present study took place at two botanical gardens (Fairchild Tropical Botanic Garden (FTBG) and Montgomery Botanical Center (MBC)) located within a mile of each other in Coral Gables, FL, USA. These botanic gardens share common geologic substrates (limestone bedrock with a few inches of topsoil) and experience similar weather conditions (5 month wet period from late spring to fall and 7 month dry period from late fall to spring).

Individuals used in this study were grown in cultivation from wild-collected seeds from populations in Belize, Florida (USA) and Mexico. Year of entry for these living collections was used to determine approximate age of individuals. Plants grown from seeds collected from the same parent were called “sisters” and had the same garden accession number. When planted in the garden, they were given distinct qualifiers to distinguish among individuals. Seven sister groups and a total of 47 individuals that varied in age from 14 to 66 years were used in this study. Two sister groups, groups 1 and 2 (n= 23 and n= 13 individuals), were wild-collected in Belize in 1999 and planted in full sun in both gardens and in partial shade at MBC. Three sister groups, groups 3, 4 and 5 (n=5, n=5, and n=4) were wild-collected in Florida in 2001 and planted in full sun at MBC. Sister group 6 (n=4) was wild-collected in Mexico in 1984, and planted in a shaded hammock at FTBG. Sister group 7 (n=4) was wild-collected in Florida in 1950, and planted in a shaded hammock at MBC.

Ramet leaf production and morphology— Leaf production was followed over a two-year period (Nov. 2012 to Nov. 2014) on two ramets per genet for 38 genets (76 ramets total) from Belize (24 plants) and Florida (14 plants); they belonged to sister groups 1–

5). Southern Florida has a wet warm season from June to November and a dry cool season from December to May (DeAngelis & White, 1994), so leaf production sampling spanned two of each season.

The most recently matured leaf on each ramet was tagged. Every three months for two years, the following measurements were recorded: number of new leaves matured (number of fully expanded leaves above tagged leaf); the number of live (green) leaves below the most recently matured leaf; and height of the ramet (from soil to apical bud of ramet). At each sampling, the current most recently matured leaf was tagged so that measurements could be repeated three months later. Internode length was calculated as the change in ramet height (cm) between measuring events divided by the number of new leaves matured. Leaf production was analyzed using a mixed within/between-subject ANOVA. The mixed design ANOVA tested the difference between life history phases (establishing and established), while subjecting individuals (ramets) to repeated measures analysis by season (winter = average of leaves produced from December-February and March-May, summer = average of leaves produced from June- August and September-November) (Teetor, 2011).

To characterize leaf and ramet morphology, leaves from 16 individuals (genets) from Belize (10 individuals) and Florida (6 individuals) belonging to sister groups 1, 2 and 4 were measured; two or three ramets of different height were selected for sampling from each genet. Three leaves/ramet--the first, fifth and tenth most recently matured leaves--were sampled (N = 94 leaves measured). The most recently matured leaf was defined as the newest leaf that had fully emerged from the apical bud of the stem and whose lamina had fully expanded. Morphological measurements included ramet height and circumference, lamina length and width, and petiole length and width. Ramet height

was measured from the base of the ramet to the apical bud. Location of the apical bud was estimated based on location of the emerging leaf. On larger plants, circumference of the ramet was measured 0.3 m below the stem apical bud, where the stem circumference stablizes. If the stem was less than 0.5 m, ramet circumference was taken at half the height of the stem. Lamina length was measured from the point of petiole attachment to the tip of the lamina, while lamina width was measured at the widest part of the lamina. Petiole length was measured from the top of the leaf sheath to lamina attachment on the abaxial side of the petiole. The abaxial side of the leaf was used because petiole and lamina are clearly demarcated on the abaxial side. Petiole width was measured on the adaxial side, where the petiole is flat. Because the data were not normally distributed, Spearman correlations were used to detect relations between height of ramet, circumference of ramet, lamina length, lamina width, petiole length, and petiole width. Analysis of the data suggested that there were two distinct growth phases, which were designated as the establishing and establishment phases. These phases were defined through break point analyses using linear models and piecewise regression; ramet height was plotted against leaf morphology variables (lamina length, lamina width and lamina length) to determine break points (Loew, 2012). Piece-wise linear regression models were used to examine variability in lamina length (using only the most recently matured leaf to avoid pseudoreplication) and ramet circumference, with ramet height as the explantory variable, across the two establishment phases.

Clonal architecture—Architectural drawings and measurements to describe clonal architecture were made for 41 genets from Belize (26 plants), Florida (11 plants) and Mexico (four plants) that were from sister groups 1–7). Architectural drawings recorded locations of ramets (dead and alive) within a genet, locations of rhizomes (dead and alive) within a genet, and locations of basal suckers (dead and alive) within a genet, with

a focus on rhizome and ramet connectivity. Clone circumference was measured with a tape ruler as the total distance around the base of the clump, including all ramets above 0.1 m. Two perpendicular diameters (diameter 1 = length and diameter 2 = width) were taken for the clumps, which were elliptical. Length and width were defined as follows: The first rhizome produced was identified as the rhizome from the most central ramet in the clump. Diameter 1 was measured perpendicular to the first rhizome and diameter 2 was measured parallel to the first rhizome. Total number of ramets over 0.5 meters tall, total number of live ramets over 0.5 meters tall, and number of tiers in a genet were counted. Tiers were defined as visually distinct levels in the canopy of a clonal palm (or plant) caused by cohorts of ramets of differential heights; not all multi-stemmed palms form tiers. Tiers were counted for each genet by visual estimates of canopy density and overlap; distinct tiers have little intersection of ramet canopies. Light was measured at breadst height on the outside of the genets with a BQM Apogee quantum meter (Apogee Instruments, Inc., Logan, UT). Four light measurements per genet were taken at high noon and averaged. Genets with average measurements < 500 μmol $m^{-2}s^{-2}$ were in shade, while those with > 500 μmol $m^{-2}s^{-2}$ were in sun.

Circumference, number of ramets, and number of tiers were measured for each genet, and variation was examined separately for each age group. Clone age groups were determined based on the year of the sampling (2014) as compared to accession date; genets had ages 13–15 yr (planted 1999-2001, full sun, n= 37) and age 30 yr (planted 1984, n=4, in shade). The following architectural relationships were examined for each genet growing in full sun aged 13–15 years: circumference (explanatory variable) versus number of ramets; circumference (explanatory variable) versus number of tiers; and number of tiers (explanatory variable) versus number of ramets.

Statistical analyses were done in the R statistical environment (R 2015; Therneau, 2015). Average circumference, average number of ramets, and average number of tiers were found for clone age groups (ages 13–15, N= 37; age 30, N=4). ThenANOVA tests analyzed differences in architectural relationships between light regimes (sun or shade). Since there were great differences in growth rates and architectural relationships for different light regimes, results presented on growth relationship calculations were from genets growing in full sun (sister groups 1–5, N=37). The *t*-tests analyzed differences in growth rates and architectural relationships between populations. Exponential regressions were reported instead of linear regression because of higher R^2 values for the exponential models.

Modeling clonal growth— Given the clonal growth and tiered architecture of *A. wrightii* individuals, an exponential architectural model was developed in order to better understand the effect of growth rate on number of ramets in a genet and to determine growth rate of *A. wrightii* under garden conditions. A basic model of exponential growth was used to predict number of ramets in a genet by manipulating growth rate,

$N_t = N(0)*R^t$,

where N_t = total number of established ramets in a genet with t tiers, N(0) = the number of ramets at initiation, R = growth rate and t = number of tiers (generation). N(0) was set to one (N(0)=1), and t, number of tiers, varied from 1 to 6. The growth rate (R), was assumed to be a function of (1) the number of offspring ramets each ramet produced (r), and (2) the survivorship of the offspring ramets (s) (Tillman1988). Thus, R= r*s. Based on observations of ramet production in the garden clones, it was assumed that only recently established ramets produced offspring ramets and that the reproduction rate was constant for all tiers.

The goal of the modeling was to determine how rates of vegetative reproduction and ramet survival affected ramet number per tier and what combination of rates most closely described genet growth in the gardens. In the model, R (finite growth rate) was manipulated using low or high vegetative reproduction (r, number of ramets produced, either 3 or 6) and low, medium or high levels of survivorship (s, ramet survival, either 0.3, 0.5, 0.8) (Table 2): Values for vegetative reproduction and survivorship were selected based on the range of observed values in the gardens.

To determine the best-fit model, models were plotted using t as the independent variable and N_t as the dependent variable. The best-fit model (R under garden conditions) was selected based on ramet accuracy for the fourth tier (t=4) by comparing measured number of established ramets (from the data) to predicted number of established ramets at the fourth tier.

RESULTS**:**

Ramet characteristics—Ramet growth varied between younger and older ramets, as reflected in leaf morphology and ramet circumference (Fig. 1; piecewise regression to determine break point of ramet height; breakpoint = 0.3 m ramet height for lamina length, lamina width and number of pinnae; p= 0.01). Leaves on establishing ramets (≤ 0.3 m) were smaller and increased linearly with ramet height up to a height of 0.3 m (Fig. 1A). Leaves on ramets > 0.3 m also increased in size linearly with ramet height but at a much lower rate than leaves on smaller ramets (Fig. 1A; t-test comparing slope of increase in leaf size on establishing and established ramets, t = 12.52, df = 45, $p < 0.05$). Ramet circumference also increased linearly until ramets were 0.3 m in height, then circumference increased much more slowly (Fig. 1B; t-test comparing slope of circumference increase on establishing and established ramets, t = 32.75, df = 45, $p <$ 0.05). These variations in morphology were used to define an establishment phase

(ramet height ≤ 0.3 m) and an established phase (ramet height > 0.3 m) for ramet growth.

Leaf production was influenced by both ramet height (establishment phase) and seasonality (Fig. 2). Ramets produced more leaves in the wet season (1.3 leaves/mo., internode length = 1 ± 1 cm) and fewer leaves in the dry season (0.3 leaves/mo.; internode length = 3 ± 3 cm) (Fig. 2; internode data not shown). Establishing and established ramets showed similar patterns of variation in leaf production across seasons, but established ramets had greater rates of leaf production than establishing ramets (Fig. 2, t-test comparing number of leaves produced between establishing and established ramets, t = 12.28, *df* = 154, $p < 0.01$). Established ramets produced an average of two more leaves than establishing ramets in the wet season and an average of one more leaf in the dry season (Fig. 2, mixed within-between ANOVA comparing leaf production of different establishment phases between dry and wet, $F_{1, 1, 150} = 15$, $p << 0.01$). Establishing ramets produced shorter internodes than established ramets in both the wet season (1.0 ± 1.1 cm, 3.5 ± 1.2, respectively), and dry season (1.4 ± 1.1 cm, 2.5 ± 2.3, respectively). There were no differences in leaf production between gardens, location in garden or country of origin (ANOVA, $p = 0.42$, N = 92). Established ramets produced more leaves than establishing ramets (repeated measures ANOVA comparing leaf production of establishing and established ramets, $F_{1, 1, 150} = 15$, $p < 0.01$), but the difference between leaf production in establishing and established ramets was more dramatic in the summer, as indicated by a significant interaction term (mixed within-between ANOVA, $p < 0.01$).

The palmately compound laminae of establishing and established ramets of *A. wrightii* were wider than long (54.5± 6.5 cm (L) x 82.1 ± 12.8cm (W); L/W ratio = 0.7 ±

0.1) and had 37 ± 6 pinnae. Petiole length was similar to lamina length (59.5 ± 14.8 cm), while petiole width was 1.3 ± 0.2 cm. Lamina length to lamina width had a 2:3 relationship regardless of establishment phase (*t*-test comparing relationship between lamina length and lamina width for both establishment phases; $p = 0.90$), but the relationship was more variable during the establishing phase (*t*-test comparing relationship between lamina length and lamina width for leaves on establishing ramets only; $p = 0.75$). All leaf variables except petiole length and width were highly correlated ($p > 0.72$) (Table 1). Petiole length was correlated with position in the canopy. The most recently matured leaf and the fifth most recently matured leaf had shorter petioles (0.5 ± 0.1 m) than the tenth most recently matured leaf (0.7 ± 0.1 m). Correlations among leaf variables were not stronger when only the most recently matured leaves were used for analysis ($p > 0.63$,) nor when leaves on only established ramets were used ($p > 0.69$). Lamina length increased more rapidly with ramet height in establishing ramets than established ramets (Fig. 1A). Number of pinnae on the compound leaves had a slightly greater increase with lamina width in establishing ramets (no. pinnae = 0.67 * lamina width + 13.65) than established ramets (no. pinnae = 0.08 * lamina width + 31.37) (ANCOVA comparing relationship between number of pinnae and lamina width between establishment phases, $F_{3, 90} = 23.4$, $p < 0.01$). However, lamina length increased with lamina width similarly in both establishing and established ramets (lamina width = 1.54 * lamina length; $F_{1, 92} = 675.5$, $p < 0.01$).

Clonal architecture—The 41 genets measured ranged in age from 14–66 years old and varied in size, but clones initiated growth similarly. All *A. wrightii* genets began growth as single stems that branched rhizomatously to form clumps. The initial stem or protoclone was not observed alive in any of the garden specimens. Death of the first stem formed a small opening in the center of the genet (Fig. 3A). The size of the empty

center increased as older ramets died and newer ramets were produced at the periphery of the clump. All vegetative reproduction occurred through sympodial rhizomatous growth. Rhizomes arose as basal suckers from axillary buds at the base of the parent ramet/rhizome (Fig. 3B). Some basal suckers elongated horizontally to form rhizomes (Fig. 3C), whereas others remained close to the parent ramet and grew vertically. An average of 3 ± 3 rhizomes were produced and survived from each ramet in our sample. Episodic rhizomatous growth occurred only at the periphery of the clump, creating a tiered canopy (Fig. 3D); interior ramets did not initiate new basal suckers or rhizomes. The innermost tier was composed of the tallest, oldest ramets, and the outermost tier was composed of the shortest, recently produced ramets. The clump expanded in circumference through growth of new rhizomatous ramets.

Genet circumference in clones in the gardens varied from 1 to 6 m, having from 1 to 14 live established ramets and 1 to 4 tiers of establishing and established ramets per genet. Genets were not circular but were elliptical (d1/d2 = 0.5). Genets increased in diameter 1 and diameter 2 at the same rate (slope = 1) (Fig. 4). Older genets were not necessarily bigger but age and light regime were confounded in the garden specimens, so results could not be compared. The number of ramets per genet increased exponentially with tier number (Fig. 5, no. ramets = $1.1e^{0.5x}$, where x = no. tiers, $F_{1\ 35} = 40.5$, $p < 0.01$) and with genet circumference (Fig. 5, no. ramets = $1.1e^{0.5x}$, where x = genet circumference, $F_{1\ 35} = 61.8$, $p < 0.01$). The number of tiers also increased exponentially with genet circumference (Fig. 5, no. tiers =$1.1e^{0.2x}$, where x = genet circumference, $F_{1\ 35} = 53.5$, $p < 0.01$).

Modeling clonal growth— The six models to estimate clonal growth had very different rates of increase and numbers of ramets by tier 4 (Table 2, Fig. 6; model 6 not

plotted). Models 1 and 2, with low rates of vegetative branching and low to medium survivorship, increased in ramet number gradually and at lower rates than the observed data (Fig. 5C, Fig. 6). Low vegetative reproduction but high survivorship, or high vegetative reproduction and medium or high survivorship quickly produced many ramets and had many more ramets than observed (Table 2, Fig. 6). Model 4, which had high vegetative reproduction and low survivorship, provided the best fit with the observed data with respect to rate of increase and number of ramets at tier 4 (Table 2, Fig. 6). At the gardens there was only one clone in the sun that had 5 tiers, but this clone had fewer ramets than would be predicted by the exponential model (Fig. 5C), which predicts 19 ramets for a clone with five tiers.

DISCUSSION:

Acoelorraphe wrightii expands clonally, producing an elliptical clone with tiers of ramets. The oval shape probably results from asymmetry in the initial growth of the protoclone, as the rate of expansion in length and width is equal in older genets. *Acoelorraphe wrightii* ramets have distinct establishing and establishment phases of growth. For *A. wrightii*, 0.3 m height corresponds with stabilization in leaf scaling, leaf production and ramet circumference; 0.3 m height defines the end of an establishment phase that begins with seed germination or branch outgrowth and that is characterized by higher relative growth rates of leaf and ramet characters and lower rates of leaf production. The presence of an establishment phase is well documented in both solitary and clonal palms (Lothian, 1959; Sarukhán, 1978; Savage & Ashton, 1983; Ash, 1988; Gupta, 1993; Joyal, 1995; McPherson & Williams, 1996; Olmstead & Alvarez-Bullya, 1995; Svenning & Balslev, 1997; Zakaria, 1997; Bernal, 1998). In these studies, establishment phase is a seedling characteristic, not a ramet characteristic. However, in

clonal palms, the transition from establishing to established ramet occurs many times, as new ramets are produced and grow out. This study is also different from previous studies on the establishment phase because prior descriptions of an establishment phase are published as duration of establishment phase (years). In this study, ramet height proved to be a reliable marker for transition between phases. Therefore, in order to quantify the establishment phase for a clonal palm, researchers could consider defining establishment phases based on morphological markers such as ramet height, rather than or in addition to, time.

The leaf phenology data reported here provide a method to age individuals of *A. wrightii* in the field. In temperate plants, a well-defined dormancy period makes it possible to age individuals because periods of dormancy produce physical markers such as bud scale scars, distinguishing between seasons and years. However, similar to most palms and many tropical plants, individuals of *A. wrightii* did not display vegetative dormancy (Tomlinson, 2006). Using our data on rates of leaf production and internode length, we can roughly estimate age of ramets by culm height. An estimated twelve leaves are produced per year with an average internode length of 2 cm. Therefore, a ramet grows an estimated 24 cm a year (12 internodes/year x 2 cm= 24 cm/year). The approximation of 24 cm of growth /year can be used in the field to age a culm by dividing ramet height (measured in cm) by 24 cm to get an estimated age. The 24 cm/ year estimation would yield a crude estimation of age, since variables used in estimation (leaf production and internode length) were variable by season and height of the ramet. The 24 cm/year estimation also does not include the time it takes for a rhizome to begin vertical growth. However, maximum rhizome age could be estimated by the difference between parent and daughter culm age.

The method described above provides a method for estimating integrated annual growth, but there were differences in growth between seasons. The phenology data showed that there is a period of slow growth during the cool, dry months and a period of active growth during the warm, wet months in southern Florida. The active growth is associated with both vegetative and reproductive growth. Flowers are produced in May and June, fruits develop in July, August and September and fruits mature in October and November in south Florida (Edelman, personal observation). Individuals of *A. wrightii* experience the highest rate of leaf production while fruits are maturing, and rhizome initiates are formed as flowers are developing. Although no data were collected on flowering and fruiting, only a few ramets in a genet produced flowers and fruit, even though many were tall enough to do so. Most ramets reproduced vegetatively, suggesting a resource trade-off between vegetative reproduction over sexual reproduction. A simple mapping of inflorescence production on ramets in a clone would show whether sexual reproduction is confined to the interior of the clone where vegetative branching has ceased. If there is no overlap between sexual and vegetative reproduction, then vegetative branching is a characteristic of younger ramets, and once ramets are sexually mature, they no longer branch vegetatively. However, if there is overlap of the two types of reproduction, determining whether ramets with inflorescences produce fewer basal branches than ramets without would provide insight into potential reproductive trade-offs.

The results from the architectural model proposed in this study serve as benchmark averages for future architectural comparisons. Deviations from model predictions may give insight into how environmental and field conditions affect clonal growth. In particular, survivorship in the field can be analyzed using this architectural model. In the model that most closely approximated the garden data, not all rhizomes survived

(survival rate = 0.3), indicating that even under garden growing conditions, fewer than half of the ramets survived. These survival rates may be more variable in nature, where *Acoelorrhaphe wrightii* genets are exposed to fire, flooding and, potentially, other environmental stresses. The estimations of the best-fit model highlighted the slow-growing nature of *A. wrightii*. Number of rhizomes and basal suckers produced is expected to be lower in the field. Therefore, clones in the wild may be more similar to the low reproduction, low survivorship model (Model 1, Fig. 6). The proposed model can also be used in the field to compare survivorship of different sized genets and to determine if there is a maximum number of ramets and tiers that can exist in a genet (carrying capacity). The deviation from the model prediction for number of ramets in the single garden clone with five tiers suggests that such limitation can occur.Tiers were used in the exponential architectural growth model as equivalent to a generation and thus as a proxy for time. However, the relationship between tier formation and time is unknown. Tiers were a better predictor of generation than year. While architectural measurements (ramet number, clone size) were not directly related to age, they were related to tier number. Tier number, not age, was a better predictor of the overall size and robustness of the genet.

The architectural model for *A. wrightii*, which used horizontal tier formation as a proxy for time, may be unique to plants such as *A. wrightii* that show episodic growth. Growth of tiers, however, has been used in other architectural models to describe the pattern of aerial branching along a vertical axis (Hallé et al., 1978, Borchert & Tomlinson, 1984; Shukla & Ramakrishnan, 1986; Tomlinson, 1987; Fisher, 1992; Hill, 1997; Sabatier & Barthelemy, 1999; Barthelemy & Caraglio, 2007). The tiers found in these models and architectural analyses are formed by the pattern of aerial branches along a main axis. In Nozeran's architecture model, the shoot tip of the seedling axis produces a

tier of horizontally oriented branches and the main shoot apex becomes determinate. A new erect axis arises below the tier, grows vertically, and repeats the process (Hallé et al., 1978). In Aubréville's model tiers are produced by a monopodial, single trunk axis with rhythmic growth and each cycle of growth produces a new tier of horizontally oriented branches (Hallé et al., 1978). The features that these models share with tier growth in *A. wrightii* are episodic branching and separation of ramets (branches) from previously formed ramets (branches).

The current study highlights the usefulness of botanic gardens in studying large, slow-growing species. Having numerous individuals in close proximity facilitated making measurements, while having access to plants in a protected location for periods long enough to quantify the slow growth made this work possible. In addition, the clonal architecture of *A. wrightii* is difficult to study in the wild because the ecological history of the individuals is not known, but life history greatly influences growth and architecture. In the gardens, careful historical records are kept so the history of the individual is easily determined and can help in understanding growth. Finally, the similar "common garden" environment reduces variation among genets. The knowledge gained from this type of study can then inform field studies.

TABLES:

Table 1: Spearman correlation coefficients for most recently matured leaves (top) and all leaves (below, in parentheses) of *A. wrightii* ramets.

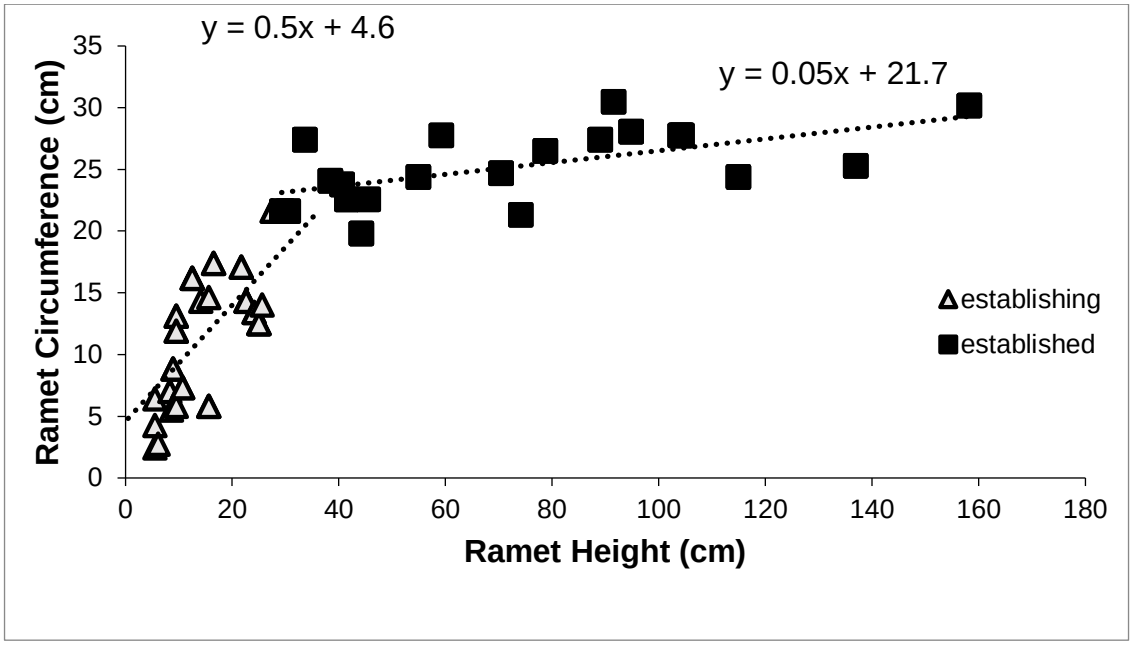
	Circumference	**Lamina length**	**Lamina width**	**Petiole length**	**Petiole width**	**No. of pinna**
Height	0.927 (0.895)	0.870 (0.793)	0.798 (0.719)	0.441 (0.311)	0.818 (0.707)	0.832 (0.766)
Circumference		0.879 (0.794)	0.811 (0.704)	0.386 (0.288)	0.837 (0.702)	0.797 (0.782)
Lamina length			0.877 (0.895)	0.482 (0.400)	0.887 (0.763)	0.804 (0.755)
Lamina width				0.449 (0.357)	0.833 (0.752)	0.724 (0.663)
Petiole length					0.420 (0.275)	0.394 (0.342)
Petiole width						0.691 (0.629)

Table 2: Parameters for models of clonal growth in *A. wrightii*. The model is $N_t = N(0) * R^t$, where N_t is the number of ramets present in a clone with a given tier number, and R, the growth rate, is determined by r (number of branches produced by a ramet) * s (ramet survivorship). Veg. reprod. = vegetative reproduction; surv. = survivorship.

Model No.	Model Description	r	s	R	N_4
1	low veg. reprod., low surv.	3	0.3	0.9	1
2	low veg. reprod., med. surv.	3	0.5	1.5	5
3	low veg. reprod., high surv.	3	0.8	2.4	33
4	high veg. reprod., low surv.	6	0.3	1.8	10
5	high veg. reprod., med. surv.	6	0.5	3.0	81
6	high veg. reprod., high, surv.	6	0.8	4.8	531
	Measured genets				10

FIGURES:

Figure 1: *Acoelorrhaphe wrightii* ramet height vs. ramet circumference (A) and lamina length (B). Left regression equations are for establishing phase (ramet height ≤ 0.3 m), while right regression equations are for established phase (ramet height > 0.3 m).



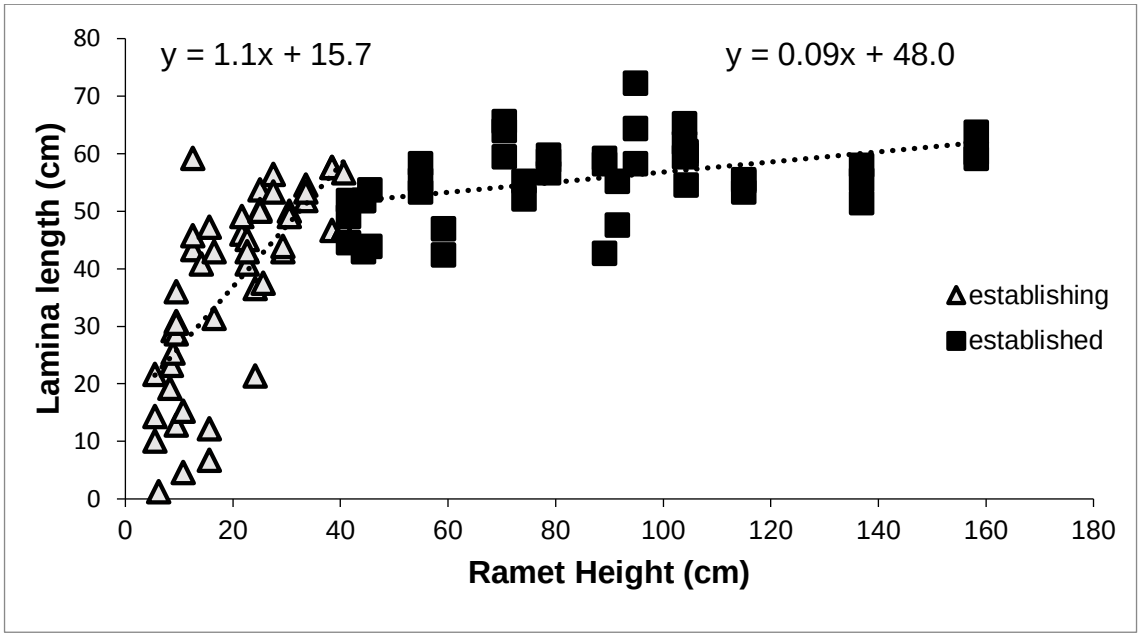


Figure 2: *Acoelorrhaphe wrightii* leaf production values on ramets of different heights in Fairchild Tropical Botanic Garden and Montgomery Botanical Center plants in Miami FL; measured from Nov. 2012 through Dec. 2014. Data divided into leaves from establishing ramets (ramet height ≤ 0.3 m) and established ramets (ramet height > 0.3 m). Error bars = standard error.

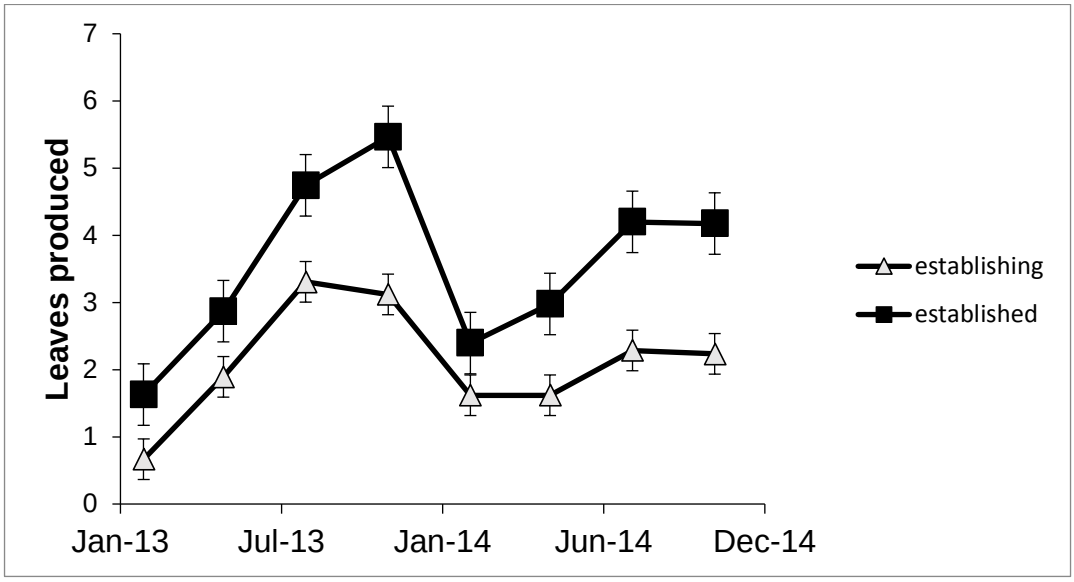


Figure 3: *Acoelorrhaphe wrightii*. (A) Absence of the protoclone results in empty-centered ring. (B) Basal node branching occurs when a basal axillary bud grows out to form a new ramet without any horizontal elongation. (C) Rhizomatous branching occurs when a basal axillary bud grows out to form a new ramet with horizontal elongation before turning upward. (D) Tiers are present in all observed *A. wrightii* individuals and decrease in height from inner to outer tiers.

Figure 4: Two perpendicular diameters (diameter 1 and 2) for 31 genets of *A. wrightii* of different sizes in Fairchild Tropical Botanic Garden and Montgomery Botanical Center plants in Miami FL; measured once in Nov. 2013.

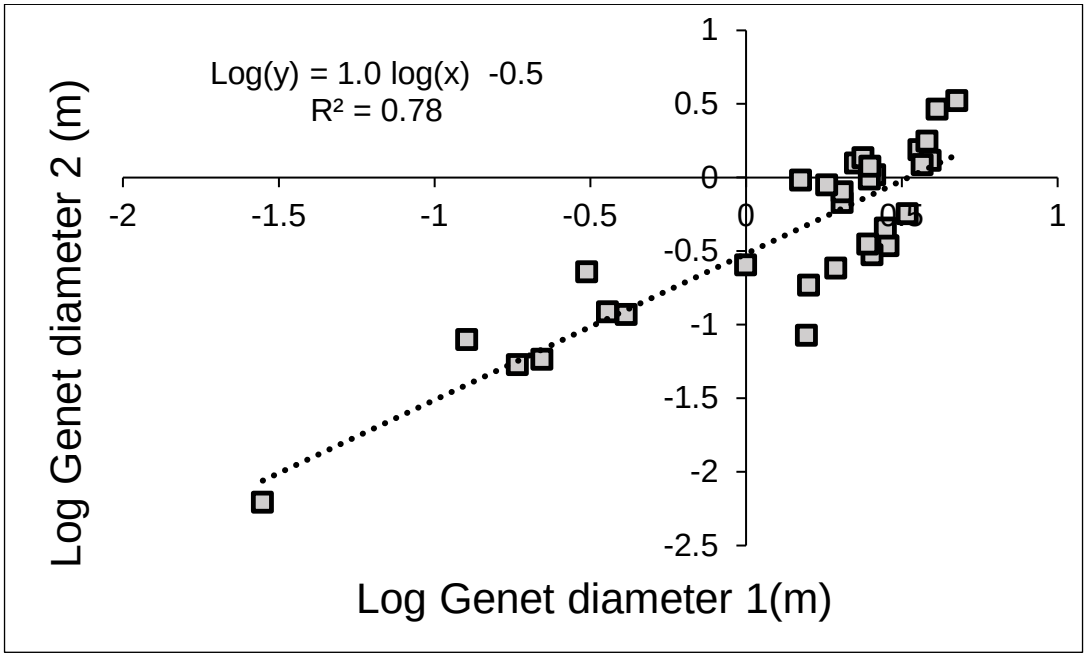


Figure 5: (A) Number of stems vs. genet circumference, (B) number of tiers vs. circumference (C) number of tiers vs. number of stems in 31 genets of *A. wrightii* in Fairchild Tropical Botanic Garden and Montgomery Botanical Center plants in Miami FL, in full sun, measured once in Nov. 2013.

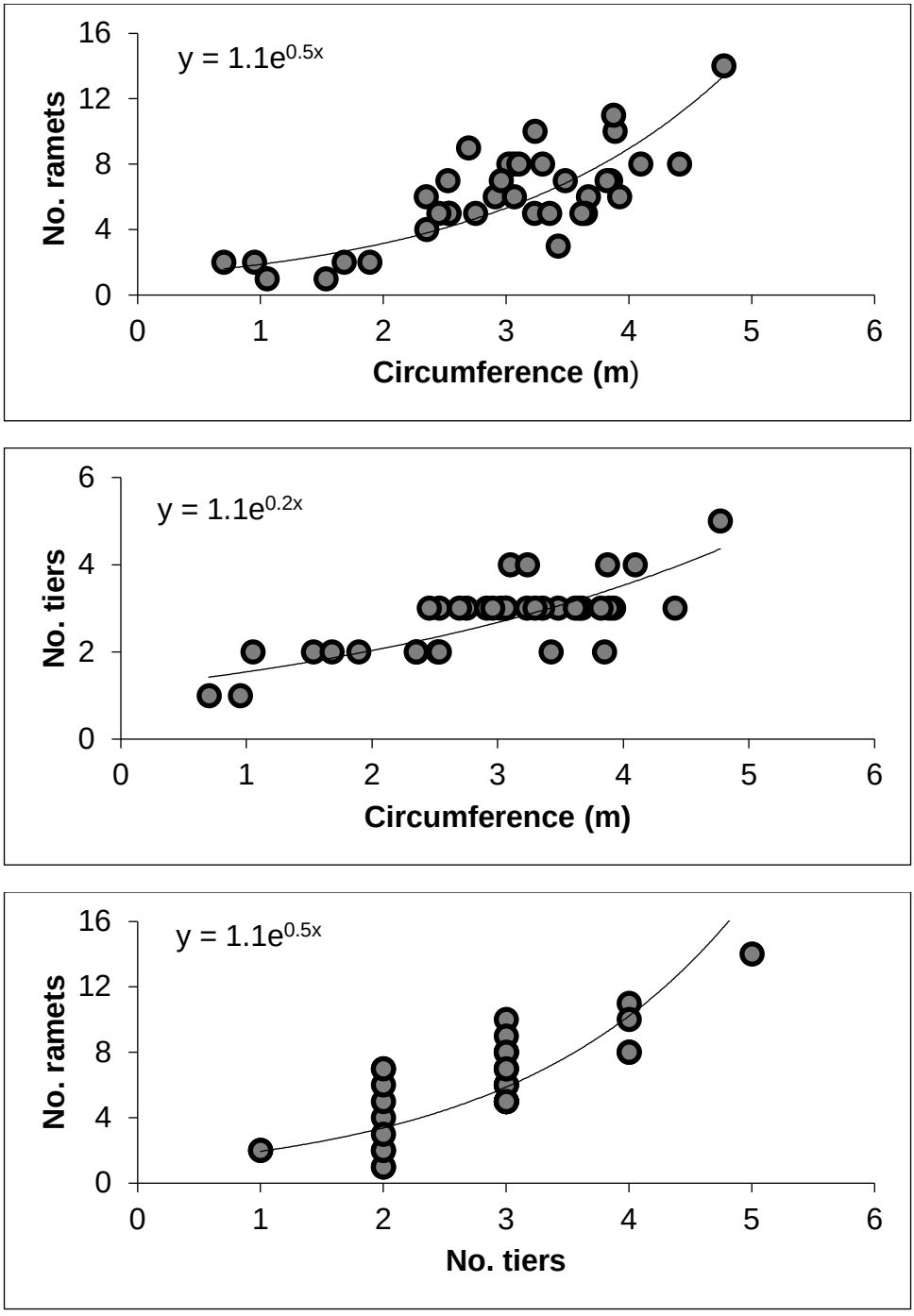
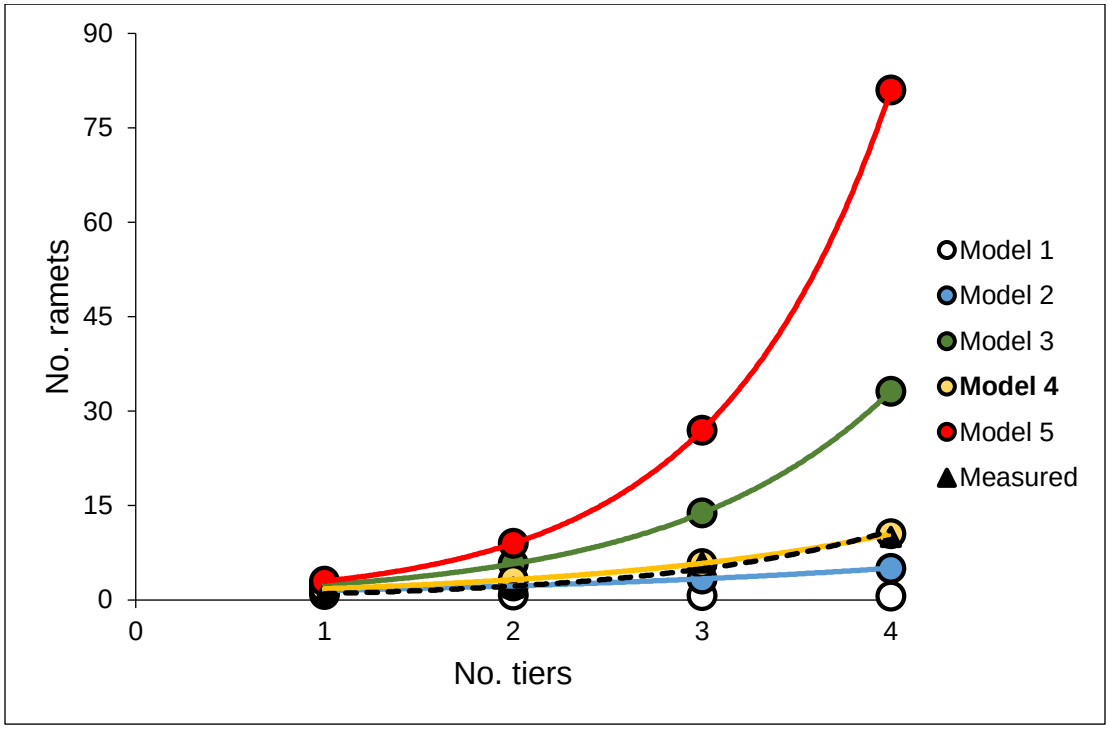


Fig. 6: Exponential clonal growth model estimations for different growth rates (R) given different levels of reproduction (r) and survival rates (s) for clonal palm, *Acoelorrhaphe wrightii*. Model 1: r = 3, s = 0.3, R = 0.9. Model 2: r = 3, s = 0.5, R = 1.5. Model 3: r = 3, s = 0.8, R = 2.4. Model 4: r = 6, s = 0.3, R = 1.8. Model 5: r = 6, s = 1.5, R = 3.0. Model 6: r = 6, s = 4.8, R = 4.8. Dashed line represents values from genets measured in the gardens. Selected model (Model 4) fits data to 1 ramet.



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CHAPTER III

GERMINATION AND JUVENILE GROWTH OF THE CLONAL PALM, *ACOELORRHAPHE WRIGHTII,* UNDER DIFFERENT WATER AND LIGHT TREATMENTS: A MESOCOSM STUDY

ABSTRACT:

Clonal growth, an important aspect of plant reproduction and survivorship, can vary under different environmental conditions, and differences in clonal growth in the juvenile stage influence adult architecture. The clonal palm *Acoelorrhaphe wrightii,* which is listed as threatened in southern Florida, can occur as solitary or clonal individuals. In order to predict its adult architecture, I determined the effects of water and light on (1) germination and (2) morphology and branching of *A. wrightii* during juvenile life stages. Germination of wild-collected seeds exposed to four conditions: emergent, saturated, low and medium water levels was monitored every month for a year. Seeds began to germinate after seven months, and soils with saturated water levels had highest seed germination. To assess the impact of water and light on stem growth, leaf production and vegetative axillary branching of juvenile plants, 64 juveniles were grown in one of four environmental treatments (low water + sun, low water + shade, medium water + sun, and medium water + shade) and measured every two months for a year. After a year, individuals were harvested to assess the impact of treatments on plant biomass, biomass allocation, and branching. Full sun and saturated soils yielded juveniles with a greater number of leaves, more root mass and more branches. The results of this study suggest that while *A. wrightii* is commonly found in flooded areas, it requires a dry-down in order to recruit successfully, and it produces more vegetative branches in high light, low water level environments. Results were used to model the effect of water level on adult vegetative architecture.

INTRODUCTION:

Axillary buds have three fates: (1) they can remain dormant; (2) they can become inflorescences; or (3) they can become vegetative branches (Bosner & Aarsen, 1996). If vegetative branching occurs at or below the soil and branches can form roots, the branches have the potential to produce clones. Through clonal growth, an individual can by-pass environmental stresses that decrease sexual reproduction and cause low recruitment, ensuring continued success and survival of the individual (Pan & Price, 2001; Honnay & Bossuyt, 2005).

Clonal growth is especially common in wetlands, as many wetland species require low water levels for seed germination, so high water levels decrease chances of recruitment from seeds (Rea & Ganf, 1994; Keddy & Ellis, 1985; Keddy & Constabel, 1986; Cronk & Fennessy, 2001). In these wetland species, clonal growth provides a way for species to persist and spread in the absence of conditions that favor germination (Santamaría, 2002). However, variations in water level can also affect clonal reproduction, and increased water levels have been observed to decrease clonal proliferation (Evans, 1991; Edwards et al., 2003; Miller & Zedler, 2003).

Light availability also impacts vegetative reproduction, and increased light availability is commonly linked to increased rates of vegetative growth and clonal expansion (Méthy et al., 1990; Dong, 1995; Stuefer & Huber, 1998; Maurer, 2002). Since younger plants often have higher branching rates, fluctuating water levels may be particularly influential on vegetative reproduction during early life history stages (De Steven, 1989; Winkler & Schmid, 1995; Miguel, Druart & Oliveira, 1996).

Environmental conditions, therefore, can stimulate axillary bud outgrowth and create a clonal individual or suppress axillary bud outgrowth and produce a solitary individual. In fact, many clonal plants have both solitary and multiple-stemmed habits, and frequently, the difference between a solitary and multiple-stemmed individual is controlled by environment rather than genetics (Hallé, Oldeman & Tomlison, 1978; Dransfield et al., 2008; Smith & Potts, 1987). Clonal plants begin as a solitary stem and through outgrowth of axillary buds, form clonal individuals. A solitary morph of a clonal individual, then, is formed by the suppression of vegetative branching (De Steven, 1989; Souza, Martins, & Bernacci, 2003; Kozlowski, 1971; Zimmerman & Brown, 1971; Penalosa, 1994; Doust, 2007). In many orthotropic, arboreal, clonal plants, such as some palms, there are two branching phases: (1) an active vegetative branching phase when basal vegetative buds on a ramet develop and expand into rhizomes; and (2) a post-vegetative branching phase when aerial buds produce inflorescences and basal vegetative buds on a ramet are no longer developing (Tomlinson & Zimmerman, 2010). The active vegetative branching phase has been shown to be associated with the juvenile phase of growth in the dicotyledonous tree *Eucalyptus occidentalis* (Jaya et al., 2009), and this is probably true in other species. Therefore, a solitary-stemmed morph of a usually clonal species can be hypothesized to be a product of environmental suppression of bud outgrowth in the juvenile phase of the stem.

In order for the environment to influence bud outgrowth and thus adult architecture, a seedling must first germinate. Conditions needed for germination could favor particular growth responses in juvenile plants, and consequently, adult architecture. Therefore, studying germination under different environmental conditions is an important aspect of understanding how environment influences juvenile growth and ultimately adult architecture. Additionally, understanding how conditions promoting

germination interact with conditions favoring different adult architectures provides a way to infer aspects of environmental history from adult populations.

Palms, members of the plant family Arecaceae, are primarily tropical and subtropical, where they occur in a variety of habitats, including wetlands (Dransfield et al., 2008). Most of the 181 palm genera have species that grow in wetland habitats or lowland moist forests (Dransfield et al., 2008), although only a limited subset of species is truly aquatic (Dransfield, 1978). Most palms do not form vegetative branches aerially because buds are suppressed hormonally or are absent; so most vegetative branching, if it occurs, is at or below ground level (Tomlinson, 1990). A number of wetland palm species have clonal branching, producing offshoots at ground level. Clonal palms that grow in wetlands encounter fluctuating water levels, so their ability to germinate, establish and begin branching vegetatively under different water levels and light availabilities is important to their success in wetland habitats (Balslev et al., 1990; Gomes, Válio, & Martins, 2006). Studies have been conducted on the germination, seedling morphology, and juvenile morphology of palms, and some studies focus on the influence of environment, specifically water and light, on germination and morphology (Djibril et al., 2005; Bonadie, 1998; Henderson, 2002; Perry & Williams, 1996; Tomlinson, 1960a; Tomlinson, 1960b). However, few of these studies include clonal palms, excepting those of Gomes et al. (2006) and Balslev et al. (2011). While Gomes et al. (2006) and Balslev et al. (2011) monitored germination and morphology of clonal palm seedlings, neither focused on growth under multiple environmental conditions.

Acoelorrhaphe wrightii, a palm classified as threatened in southern Florida (Ward, Austin & Colie, 2003), grows as a solitary stem, or more commonly, in rhizomatous clumps in seasonally flooded grasslands (Gann et al., 2016; Henderson et

al., 1997). *Acoelorrhaphe wrightii* reproduces sexually: in southern Florida flowers are produced in May, and seeds ripen in November (Henderson et al., 1997). *Acoelorrhaphe wrightii* also reproduces asexually through rhizomatous branching, which occurs on the periphery of a clone and builds up a multi-stemmed genet over time (Edelman, Chapter 2). The species, however, can also occur as solitary individuals (Edelman, 2015). Whether the difference between solitary or multiple-stemmed palms is genetically controlled or environmentally induced is unknown.

The purpose of the current study was to understand the effects of water and light on germination and early growth of the clonal palm *A. wrightii*. The effect of water and light on germination and juvenile morphology and branching of *A. wrightii* was evaluated to understand the effect of these environmental variables on early life history stages, considering as well how environmental effects on bud outgrowth influence adult architecture.

MATERIALS AND METHODS:

This study took place at Florida International University in Miami, Florida from November 2014-April 2016. Seeds and plants of *A. wrightii* were grown outdoors in water-filled mesocosms. Mesocosms used in this experiment were 3410 L (900 gal) round, polypropylene, cattle tanks (1 m deep × 2.1 m wide) and had shelves suspended within them where potted seeds or plants were placed. The shelves could be raised or lowered to establish different water levels within a single tank. Tanks were emptied and refilled with tap water before the start of the experiments. Water levels used for this study were informed by hydrologic data averaged over a year from the Everglades Depth Estimation Network (EDEN) (USGS, 2016), using values from the EDEN dataset

that coincided with collected GIS points from individuals of *A. wrightii* in the marshes of southern Everglades, Everglades National Park, FL, USA.

Seedling germination under varying water levels: Seeds were collected from individuals growing in non-wilderness areas of Everglades National Park (collecting permit no. EVER-2014-SCI-0015). In total, 3000 fruits were collected from ten individuals (300 seeds/individual) and bulked in November 2014. Of the 3000 fruits, 1600 were randomly selected for the germination experiment. Fruit walls were removed down to the endocarp. Fruits were gently placed at soil level. Fruits were planted in Nov., 2014. To assess the impact of water level on seedling germination and survivorship, I established four water levels in a single tank by manipulating shelf heights. The four treatments were (1) emergent (water 5 cm below soil surface), (2) saturated soil (water at soil surface), (3) submerged shallowly (low water level; water 5 cm above soil surface) and (4) submerged deeply (medium water level; water 10 cm above soil surface). These levels were selected using environmental conditions present in the species' habitats over the range where *A. wrightii* plants grow and on results of preliminary studies (Taylor, 1963; Armentato et al. 2002). Each water level had eight 1-gal pots with 50 seeds per pot scattered on the surface of the soil (n=1600). Germination was monitored, and the number of germinated seeds present was counted every other month for a year.

Juvenile morphology and branching response to variation in light and water levels: Twenty-six 5-gallon pots of 3-5 year-old juvenile *A. wrightii* plants were purchased from Action Theory Nursery (Homestead, FL) in Dec. 2014. Pots contained multiple individuals that had been germinated from seed, so individuals were separated and repotted in 5-gallon plastic pots using soil obtained from a commercial composting facility (EPS Organics, Hialeah Gardens, FL). A total of 64 individuals was repotted and

distributed among four mesocosms in Feb. 2015. A single stem from the seedling pots was repotted into each 5-gallon pot. These stems were the protoclones, the original stem of the genet. Treatments were set up to assess the impact of water level and light availability on juvenile stem growth, leaf production and branching using a randomized block experimental design with two factors completely crossed: water level (medium or low) and light availability (shade or sun). The four treatments were low water + sun, low water + shade, medium water + sun, and medium water + shade. Each of the four tanks was a block with all four treatments in each block. Each tank had four individuals per treatment for a total of 16 individuals per tank. Water levels, either medium or low, were selected following the environmental conditions present in the Everglades in habitats where *A. wrightii* plants grow (Taylor, 1963; Armentato et al., 2002). The medium water level treatment had water 10 cm above the soil level and the low water level treatment had water at the soil line. Water levels were manipulated using shelves in the mesocosms. Light availabilities were either shade or sun. Shade was created using 50 x 50 x 70 cm shade boxes made with wood stakes and covered with 80% shade cloth on the sides but open on top; the shade boxes were placed over individual pots. Individuals in sun were not covered by shade boxes and sat in direct sun light.

The following measurements were taken on the main stem in a pot every other month for a year: height (cm), circumference (cm), number of green leaves, and number of branches. Height was measured from the soil to the tip of the stem, where the leaves emerged. Circumference was measured at half the height of the stem. The number of green leaves was counted as the number of fully and partially expanded leaves but did not include the spear (unexpanded) leaves. The number of branches was counted as the number of basal suckers growing from the stem. Stem growth rate (change in height/year), leaf production rate (change in number of green leaves/year) and

branching rate (change in number of branches/year) were found by subtracting the initial measurement from the final measurement for each plant. Morphological measurements (height, circumference, number of green leaves and number of branches), as well as growth rates (stem growth rate, leaf production rate and branching rate) were compared between and among water levels and light availabilities. The following measurements were taken on the branches for the last two sampling periods: height of branch measured perpendicular from the soil level to the meristem of the branch (where all the leaves emerged); and rhizome length (distance between the branch and the juvenile) measured parallel to the soil from the meristem of the branch to the stem of the juvenile.

After a year, plants were harvested from March 14, 2016 to April 1, 2016. Each individual was removed from its pot, washed to remove all soil, and separated into roots, stems, dead leaves and green leaves. During the harvesting process, the shoot was dissected to examine expanding axillary bud outgrowth. Expanding buds were developing branches that had not emerged from the leaf base and, therefore, were not visible prior to dissection. Expanding axillary buds were counted, and numbers of buds per individual were compared among treatments. Total number of branches plus expanding buds were compared among treatments. The relationship between the rhizome length and height of branch, height of the juvenile plant and treatment was analyzed over time. The percent of individuals in each treatment for which no bud outgrowth occurred was compared among treatments.

Branches and expanding buds were mapped for each juvenile plant to analyze distribution of branches/buds and the sequence in which they emerged. To map the branches/buds, the base of each harvested protoclone stem was projected onto a circle. Each stem had a horizontal portion that terminated in an erect portion that supported the

leaves. On the erect portion, the leaf bases formed a cylinder surrounding the shoot apical meristem and younger stem and leaves (Fig. 1A). The horizontal stem was not visible until leaf bases and leaves were removed during dissection. The direction of curvature of the horizontal portion was used as a reference point for mapping (Fig. 1A). The horizontal axis was oriented parallel to 0^{o}–180^{o} and the plant was centered in the middle of the circle. The positions of branches and expanding buds were mapped in reference to the horizontal axis (Fig. 1B). The locations of branches/expanding buds were drawn on the circle map, and the heights of each were measured. Only expanding buds greater than three millimeters in length (observable to the naked eye) were counted. After all branches and expanding buds were mapped, a 360°protractor was used to measure the angles between the base of the horizontal portion (0°) and the branches/expanding buds. The resulting angles were grouped into quadrants: region 1 was 315–44°, region 2 was 45–134°, region 3 was 135–224° and region 4 was 225–314° (Fig. 1B). The distribution of branches and expanding buds among the quadrants was analyzed using contingency tables, predicting equal distribution of branches and expanding buds among quadrants. A 360° protractor was used to measure the smallest angle between the first and second buds to expand.

Harvested roots, stems, dead leaves/leaf bases and green leaves/leaf bases were oven-dried at 80 °C in drying ovens. Once dry, plant parts (living leaves, dead leaves, stems, and roots) were weighed to the nearest milligram. Parts were summed to determine total biomass per individual, while total live biomass included all of the above except dead leaves. Root to shoot ratios were found by dividing root biomass by shoot biomass (sum of stem, living leaves and dead leaves biomass). Leaf mass fractions (LMF), stem mass fractions (SMF) and root mass fractions (RMF) were found for all

individuals and calculated by dividing leaf mass (LM), stem mass (SM) and root mass (RM) by total mass (TM).

Statistical analysis:

The R environment was used to analyze results (R Core Team, 2013). Cox's proportional hazards test was used to analyze the effect of treatment on proportion of seedlings germinated (Springate, 2012; Therneau, 2015). Average germination rates were calculated for each water level (emerged, saturated, low and medium).

Differences in morphological and growth rate variables between water levels and between light availabilities and interaction between water and light were analyzed with two-way ANOVAS. The relationships among morphological variables were analyzed with linear regression models.

A Pearson chi-squared test was used to determine whether branches and/or buds were evenly distributed around the stem (numbers of branches and/or buds by quadrant and sequence of expansion). Since the phyllotaxy was not known for each plant, I expected an even distribution of branches and/or buds among quadrants; the expected numbers for the chi-squared test were obtained by dividing the total number of first, second and third branches and/or buds by number of quadrants (four). Analysis could only be done on first, second and third branches and/or buds to expand because one or more of the expected frequencies for fourth order branching was less than five.

Two-ways ANOVAS were also used to analyze differences between water levels and light availability in biomass variables. Differences between water levels and light availability in relative biomass allocation were analyzed with generalized linear models (GLMs) and GLMs were used to compare the slopes between water levels and light

availability of log transformed biomass data. Slopes were equivalent to leaf, stem and root mass fractions (Poorter & Sack, 2012). All values are reported as mean ± standard deviation.

RESULTS:

Germination: *A. wrightii* seeds began to germinate in June, 2015, seven months after sowing, and germination then increased over time (Fig. 2). A higher proportion of seeds germinated in saturated soil conditions than all other treatments (Table 1; Fig. 2; Cox proportional hazard tests comparing germination proportions over time between water treatments, Likelihood ratio= 64.9, df=3, p<<0.01).

Juvenile morphology and branching: Initial stem height was 5.7 ± 2.6 cm, initial number of leaves was 3 ± 1 and initial number of branches was 0 ± 0. At final sampling, stem height was 10.8 cm ± 5.4 cm, circumference was 6.4 ± 2.8 cm, number of leaves was 6 ± 2 leaves, and number of vegetative branches was 1 ± 1. Height and average number of leaves did not vary among water level-light availability treatments (Table 2A; two-way ANOVAs, p>0.20). Stems of individuals growing in the shade had smaller circumferences (Table 2; two-way ANOVA , df = 46, p < 0.05). Individuals growing in low water levels and full sun branched more, but there was no difference between individuals growing in the different light availabilities (Table 2; two-way ANOVA test comparing number of buds between water levels and light availabilities; df = 46, p < 0.05 for water levels, p > 0.20 for light availability). The deep water + shade treatment had the highest percentage of individuals that did not branch (87.5%); 62.5.5% of individuals growing in low water + shade and deep water + sun did not branch, and 32.5% of individuals growing in low water + sun did not branch. Average number of expanding buds was 1 ± 1. The average number of expanding buds was not different based on

water level or light availability (Table 2; Two-way ANOVA, $p > 0.20$). There were no interactions between water level and light availability.

Most growth occurred between June and October. Over the sampling period, the juveniles increased in height, circumference, number of leaves, and number of emerged vegetative axillary buds (Fig. 3). Stem growth was 2.9 ± 6.1 cm/year, leaf production rate was 2 ± 3 leaves/year, and branching rate was 1 ± 1 branches/year. Stem growth rate was not different between water levels or light availabilities (Table 3; two-way ANOVA, $p>0.20$). An average of 1 more leaf/year was produced in medium water levels than in low water levels, and an average of 1 more leaf/year was produced in full sun than shade (Table 3; two-way ANOVA comparing differences in leaf production rate between water levels, $df = 60$, $p<0.05$ and between light availabilities, $df = 60$, $p<0.05$.). One more branch/year was produced in the sun than in the shade, but there was no difference in branch production rates between water levels (Table 3; two-way ANOVA comparing differences in branching rate between light availabilities, $df = 60$, $p<0.05$ and water levels $p > 0.20$). There were no significant interactions between water level and light availability for any of the measured variables. Rhizome length (distance between the juvenile and the branch or expanded bud) increased linearly with height of the branch or expanded bud and time (linear regression, $F_{2,40} = 7.1$, $p = 0.002$)

Vegetative axillary buds were not evenly distributed around the base of the main stem (Fig. 4). The first buds to expand were more likely to be located at the forward base of the erect stem (quadrant 3) (Pearson chi-squared, $df = 3$, $p = 0.05$, Fig. 4B). There was no evidence in the pattern for second or third buds to expand based on their location on the stem (Pearson chi-squared, $p>0.20$). The average angle between the

first and second bud to expand was 123.9° ± 26.7°; 92% of the second buds to expand were located 90-270° from the direction of the first bud.

Juvenile biomass and biomass allocation: Total living biomass of plants was 75.7 ± 54.9 g. The biomass and biomass allocation of leaves, stem, shoot, and root can be found in Table 4. Individuals growing in shallow water were heavier overall; living leaves, dead leaves, stems, shoots, roots and total plant weight were greater than for individuals growing in deep water but there were no differences in biomass between light availabilities (Table 4; two-way ANOVAs comparing biomass of living leaves, dead leaves, stem, shoot and root between water level $df = 60$, $p < 0.05$, between light availability $p > 0.50$). There were no differences in biomass allocation or root:shoot ratio between water levels or light availabilities (Fig. 5; Table 4; GLMs comparing leaf mass fractions, stem mass fractions, root mass fractions and root:shoot ratio between water levels and light availabilities, $p > 0.20$).

DISCUSSION:

Development of solitary vs. clonal architecture in A. wrightii: The results of this study demonstrate that different water levels could induce different adult architectural habits (solitary or clonal) in *A. wrightii* by inhibiting or promoting growth and vegetative branching at the juvenile stage. Juvenile plants grew more vigorously in low water and full sun, as demonstrated by greater biomass, greater leaf production and greater branch outgrowth and survival. These results suggest that in native habitats, a juvenile growing in full sun and low water has more root biomass, can successfully produce more branches, and is therefore likely to produce a clonal individual.

The timing of the water level variation has an important effect on whole plant architecture because there is a limited time in the life of the individual in which ramets

can successfully produce rhizomes. In palms, the stem must be in the active branching phase (juvenile) in order to produce basal vegetative buds (Tomlinson & Zimmerman, 1978). Additionally, buds in monocots have a limited life span, as they are not maintained by development of a vascular cambium in the stem; thus the environment can affect bud outgrowth only for a limited time. For example, in order for buds in grasses to expand successfully in wetlands, the duration of high water must be shorter than the lifespan of the bud (Hendrickson & Briske, 1997).

These two constraints (length of the juvenile phase and life span of the axillary bud) can be used to develop hypotheses to explain the development of solitary and clonal habits in *A. wrightii*. The two architectures can be achieved through plants experiencing different water levels (medium or low) for different periods of time during the active vegetative branching phase (Fig. 6). Low water levels during active vegetative branching phases would form a clonal architecture irrespective of bud life span. High water levels, if they were shorter than the life span of some vegetative buds, could also yield a clonal architecture, as buds that were still alive when waters receded could expand. High water levels that persisted longer than the life span of the buds, however, would yield a solitary habitat. Once the stem reached the post-vegetative branching phase, the stem could not produce vegetative branches even if water levels were low, and the stem would remain solitary (Fig. 6). It is important to note that water levels in wetland habitats are typically seasonal; there is a clear distinction between high and low water levels, and over a year, a plant may experience both low water levels that allow branching and high water levels that inhibit branching. While results from the growth data in this study did not suggest seasonality of bud outgrowth, as new branches were produced throughout the year, studies on other tropical plants demonstrate that bud outgrowth may be controlled temporally by season (Shimizu-Sato & Mori, 2001), and

branching on ramets of *A. wrightii* appears to be seasonal (Chap. 2). Therefore, in order for high water levels to influence bud expansion and survival, seasonally high waters must persist for long enough to abort expanding branches and return every year until the vegetative branching phase has passed.

Environmental effects on germination: In a greenhouse study by Wagner (1982), germination rates of 70% were reported for *A. wrightii*. Germination rates in our study, however, were low and similar to data from germination studies on other palms (Wagner, 1982; Broschat, 1993; Makus, 2006). In particular, germination rates of *A. wrightii* in saturated soil (8%) were equal to germination rates of uncleaned *Sabal palmetto* seeds (Makus, 2006). Our data show that environmental conditions constrain germination; seeds germinated only in saturated soil conditions. The saturated soil condition, if maintained during the juvenile branching phase, would induce vegetative branching and a clonal individual. However, since *A. wrightii* individuals grow in wetlands with fluctuating water conditions, different architectures can occur even after low water levels are experienced for germination. Germination has to occur during a dry-down; but after germination, branching will be encouraged by continued low water level or discouraged by rising water level.

Effects of A. wrightii *germination rates on population structure:* Germination rates for *A. wrightii* observed in this study were low compared to those reported for other palms and were affected by water level (Wagner, 1982). Relative annual recruitment (F) can be estimated using germination rates (R_g) and seedling survival rates (R_s). Using results from this study, the relative annual recruitment of a genet (F) under high and low water levels can be estimated: $F= R_g*R_s$;

Relative annual recruitment under high water levels (F_{high}) and low water levels (F_{low}) were estimated using germination rates from this study (R_g = 2% for low water and 8% for high water). Survival rates (R_s) were estimated using data from other studies. Seedling survival rates for *Serenoa repens* and *Sabal etonia* in dry soils was 39-57% (Abrahamson & Abrahamson 2009), so 50% seedling survival was used in low water. Seedling survival rates for *Sabal palmetto* in flooded conditions were 0% (Perry & Williams, 1996). Since some germination was observed in high water levels, slightly greater (0.5%) seedling survival was used in high water. These numbers gave annual recruitments of F_{low} = (0.08)*(0.5) = 0.04 and F_{high} = (0.02)*(0.005) = 0.0001.

Annual recruitment in the field appears to be very low (Edelman, personal observation). In this study, seeds planted in December began germinating in June. In the Caribbean basin, as in south Florida, the wet season lasts from May until November (Duever et al., 1994; Giannini, Kushnir & Cane, 2000). During the wet season, high water levels and flooded soils are present in the wetland habitat during germination of *A. wrightii*. Under high water levels, there should be little to no annual recruitment. However, topography and water level are not homogeneous. Seedling recruitment is possible if germination occurs on raised patches of soil within the wetland landscape or during dry years. Recruitment would occur annually but only in these elevated microhabitats.

Recruitment also has the ability to influence population structure (Rea & Ganf, 1994). If seedling recruitment occurs annually on elevated microhabits, only a few individuals would germinate in any one year, and the population would consist of individuals of different ages growing in similar environmental conditions. A population structure with individuals growing in similar conditions is present in the Everglades,

where similarly sized *A. wrightii* line the ditches of the road between Mahoganny Hammock and West Lake (Edelman, personal observation). Alternatively, when environmental conditions are not conducive for germination and survivorship (such as high water levels), recruitment is limited to temporally rare environmental events when water levels remain low from germination to establishment (Rea & Ganf, 1994). If recruitment is limited to temporally rare events, individuals sexually reproduce successfully only once in many years when the environment is conducive to mass recruitment, leading to a population structured with many individuals in a few age classes.

The recruitment and architecture models proposed here used data on growth of juvenile plants to predict adult vegetative architecture and population structure. Using these models, the architecture of wild populations of adult genets can be analyzed in order to develop hypotheses about their historical environment and to predict future growth of this threatened species. Information on the historical environment and future growth of *A. wrightii* is of particular interest in the Everglades, where water levels have been manipulated over the past 100 years and where restoration will produce further changes. If seasonal water levels increased in the current habitat, decreased germination of *A. wrightii* would be expected, resulting in fewer seedlings and juveniles and potentially solitary individuals. Less vigorous vegetative branching on adult clones would also be expected. If water levels decreased, increased germination would be expected, resulting in more seedlings and juveniles, clonal juvenile plants, and vigorous vegetative branching on adult clones.

TABLES:

Table 1: Total percent germination of *A. wrightii* seeds after 1 year under different water levels; water depths are emergent (water level 5 cm below soil level), saturated (water level at soil level), submerged (water level 5 cm above soil level) and submerged deeply (water level 10 cm above soil level). Values are mean percent ± standard deviation. Different superscripts signify that means were significantly different.

LEVEL OF WATER			
Emergent	Saturated Soil	Submerged	Submerged, deeply
0.75 ± 1.49%[a]	8.00 ± 10.64%[b]	0.50 ± 0.93%[a]	0.25 ± 0.71%[a]

Table 2: Average measurements of height, circumference, number of leaves, number of branches at final sampling, and number of developing buds at harvest under different water levels and light availabilities. Values are mean ± standard deviation. Different superscripts signify that row means were significantly different.

	LOW WATER		**MEDIUM WATER**	
	SHADE	**SUN**	**SHADE**	**SUN**
Height (cm)	12.7 ± 5.8^{a}	10.7 ± 4.8^{a}	11.3 ± 6.8^{a}	8.2 ± 3.3^{a}
Circumference (cm)	7.7 ± 3.3^{a}	5.4 ± 1.4^{b}	7.2 ± 4.0^{a}	5.7 ± 1.9^{b}
No. Leaves	7 ± 2^{a}	8 ± 2^{a}	6 ± 2^{a}	7 ± 2^{a}
No. Branches	0 ± 1^{a}	2 ± 1^{b}	0 ± 1^{a}	1 ± 1^{c}
No. Buds	0 ± 1^{a}	1 ± 1^{a}	0 ± 1^{a}	1 ± 1^{a}
No. Branches and Buds	1 ± 1^{a}	3 ± 1^{b}	1 ± 1^{a}	2 ± 1^{c}

Table 3: Annual growth rates under different water levels and light availability for stem height, number of leaves matured, and number of branches produced. Values are mean growth rate ± 1 standard deviation. Different superscripts signify that row means were significantly different.

Growth rates:	LOW WATER		MEDIUM WATER	
	SHADE	SUN	SHADE	SUN
Stem (cm/year)	3.6 ± 4.5^{a}	4.5 ± 6.1^{a}	1.5 ± 8.6^{a}	1.8 ± 5.2^{a}
Leaves (No./year)	2 ± 3^{a}	3 ± 3^{b}	0 ± 3^{c}	2 ± 3^{b}
Branches (No./year)	0 ± 1^{a}	1 ± 1^{b}	0 ± 1^{a}	1 ± 1^{a}

Table 4: **A.** Variation among water levels and light availabilities in biomass of living leaves, dead leaves, stem, shoot (stem + all leaves), root and total living plant. Values are mean biomass ± 1 standard deviation. **B.** Variation among water levels and light availabilities in biomass allocation for living leaves, stem, root and root:shoot ratio among water levels and light availabilities. Values are mean mass fractions ± 1 standard deviation. Different superscripts signify that row means were significantly different.

	LOW WATER		**MEDIUM WATER**		**TOTAL**
A. *Biomass (g)*	**SHADE**	**SUN**	**SHADE**	**SUN**	
Living leaves	22.8 ± 18.5[a]	22.2 ± 16.3 [a]	15.5 ± 13.6[b]	14.6 ± 12.3 [b]	18.8 ± 15.5
Dead leaves	5.1 ± 4.74 [a]	5.1 ± 3.4 [a]	2.4 ± 1.8 [b]	3.8 ± 5.1 [b]	4.1 ± 4.0
Stem	8.4 ± 5.9 [a]	7.8 ± 5.0 [a]	4.3 ± 2.9 [b]	6.1 ± 6.6 [b]	6.7 ± 5.4
Shoot	36.3 ± 24.9 [a]	35.0 ± 23.0 [a]	22.2 ± 16.0 [b]	24.5 ± 17.9 [b]	29.5 ± 21.2
Root	27.9 ± 20.7 [a]	23.5 ± 15.3 [a]	14.5 ± 10.2 [b]	17.1 ± 16.7 [b]	20.8 ± 16.7
Total living plant	59.1 ± 421.1 [a]	53.5 ± 34.7 [a]	34.3 ± 23.7 [b]	37.8 ± 29.3 [b]	75.7 ± 54.9
B. *Biomass allocation (%)*					
Leaves	0.33 ± 0.17 [a]	0.42 ± 0.14 [a]	0.40 ± 0.18 [a]	0.37 ± 0.18 [a]	37.9 ± 16.9
Stems	0.17 ± 0.08 [a]	0.15 ± 0.04 [a]	0.15 ± 0.06 [a]	0.19 ± 0.14 [a]	16.5 ± 9.2
Roots	0.49 ± 0.11 [a]	0.43 ± 0.10[a]	0.45 ± 0.15 [a]	0.45 ± 0.13 [a]	45.6 ± 12.2
Root: Shoot	0.84 ± 0.32 [a]	0.71 ± 0.36 [a]	0.76 ± 0.37 [a]	0.74 ± 0.42 [a]	0.76 ± 0.6

FIGURES:

Figure 1: **A**. Dissected shoot of *A. wrightii* showing a small rhizome with a slight protrusion at the base of the erect stem. The origin of the rhizome is at 0° and the erect stem is at 180°. Arrow points to axillary bud. **B**. Diagram displays in plan view how buds and branches were categorized into quadrants. If viewed from above, 0° is the origin of the rhizome, 180° is the erect stem, 270° is behind the erect stem and 90° is over the bud. Dashed inner circle represents where erect stem was placed during angle measurements.

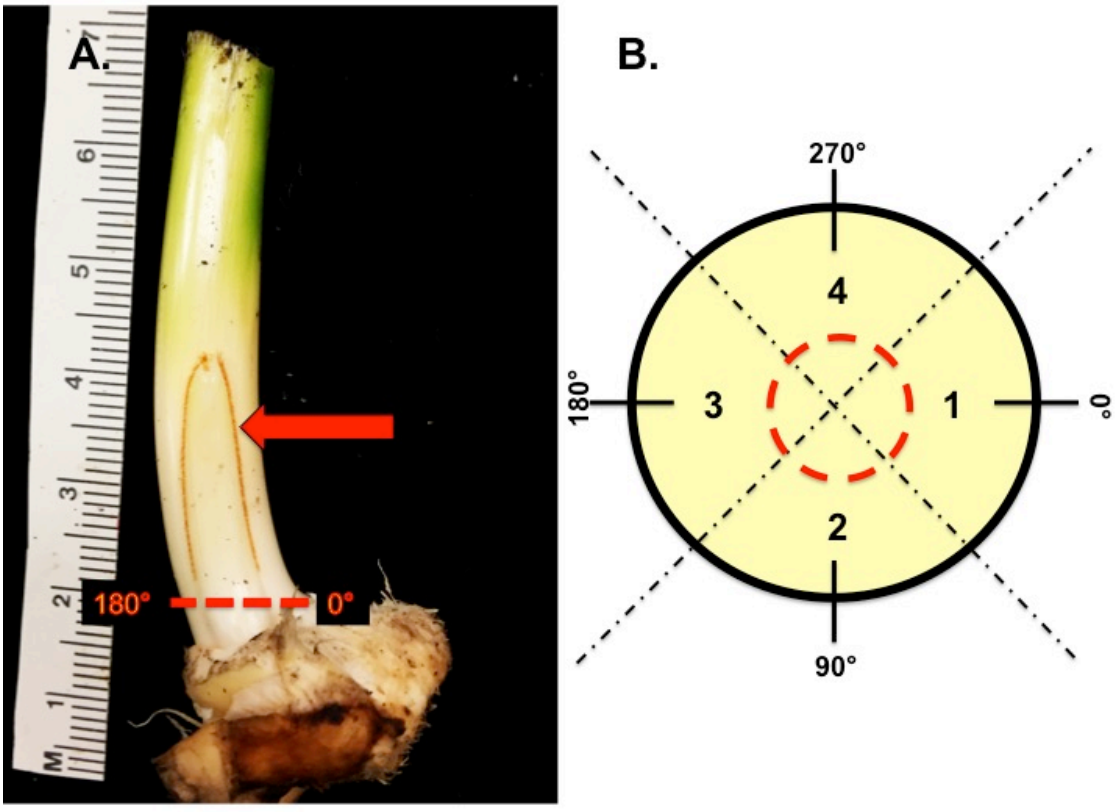


Figure 2: Cumulative number of *A. wrightii* seeds germinated for each of the four water levels over the 1-year sampling period. The four water levels were emergent (-5 cm), saturated soil (0 cm), low water level (5 cm) and medium water level (10 cm). Error bars represent ± 1 standard error but only the saturated soil water level had standard error large enough for error bars to be visible.

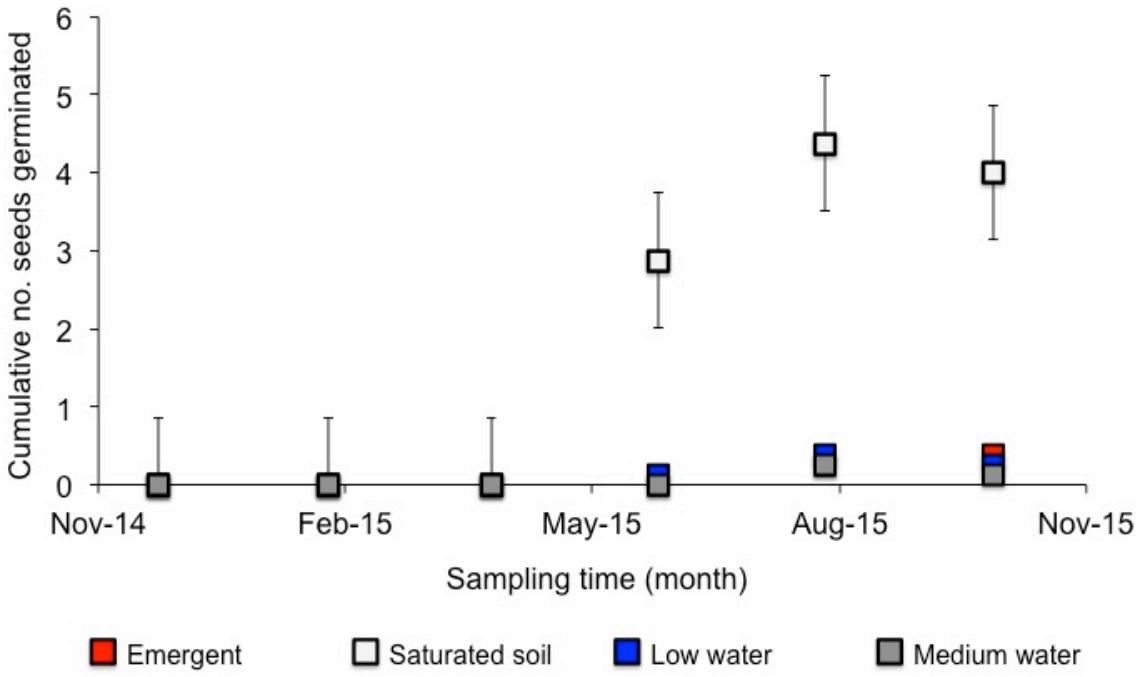


Figure 3: **A.** Average stem height, **B.** average number of mature leaves, and **C.** average number of visible buds for juveniles of *A. wrightii* growing in four treatments (low water level + shade, low water level + sun, medium water level + shade, and medium water level + sun). Error bars represent ± 1 standard error but only the saturated soil water level had standard errors large enough for error bars to be visible.

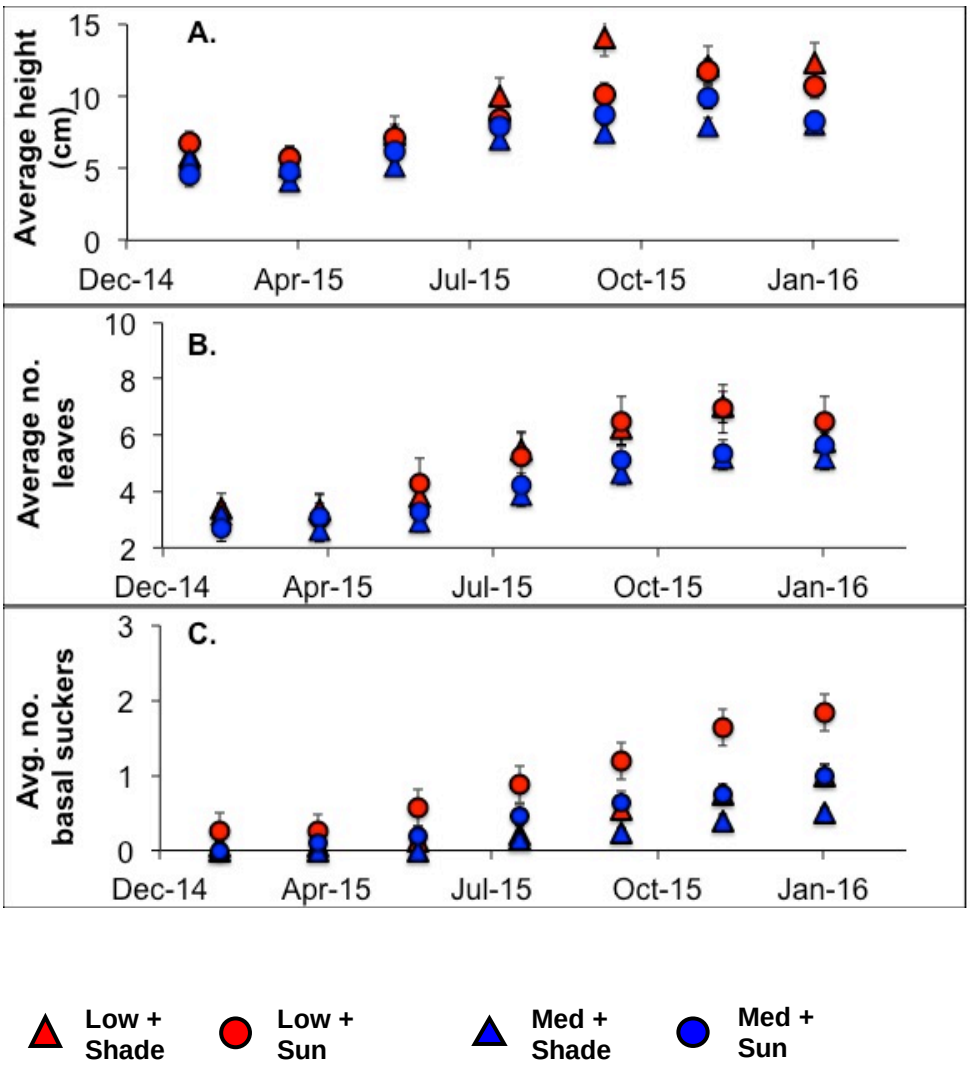


Fig. 4: **A**. Distribution of developing and emerged axillary branches around the base of the stem, based on sequence of emergence. Numbers in parentheses are the cumulative numbers of buds/branches in each region. Categories 1-4 correspond with degrees from Figure 1, with the midpoint of 3 being 180^{o}. **B**. Frequency of developing and emerged bud/branch locations (region 1, 2, 3, 4) and their sequence of emergence (first, second or third).

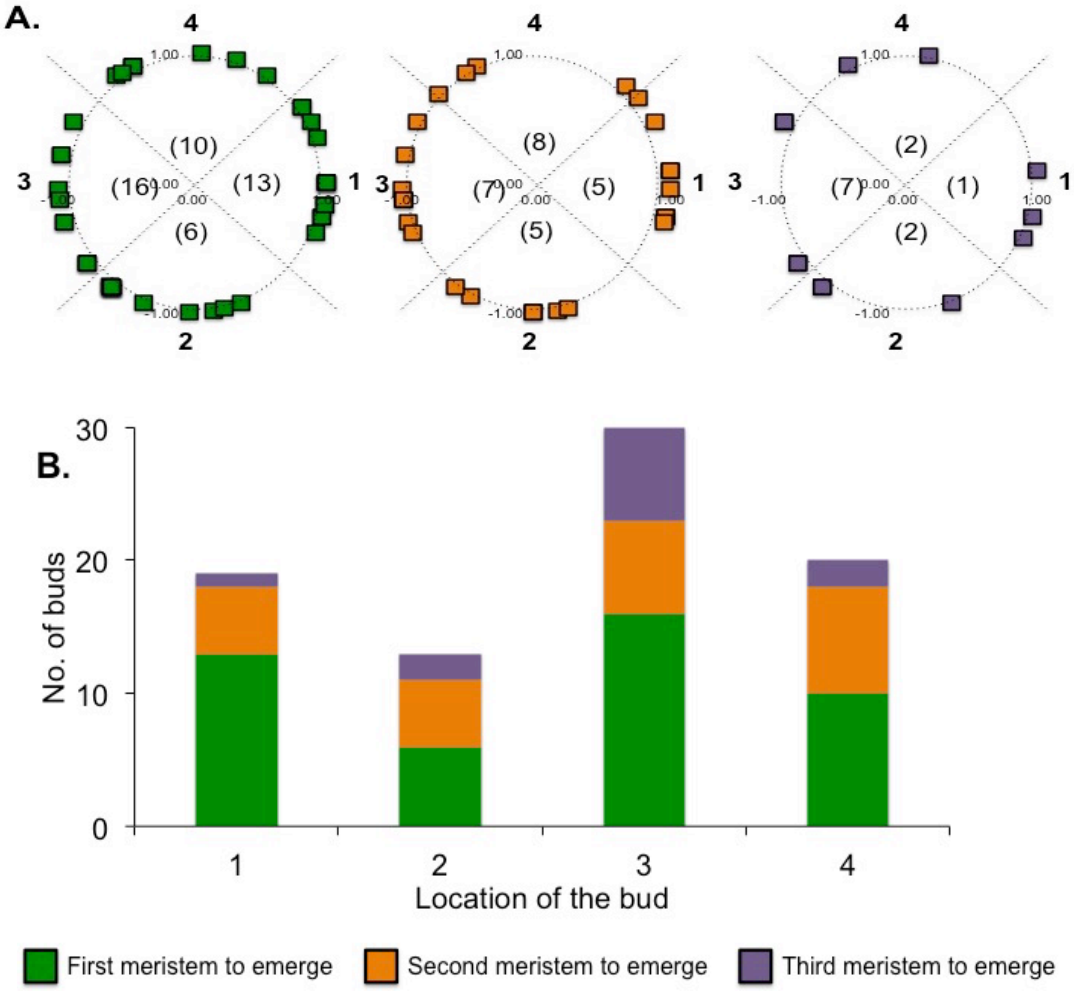


Fig. 5: **A.** Log leaf mass (LM), **B.** log stem mass (SM), and **C.** log root mass (RM) plotted against log total plant mass (TM) for juveniles of *A. wrightii* growing in four treatments (low water level + shade, low water level + sun, medium water level + shade, and medium water level + sun).

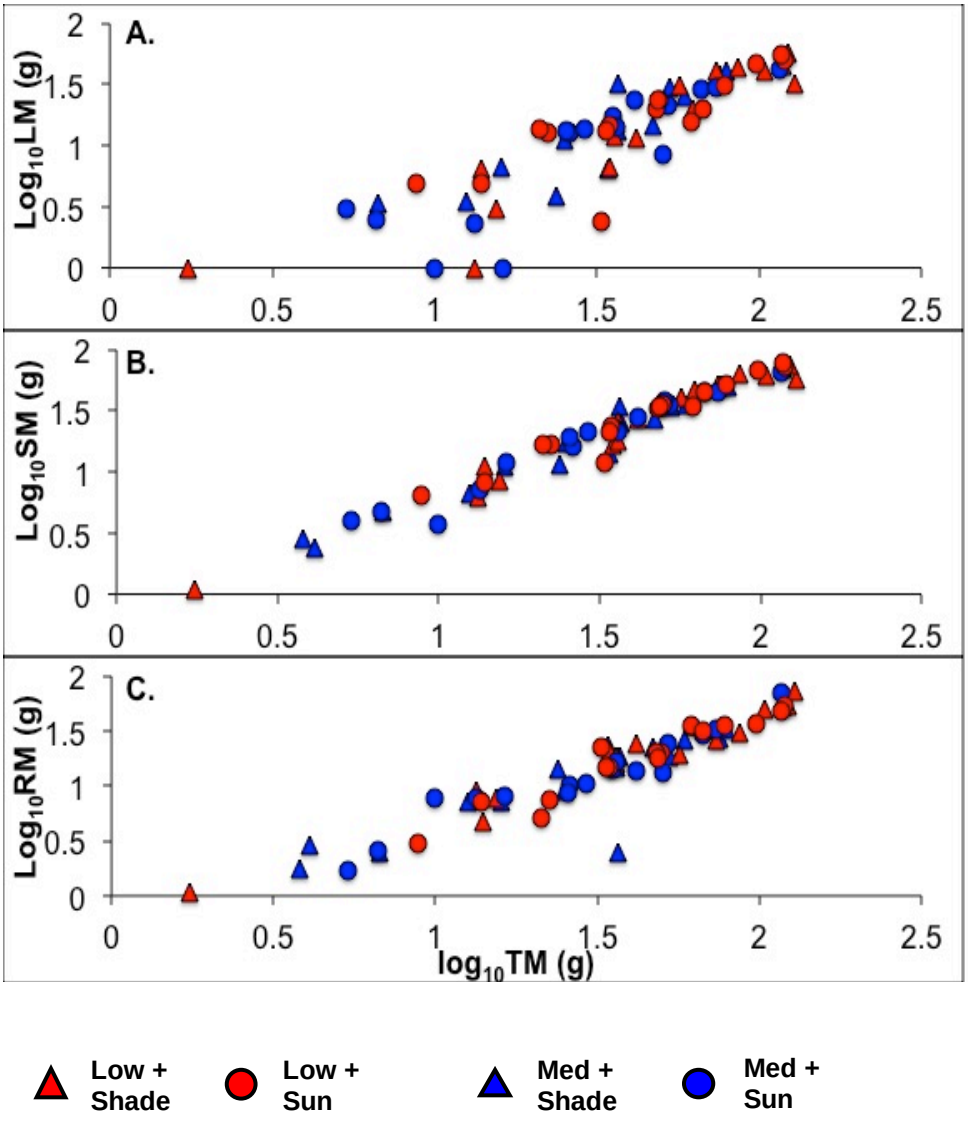
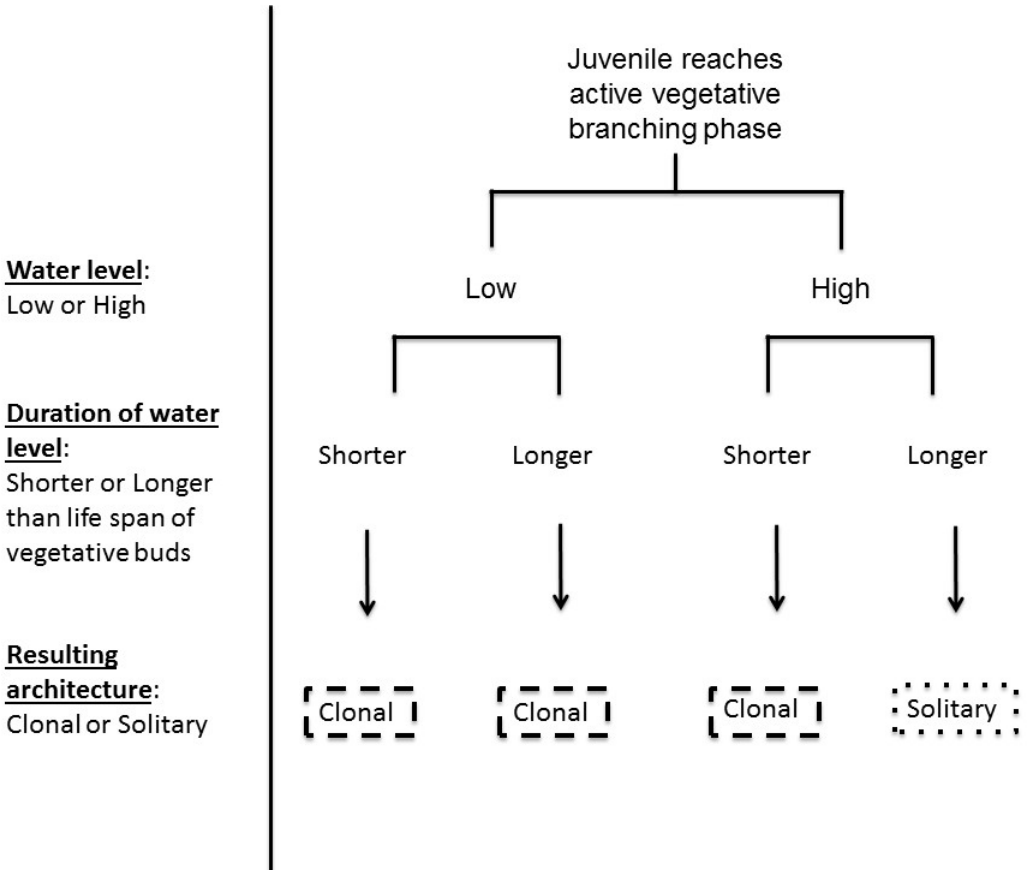


Figure 6: Conceptual model for how high and low water levels could result in solitary or multiple stemmed architecture. Production of solitary individuals occurs under a single combination of environmental conditions.



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CHAPTER IV

ARCHITECTURAL VARIABILITY OF THE CLONAL PALM *ACOELORRHAPHE WRIGHTII* ACROSS A GEOGRAPHIC RANGE

ABSTRACT:

Morphological or architectural variability is the ability of an organism to change its shape or form in response to changes in the environment. Clonal plants make good subjects for the study of architectural variability because the ramet can be used as an additional measure of architectural variability. The purpose of this study was to describe leaf mophology and clonal architecture of *A. wrightii* in different parts of its geogrphic range and to analyze variability of these characters in different environmental conditions. A total of 96 genets (clonal individuals); from four populations were studied: three populations in Belize and one in Florida. Leaf morphology and ramet measurements were taken on one to three leaves for one ramet/genet (N_{leaves} = 179). The variability in leaf morphology was compared in relation to light regime, presence of fire, habit and elevation. Architectural variability was studied on clumping individuals (N_{genets} = 87), and variability was analyzed for different light regimes, presence of fire and elevations. Circumference size was used to create size classes, and the distribution of individuals among size classes was compared among populations. Leaf morphology differed among populations and within populations with fire, light regime and elevation. Clonal architecture differed among populations and elevations. However, differences in average values among populations, light and fire regimes were not great, suggesting that leaf morphology and clonal architecture were not highly variable across the geographic range of *A. wrightii*. Size class distribution differed among populations, suggesting different population dynamics.

INTRODUCTION:

Morphological or architectural variability is the ability of an organism to change its shape or form in response to changes in the environment (Sultan, 2000). Examples of environmental conditions that induce variations are changes in temperature, topography, and altitude (de Kroons & Hutchings, 1995). Historically, plant species were delineated based on their morphology and/or architecture (Stace, 1989). Recent findings in genetics show that these delimitations were not always correct (Judd et al., 2000). Moreover, variability in plant form and architecture may make these historical delimitations even less reliable (Bradshaw, 1965; Sultan, 1987; Sultan, 2000). These considerations are especially important for slow-growing, long-lived species such as palms because conditions can change through the lifespan of individuals and conditions experienced early on can induce differences later.

Clonal plants make good subjects for the study of architectural variability because there is an additional layer of study -- the ramet within the genet. The number of ramets within a genet and overall clone circumference have been used to measure architectural variability (Doust, 1991; Cain & Damman, 1997; Price & Marshall, 1999; Sultan, 2000; Benot et al., 2011). Clone circumference, commonly used in studies of architectural variability, can also be used to analyze population structure, where size is taken as a proxy for time or developmental stage (Condit et al., 1998; Lykke, 1998). In these types of studies, the population is split into discrete size classes. The distribution of size classes within the population are used to predict the fate of a population (Ahmed & Ogden, 1987; Crouse, Crowder & Caswell, 1987; Boot & Gullison, 1995; Olmstead & Alvarez-Bullya, 1995; Frederiksen, Lebreton & Bregnballe, 2001; Hunt, 2001; Kaye et al., 2001; Feeley et al., 2007). Analysis of population structure can provide information on the overall health of a population. Populations skewed to small size classes are

increasing in population size; populations skewed to larger size classes are decreasing; populations with an even distribution of size classes are not changing in size; and populations with missing classes are not reproducing every year (Ricklefs & Miller, 2000). These types of analyses can be used to understand the health of a population and can be used further to compare among populations (Ahmed & Ogden, 1987).

Clonal palms are large, woody monocots that branch vegetatively, primarily through basal suckering (Tomlinson, 2006; Edelman, chap. 1). While studies on clonal palm architecture have mostly focused on the effect of harvesting on regrowth and basal suckering, some studies have found that the circumference and number of ramets in a genet is variable among clone sizes (Olmstead & Alvarez-Buylla, 1995; Alvarez-Buylla et al., 1996; Bernal, 1998; Silva Matos, Freckleton & Watkinson, 1999; Siebert et al., 2000; Floreze & Ashton, 2000; Souza et al., 2003).

Acoelorrhaphe wrightii is a clonal palm native to the Caribbean basin (Atlantic coast of Central America, from the Yucatan Peninsula to northern Costa Rica; Cuba; Southern Florida; Bahamas) (Henderson et al., 1997). Historically, *A. wrigthii* was seperated into eight species demarcated by differences in morphology and architecture (Small, 1922; Goevarts & Dransfield, 2003); species delimitation also depended on the original author. A subspecies of *A. wrightii* was distinguished based on presence of a solitary habit (Small, 1922; Dransfield et al., 2008; WCSP, 2017). However, as more researchers viewed herbarium specimens, the eight species and subspecies were lumped into *A. wrigthii* as a result of a consensus on leaf and floral morphological similarities among herbarium specimens (Small, 1922; Bailey, 1934).

Thus, both leaf morphology and whole plant habit (architecture) have been used to classify species or subspecies in the genus *Acoelorraphe*. The purpose of this study

was to describe the leaf morphology and clonal architecture of *A. wrightii* in distinct natural populations from different parts of its geographic range in order to examine morphological and architectural variability in these characters in the field. The findings were used to analyze population structure in different locations and to evaluate the bases for historical species classification.

MATERIALS AND METHODS:

Study sites and selection of individuals: Individuals were sampled from relatively undisturbed, native areas, excluding individuals found on the side of the road and individuals known to be planted and/or managed by people. Solitary and mulitple-stemmed genets were used in this study but solitary individuals were not included in the architectural measurements, because they lacked tiers and genet circumference (Fig. 1A & 1B; $n_{solitary} = 9$; $n_{multiple} = 91$). Two countries, Belize and U.S.A., and multiple populations were visited for this *in-situ* study (Fig. 2; population information available in Table 1). In Belize, three populations were sampled ($N_{Belize} = 80$ genets): (1) Monkey Bay Wildlife Sanctuary ($n_{BZmb} = 38$ genets); (2) the northern Western Highway from La Democracia to Burrell Boom ($n_{BZnh} = 14$ genets); and (3) the Coastal Highway ($n_{BZch} = 32$ genets). In the USA one population was sampled in the southern Everglades of Florida; the Everglades population was located off the Main Highway between Mahoganny Hammock and Nine Mile Pond ($n_{FL} = 18$ genets). Population locations are given in Table 1. Data from garden-cultivated individuals from Edelman, Chapter 2 ($n_{garden} = 45$) were also used in this study.

Sampled individuals were mapped using a Garmin ETrex 10 GPS (GPS accuracy ± 15 m). Sampled individuals occurred in different light regimes and varied in their fire interval. Light regime was visually determined by amount of interception of

sunlight by the outermost tier when the sun was most vertical, between 10-3pm. Light regime was defined as sun or shade; if more than 50% of the leaves on the outermost tier of a genet were in the sun, then the individual was said to be growing in the sun, otherwise it was said to be in shade. Presence of fire was assigned based on physical evidence of fire. Presence or absence of fire was a genet characteristic based on evidence of fire, such as burn marks on stems, rhizomes or leaves (Fig. 3A & 3B). A class of no fire was assigned if there were no signs of fire on the indivdual (Fig. 3C). All sampled individuals in all three countries were growing in seasonally flooded conditions. Gross elevation was determined to examine interpopulation variation of elevation in the Google geoplanar application (accuracy of geoplanar was ± 10m elevation; Google, 2016) using GPS coordinates obtained from the field, since field elevation from the GPS was not accurate enough for this study (accuracy of GPS was ± 20 m elevation).

Leaf morphology: To characterize leaf and ramet morphology, 179 leaves from 79 individual genets (ramet/genet, 2-3 leaves/ramet) were measured. Leaves from four populations (n_{BZcr} = 48 leaves, n_{BZnh} = 11 leaves, n_{BZmb} 93 leaves, and n_{FL} = 27 leaves) were measured in this study. One ramet/genet were selected to measure. Ramets were selected based on size (between 0.4 and 1.5 m) and location in the genet (in the outermost tier). At heights above 0.4 m, ramets are established and their leaf characteristics are more similar within a ramet (Edelman, Chapter 2), so selecting established ramets diminished the effect of ramet size on leaf morphology. Ramets found in the outermost tier were used in order to reduce the potential effects of shading on leaf morphology. Up to three leaves/ramet--the first, fifth and tenth most recently matured leaves--were measured, if available. The most recently matured leaf was defined as the newest leaf that had fully emerged from the apical bud of the stem and whose lamina had fully expanded. Morphological measurements included ramet height

and circumference, lamina length and width, petiole length and width, and number of pinnae. Ramet height was measured from the base of the ramet to the apical bud. Circumference of the ramet was measured 0.3 meters below the stem apical bud, where the stem circumference has stablized after primary thickening growth. Lamina length was measured from petiole attachment to the tip of the lamina, while lamina width was taken at the widest part. Petiole length was measured from the top of the leaf sheath to lamina attachment on the abaxial side of the petiole. The abaxial side was used since there is a clear distinction of where the petiole begins and ends on the abaxial side. Petiole width was measured on the adaxial side, where the petiole is flat. Leaf morphological characters were compared among wild populations and to garden-cultivated individuals from Edelman, Chapter 2 (n_{garden} = 94 leaves).

Clonal architecture: Measurements to describe clonal architecture were taken for 87 multi-stemmed or clumping genets from four populations (N_{BZcr} = 30, N_{BZmb} = 36, N_{BZnh} = 7, and N_{FL} = 14). Clone circumference was measured with a tape ruler as the total distance around the base of the clump, including all ramets above 0.1 m. Total number of ramets over 0.5 meters tall, total number of live ramets over 0.5 meters, and number of tiers in a genet were counted. Tiers were defined by visual estimates of canopy density and overlap; distinct tiers had little intersection of ramet canopies. Three architectural relationships were analyzed, as in Edelman, Chap. 2: (1) circumference x number of established ramets; (2) circumference x number of tiers; and (3) number of ramets x number of tiers. These relationships were used to determine if there were differences in clonal architecture between populations, light regimes, fire intervals, and elevations. Relationships were compared among wild populations and to garden-cultivated individuals, using data from Edelman, Chapter 2 for the latter (N_{garden} = 45).

Population structure, defined as the distribution of size classes within a population, was analyzed using circumference as a measurement for size class and then finding the number of genets in each size class for each population. Number and size of size classes were defined to balance the number of sampled individuals across size classes as in Condit et al. (1998). The following circumference size classes were used to accommodate the decrease in number of individuals with increasing class size (Condit et al., 1998): 0-2, 2.01-4, 4.01-6, 6.01-8, 8.01-12, 12.01-16, 16.01-24, 24.01-32 m. The number of individuals in each class for each population was tallied, and numbers were compared between classes within populations to determine if the distribution of class sizes within a population was even. Class size distributions were also compared among populations to determine whether population structure was similar.

Statistical analysis: The R environment was used to analyze results (R Core Team, 2013). Leaf variability was examined using linear regression with lamina length as the independent variable and lamina width as the dependent variable. To determine if there were differences in leaf morphology among populations (wild and garden-cultivated), light regime, presence of fire, and habit, average lamina length, lamina width, petiole length, petiole width and number of pinnae were analyzed using ANOVA tests. To determine if there were differences in leaf morphology among elevations, average lamina length, lamina width, petiole length, petiole width and number of pinnae were analyzed using ANCOVA tests Since differences existed among populations, nested ANOVA tests were used to examine differences in leaf morphology variables between light regimes (shade or sun), habit (solitary or clumping), and between presence of fire (fire or no fire) within populations. Scaling relationships between morphological variables were compared among wild populations, light regimes, fire, elevation and habit using

ANCOVA tests. The effect of genet within the population on leaf morphology variables was examined with nested-mixed effects models using the lme4 package in R; population was the random variable and ramet within genet was the fixed effect (Bates, 2011). The genet could not be used as a fixed effect since there was only one ramet per genet. The nested mixed effect model thus compared variation within a ramet to variation within a population to variation between populations.

The architectural relationship between circumference and number of established ramets was analyzed using linear, exponential and log-transformed equations, and the best fit equation was selected using AIC values. Log-transformed models were the best fit and were used to analyze the relationship between circumference and number of established ramets (see also Edelman, Chap. 2). The relationship between circumference and number of established ramets was compared among populations (wild and garden-cultivated), light regimes, and presence of fire using ANCOVA tests. The relationship between circumference and number of established ramets was compared among elevations using regression analysis, where circumference and elevation were the indepdent variables.

The architectural relationship between circumference and number of tiers and number of established ramets and number of tiers were compared using ANOVA tests. The relationships between circumference and number of tiers and number of established ramets and number of tiers were compared among populations (wild and garden-cultivated), light regimes, and presence of fire using two-way ANOVA tests, while the relationships among elevations were compared using ANCOVA tests.

As per Lykke (1998), for each population, a regression was calculated with size class midpoint (m) as the independent variable and number of individuals (N_i) in that size class as the dependent variable. Class mid point was the average circumference for

each size class in each population. The size class variable was ln-transformed, and the average number of individuals was transformed by ln (Ni+1) (1 was added beause some size classes had 0 individuals). A regression was calculated for each of the populations. Slopes of these regression were called SCD (size class distribution) slopes and were used as indicators of population structure. SCD slopes among populations were compared using linear regression analysis.

RESULTS:

Leaf morphology– Leaf morphology (lamina length, lamina width and petiole length) is variable among populations (Table 2; ANOVA tests for differences in lamina length, lamina width and petiole length among populations, $p < 0.05$). However, there was little morphological variation observed within a ramet for leaf morphology variables (nested mixed-effect model testing the variation within a ramet within a population for lamina length, lamina width, number of pinnae and petiole length, $p > 0.10$).

Leaves in BZ_{MB} had the largest laminas (Table 2; ANOVA tests for differences in lamina length and lamina width, $p < 0.05$, Tukey post hoc among populations). Leaves in BZ_{NH} had the longest petioles (Table 2; ANOVA tests for differences in petiole length, $p < 0.05$, Tukey post hoc among populations). Lamina length and lamina width had a positive linear relationship (lamina width = 1.39 lamina length + 0.0006, $p < 0.01$). Garden-cultivated individuals were larger for leaf variables except petiole width (Table 2; ANOVA tests for differences in lamina length, lamina width and petiole length among populations, $p < 0.05$).

Leaf morphology was also variable between environmental conditions within populations. Different light regimes, presence of fire and elevations were correlated with variability in lamina length, lamina width and petiole length within populations. Individuals that had experienced fire had narrower and shorter laminas and shorter petioles (Table

3; nested anova for differences in lamina length, lamina width and petiole length between light regimes within populations, $p = 0.05$). Individuals in the shade had longer and wider laminas and longer petioles (nested anova for differences in lamina length, lamina width and petiole length between light regimes within populations, $p = 0.05$). Ramet circumference, number of pinnae, and petiole width were not variable between light or fire regime or habit within populations (Tables 2A and 2B; nested analysis for differences in ramet circumference, number of pinnae, and petiole width within populations, between light regimes and presence of fire, $p > 0.05$; ANCOVA test for differences between elevations, $p > 0.05$). The relationship between lamina length and lamina width did not vary significantly within wild populations for light or fire regime, elevation or habit (ANCOVA test, $p > 0.05$). Elevation within populations were not variable so statistical analysis could not be completed on differences in leaf shape within populations based on elevation.

Clonal architecture: Architecture and population structure (size class distributions) were variable among populations, however, similar growth patterns were found throughout all populations. Solitary individuals were present in every population. There were two solitary individuals observed in the southern Everglades (8% of total observed individuals), two in Monkey Bay Wildlife Sanctuary (5% of total observed individuals), three in northern Western Highway (20% of total observed individuals), and two in Coastal Highway (6% of total observed individuals).

All mulitple-stemmed individuals (genets) had similar overall architecture; they all had empty centers, presumably caused by death of the protoclone, and formed tiers. Tiers were less obvious in genets growing in shaded conditions without fire. The maximum number of ramets observed in a genet was 60 and the maximum number of tiers observed was five. However, there was more variability in clone circumference and

number of ramets among genets with five tiers than in genets with four or fewer tiers (Fig. 4) The relationship between circumference and number of established ramets can be expressed as log (no. ramets) = 0.13 * circ + 0.61 (semi-log linear regression analysis, $F_{1,85}$= 208.5, p< 0.01).

Architectural relationships, as reflected in circumference, tiers and number of ramets, differed among wild populations (Fig. 5; two-way ANOVA for differences among populations in relationships between 1- circumference and no. tiers, $F_{5,3,78}$= 2.8, p= 0.05; 2- no. ramets and no. tiers, $F_{5,3,78}$= 3.8, p= 0.01). The Monkey Bay Wildlife Sanctuary population produced more ramets and larger circumference than other populations (Fig. 5). The Western Highway population had fewer ramets given circumference and displayed a greater increase in number of tiers with increase in circumference than other populations (Fig. 5). The southern Everglades population had a smaller increase in number of tiers with increase in circumference than other populations. Genets growing in higher elevations had fewer ramets and fewer tiers given circumference.The Coastal Road, Belize, population had the largest circumferences and greatest number of ramets for genets with one to five tiers (Table 4). Differences in elevation may have induced the architectural variability observed among populations (linear regression for relationship between ramets and circumference + elevation, $F_{3,83}$= 75.07, p< 0.001; ANCOVA for relationship between circumference and no. tiers + elevation, $F_{5,1,80}$= 2.0, p= 0.10; and ANCOVA for relationship between no. ramets and no. tiers + elevation, $F_{5,1,80}$= 5.0, p= 0.02). However, environmental differences within populations (fire, light, elevation) did not induce variability in architectural relationships (ANCOVAs for differences in relationship between ramets and circumference, circumference and number of tiers, and number of ramets and number of tiers between light, fire and elevation within populations, p> 0.10). Architecture of garden-cultivated individuals were different from

wild populations but most similar to southern Everglades (Fig. 5; ANCOVA test for differences among populations in architectural relationships, $p < 0.10$).

Population structure, measured by size class distributions, varied among populations (linear regression comparing size class midpoint (independent variable) to number of individuals in each size class among populations, $F_{1,3,27} = 6.62$, $p = 0.001$). While all populations had a greater proportion of the population in smaller class sizes, Coastal Highway and Monkey Bay populations had a more even distribution of individuals among size classes than Western Highway and Southern Everglades populations (Fig. 6A - D). Western Highway and Southern Everglades popoulations lacked larger-sized individuals (larger size classes) (Figs. 6C & 6D).

DISCUSSION:

Results of the leaf morphological and architectural analyses in this study support the current classification of *A. wrightii* into a single species. At the time of *A. wrightii*'s discovery and classification, palm biologists sometimes drew species lines based on analysis of a single herbarium sheet with one leaf and one inflorescence or infructescence (Small, 1922; Bailey, 1934). In this study, the variation among ramets captured the variation in an entire population; one clone had the ability to display all the variability observed within the population. However, the variability between populations was only a few centimeters, similar to leaf variability of other palms (Henderson, 2002). Most likely, *A. wrightii* was split into taxonomic species as a result of lack of communication between authors or lack of understanding of the range of variation among individuals and populations, not because of significant morphological differences based on genetic differences (Bailey, 1934).

While results of this study demonstrate that variability occurs among populations, it is important to note that this study did not include samples from the entire range of the species. *A. wrightii* also occurs in Costa Rica, Cuba, Guatemala, Honduras, Mexico, and Nicaragua. Populations used in this study were from Belize (the center of the range) and Florida (the northern edge of the range). A study of additional populations would provide information about morphological and architectural variability throughout the range. It would be especially interesting to look at the edge of the range: Costa Rica (southern range), Nicaragua (western range) and Cuba (eastern range). Cuba has some populations that have been reported to have only solitary individuals (Henderson et al., 1997). Examination of these populations and their environmental history would be especially interesting. Results of the experiments in Edelman, Chap. 3, suggest that these could be populations with wet/dry hydroperiods where the dry period is short but shallow enough to allow germination, and water levels in the wet season are relatively high, inhibiting bud expansion in the juvenile stage. Additional data on morphological and architectural variability throughout the range could be used to determine if architectural variability reported from this study was typical.

Additional data on morphological and architectural variability throughout the range could be used to determine if architectural variability reported from this study was typical. The number of countries sampled could increase the variability measured. Gaston (2000) hypothesized that variability in plant architecture changed with extent of geographic range such that species with larger geographic ranges display greater variability. Studies suggest that species with larger geographic ranges display greater variability because these species experience more environmental variability (Brown et al., 1996). The range of *A. wrightii* spans the Caribbean basin. Belize populations (Coastal Highway, Monkey Bay Wildlife Sanctuary, and Western Highway) were located

at the center of the geographic range, while the Florida population (southern Everglades) was located at the northern edge of the geographic range. The Florida population, however, was not different morphologically or architecturally from two of the three Belize populations. The third Belize population, Western Highway, was different from all other populations, suggesting that location within range may not be as important as other environmental factors.

Generally, a larger range has more environmental conditions. In this study, environmental conditions observed (light and fire) did not influence overall architecture. And while elevation is usually a proxy for climate, sites used in this study span about 40 m of elevation, a relatively narrow range. A wider range of elevations, achieved by sampling more populations, is needed in order to determine the shape of the curve describing the relationship of elevation to morphology and architecture in *A. wrightii*.

The importance of environmental variables on leaf morphology is further supported by the fact that garden individuals were different in leaf morphology from wild populations. Leaves of garden individuals were larger than all wild populations except BZ_{NH} . Larger leaves in the garden is most likely caused by the additional fertilizer and nutrients available to garden-cultivated individuals. Nutrient analysis was not included in this study but has been shown to play a role in leaf morphology of other plants, including palms (De Steven, 1989; Poorter & Nagel, 2000)

Regardless of architectural variability, genets displayed clear carrying capacities. The maximum number of tiers found on a genet was five, but circumference was quite variable, suggesting that there is a maximum number of tiers a genet can support. Number of tiers have been used to estimate age in *A. wrightii* (Edelman, Chapter 2) however, the results reported here suggests that circumference may be a better proxy for time. Individuals in wild populations were much larger than garden individuals,

suggesting that they were older. We could not find a relationship between time and circumference (Edelman, Chapter 2), when we knew the ages of the clones, because most of the garden clones were the same or similar ages. If garden clones are monitored for growth over many years in a long term study, the relationship between time and circumference could be clarified.

The distribution of circumference size within a population was used to describe population structure. While stability of a population can only be determined through a life history study, population structure is often indicative of population stability (Tilman & Kareiva, 1997). A population with an even distribution of proportions among classes (here, size classes) or more young individuals than old individuals is usually a stable population. The results from this study suggest that the Coastal Highway population is stable. However, populations with skewed distributions are generally unstable (Ricklefs & Miller, 2000). A skewed small class size, as in Monkey Bay, is an increasing population. However, greatly uneven distributions with missing classes, such as Western Highway and Southern Everglades population, are indicative of an unstable population that is not consistently reproducing and replacing itself. Thus, clone size provides an easy and convenient way to assess population characteristics in native habitats.

The use of clone size to examine population structure could be applied to other populations of *A. wrighitt*. When coupled with findings on morphological and architectural variability, results from the study can be used for baseline comparisons to other populations of *A. wrightii* not covered in this study. More widely, results on population structure, morphology and architecture can also be used to compare variability among clonally-reproducing palms or similar large, slow-growing monocots.

TABLES:

Table 1: Location and sample sized for the five populations sampled, including the Bahamian population that was excluded from analyses. Population acronyms are: MB = Monkey Bay Wildlife Sanctuary located in Belize; NH= North Western Highway located in Belize; CH= Coastal Highway located in Belize; FL= Southern Everglades located in Florida, USA. Numbers in parenthesis were not used in the study.

Pop	Country	Lat.	Long.	Avg. elevation (m)	No. genets	No. genets with multiple stems	No. solitary individuals	No. leaves sampled
MB	Belize	17°19.103' - 17°24.375' N	88°28.827' - 88°34.045' W	40.7 ± 6.8	34	32	2	48
NH	Belize	17°47.079' - 17°51.890' N	88°18.477' - 88°19.071' W	14.1 ± 0.5	18	15	3	36

CH	Belize	17°17.601’ - 17°17.837’ N	88°28.113’ - 88°28.440’ W	18.2 ± 1.6	32	30	2	93
FL	USA	25°15.859’ - 25°20.721’ N	80°47.891’ - 80°49.913’ W	1.4 ± 0.8	18	17	2	27

Table 2: Average ramet circumference and leaf morphological variables by population. Different letters to the right of the value indicates that these means differed significantly (ANOVA $p<0.05$).

	Population					
	Coastal Road, Belize (n= 48)	Monkey Bay Wildlife Sanctuary, Belize (n= 93)	Western Highway, Belize (n= 11)	Southern Everglades, U.S.A. (n= 27)	Overall Average	Garden individuals
Ramet circum. (cm)	22.9 ± 1.6[a]	26.0 ± 17.9[a]	25.6 ± 1.9[a]	29.9 ± 2.8[a]	25.3 ± 13.1	20.0 ± 7.6 [b]
Lamina length (cm)	48.5 ± 5.5[a]	53.2 ± 7.9 [b]	51.8 ± 10.3 [a]	48.6 ± 7.4[a]	51.1 ± 7.9	54.5± 6.5 [c]
Lamina width (cm)	66.1 ± 9.0[a]	74.6 ± 13.5[b]	73.3 ± 15.5[a]	68.4 ± 15.2[a]	71.2 ± 13.4	82.1 ± 12.8 [c]
No. pinnae	37 ± 3[a]	38 ± 5[a]	36 ± 3[a]	36 ± 6[a]	37 ± 5	37 ± 6 [b]
Petiole length (cm)	43.3 ± 39.8[a]	44.1 ± 18.0 [a]	59.8 ± 35.1[b]	52.8 ± 23.3[c]	47.2 ± 28.7	59.5 ± 14.8 [d]
Petiole width (cm)	1.0 ± 0.0[a]	1.1 ± 0.9[a]	1.0 ± 0.0[a]	1.1 ± 0.1[a]	1.1 ± 0.1	1.3 ± 0.2 [a]

Table 3: Average ramet circumference and leaf morphological variables for light, fire and habit within populations (A, Coastal Road; B, Monkey Bay; C, Western Highway; D, Southern Everglades). Different letters to the right of the value indicate that these means differed significantly (ANOVA $p<0.05$). C= circumference (cm); LL= lamina length (cm); LW= lamina width (cm); No. p = number of pinnae (count); PL= petiole length (cm); PW= petiole width (cm).

A. **CR**	LIGHT	FIRE		HABIT	
	full	fire	no fire	clumping	solitary
C (cm)	22.9 ± 1.6	22.1 ± 1.6 [a]	23.4 ± 1.5 [a]	22.9 ± 1.6 [a]	23.2 ± 1.3 [a]
LL (cm)	48.5 ± 5.5	47.7 ± 4.7 [a]	48.4 ± 5.9 [a]	48.3 ± 5.5 [a]	50.2 ± 6.1 [a]
LW (cm)	66.1 ± 9.1	61.8 ± 5.0 [a]	66.1 ± 7.8 [b]	64.9 ± 7.1 [a]	74.2 ± 16.1 [a]
No. P	37 ± 3	37 ± 4 [a]	36 ± 3 [a]	37 ± 3 [a]	40 ± 3 [a]
PL (cm)	43.3 ± 4.0	18.8 ± 31.1 [a]	45.5 ± 44.6 [b]	42.6 ± 42.3 [a]	47.6 ± 14.4 [a]
PW (cm)	1.0 ± 0.0	1.0 ± 0.0 [a]	1.0 ± 0.0 [a]	1.0 ± 0.0 [a]	1.0 ± 0.0 [a]

B. **MB**	LIGHT	FIRE		HABIT	
	full	fire	no fire	clumping	solitary
C (cm)	26.0 ± 17.9	23.2 ± 1.1 [a]	26.2 ± 19.0 [a]	26 ± 18.1 [a]	28 ± 0.0 [a]
LL (cm)	52.1 ± 8.2	46.1 ± 9.1 [a]	52.6 ± 8.2 [b]	52.3 ± 8.2 [a]	44.7 ± 0.7 [a]
LW (cm)	73.1 ± 13.8	63.3 ± 10.4 [a]	74.2 ± 13.8 [b]	73.4 ± 13.7 [a]	56.3 ± 9.8 [a]
No. P	38 ± 5	36 ± 6 [a]	38 ± 5 [a]	38 ± 5 [a]	36 ± 1 [a]
PL (cm)	44.7 ± 22.4	27.1 ± 5.3 [a]	46.5 ± 23.0 [b]	45.0 ± 22.6 [a]	30.4 ± 9.6 [a]
PW (cm)	1.1 ± 0.1	1.0 ± 0.1 [a]	1.1 ± 0.1 [a]	1.1 ± 0.1 [a]	1.0 ± 0.0 [a]

C. **NH**	LIGHT		FIRE		HABIT	
	full	shade	fire	no fire	clumping	solitary
C (cm)	28.0 ± 0.0 [a]	24.8 ± 1.3 [a]	28.0 ± 0 [a]	24.7 ± 1.3 [a]	25.7 ±2.4 [a]	25.5 ± 0.6 [a]
LL (cm)	62.6 ± 5.9 [a]	60.6 ± 8.0 [a]	62.6 ± 5.9 [a]	60.6 ± 8.0 [a]	58.2 ± 6.4 [a]	67.5 ± 3.1 [a]
LW (cm)	85.1 ± 8.0 [a]	88.3 ± 5.4 [a]	85.0 ± 8.0 [a]	90.5 ± 15.0 [b]	84.5 ± 5.9 [a]	92.1 ± 2.5 [a]
No. P	39 ± 1 [a]	35 ± 2 [a]	39 ± 1 [a]	35 ± 2 [a]	36 ± 3 [a]	36 ± 2 [a]
PL (cm)	63.8 ± 13.7 [a]	82.1 ± 10.4 [b]	63.8 ± 13.7 [a]	82.1 ± 10.3 [b]	71.0 ± 13.2 [a]	86.0 ± 11.5 [a]
PW (cm)	1.1 ± 0.1 [a]	1.0 ± 0.0 [a]	1.1 ± 0.1 [a]	1.0 ± 0.0 [a]	1.1 ± 0.1 [a]	1.0 ± 0.0 [a]

D. FL	LIGHT		FIRE	HABIT	
	full	shade	no fire	clumping	solitary
C (cm)	26.3 ± 1.9 [a]	27.8 ± 3.7 [a]	26.9 ± 2.8 [a]	26.7 ± 2.7 [a]	28.5 ± 4.4 [a]
LL (cm)	47.3 ± 8.8 [a]	50.6 ± 4.0 [a]	48.6 ± 7.4 [a]	48.4 ± 7.5 [a]	50.3 ± 7.0 [a]
LW (cm)	65.8 ± 18.6 [a]	72.1 ± 7.6 [b]	68.4 ± 15.2 [a]	68.1 ± 15.6 [a]	70.1 ± 13.8 [a]
No. P	35 ± 6 [a]	37 ± 5 [a]	36 ± 6 [a]	36 ± 6 [a]	33 ± 6 [a]
PL (cm)	48.2 ± 19.8 [a]	59.5 ± 27.2 [b]	52.3 ± 23.3 [a]	55.2 ± 21.2 [a]	33.1 ± 34.7 [a]
PW (cm)	1.1 ± 0.1 [a]	1.2 ± 0.1 [a]	1.2 ± 0.1 [a]	1.2 ± 0.2 [a]	1.2 ± 0.0 [a]

Table 4: Number of ramets and average circumference of outermost tier based on number of tiers for each wild population and garden-cultivated individuals (data from Edelman, Chapter 2).

Population		**No. tiers**			
		1	2	3	4
Coastal Road, Belize (n=30)	No. ramets	1 ± 0	2 ± 1	8 ± 6	21 ± 8
	Circumference	2.7 ± 1.0 m	9.1 ±7.7 m	16.4 ± 7.1 m	20.5 ± 3.8 m
Monkey Bay Wildlife Sanctuary, Belize (n=36)	No. ramets	1 ± 1	4 ± 4	12 ± 12	25 ± 20
	Circumference	2.2 ± 1.3 m	4.0 ± 3.0 m	9.0 ± 6.5 m	12.1 ± 19.7 m
Western Highway, Belize (n=7)	No. ramets	1 ± 0	2 ± 1	n/a	6 ± 0
	Circumference	1.0 ± 0 m	3.0 ± 2 m	n/a	4.51 ± 0 m
Southern Everglades, USA (n=14)	No. ramets	n/a	4 ± 4	5 ± 2	9 ± 4
	Circumference	n/a	6.7 ± 2.2 m	4.3 ± 1.3 m	7.9 ± 1.9 m
Garden-cultivated, Miami, USA (n=37)	*No. ramets*	*1 ± 1*	*2 ± 1*	*6 ± 1*	*10*
	Circumference	*0.83 m*	*2.56 m*	*3.17 m*	*3.82 m*

FIGURES:

Fig. 1*: Acoelorrhaphe wrightii* is found naturally as a (A) single-stemmed (solitary) or (B) multiple-stemmed (clumping) individual.

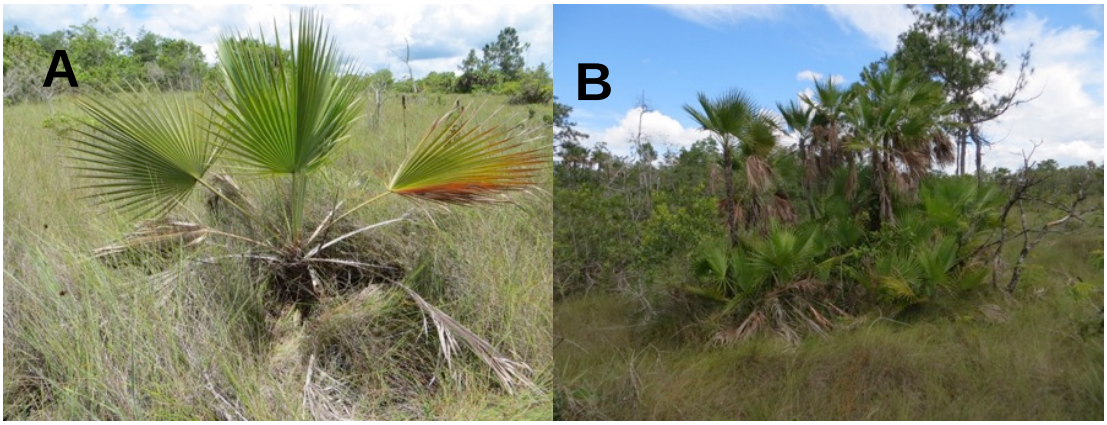


Fig. 2: Range of *Acoelorrhaphe wrightii* highlighted in green. Populations visited marked with icon (Google Earth).

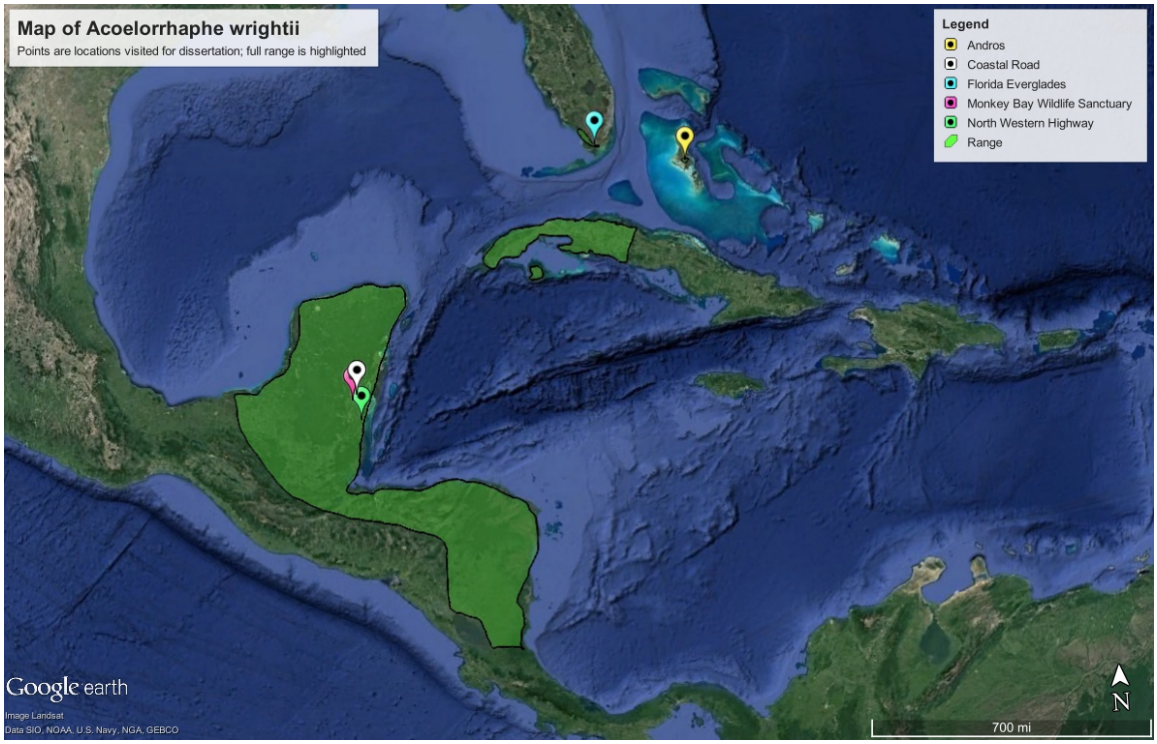


Fig. 3: Fire interval assigned based on fire evidence. Fire (A): evidence of fire on rhizomes, stems and 3 newest leaves and (B): evidence of fire on rhizomes and stems but canopy has returned to normal. No fire (C): no evidence of fire on stem or rhizome.

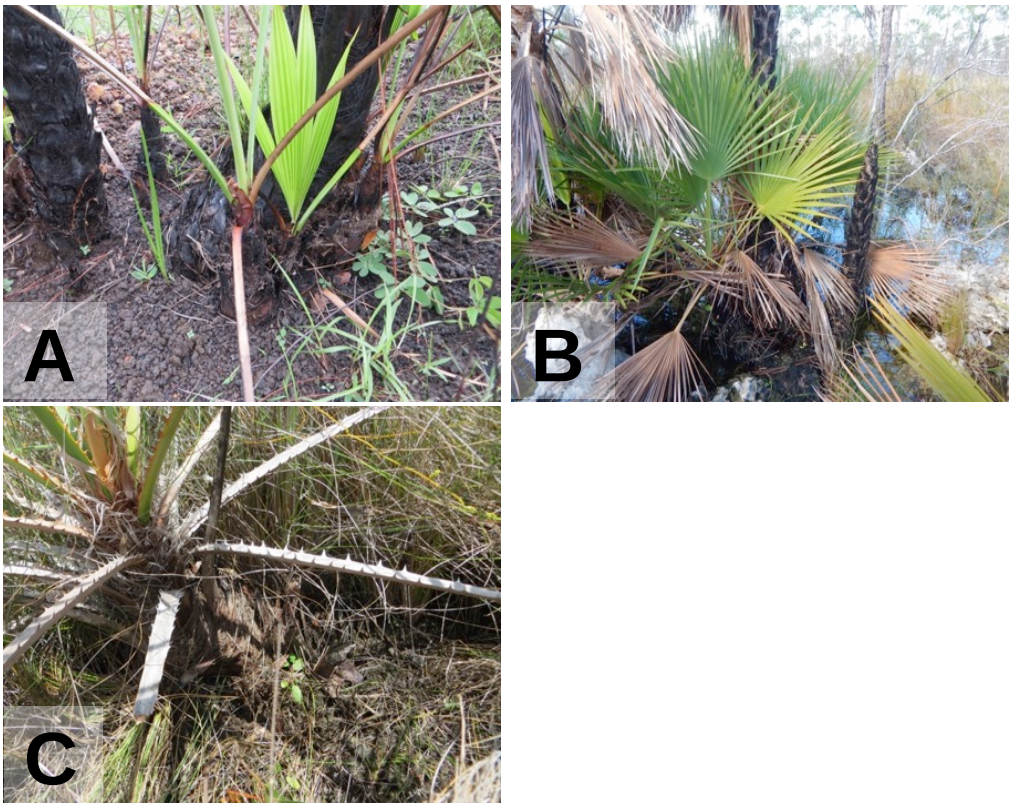


Fig. 4: The relationship of **(A)** the circumference for genets with different numbers of tiers and **(B)** the number of ramets for genets with different numbers of tiers for all wild populations.

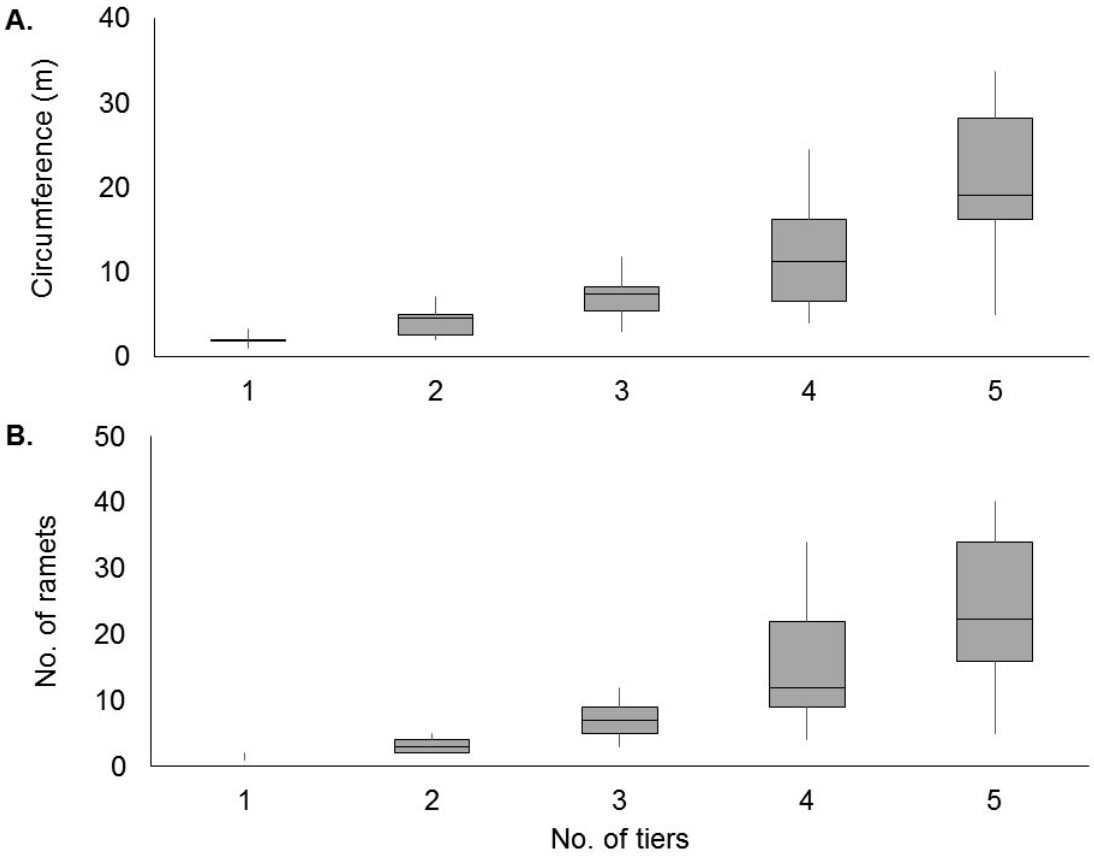


Fig. 5: The relationship of **(A)** the circumference for genets with different numbers of tiers and **(B)** the number of ramets for genets with different numbers of tiers for all wild populations, separated by population.

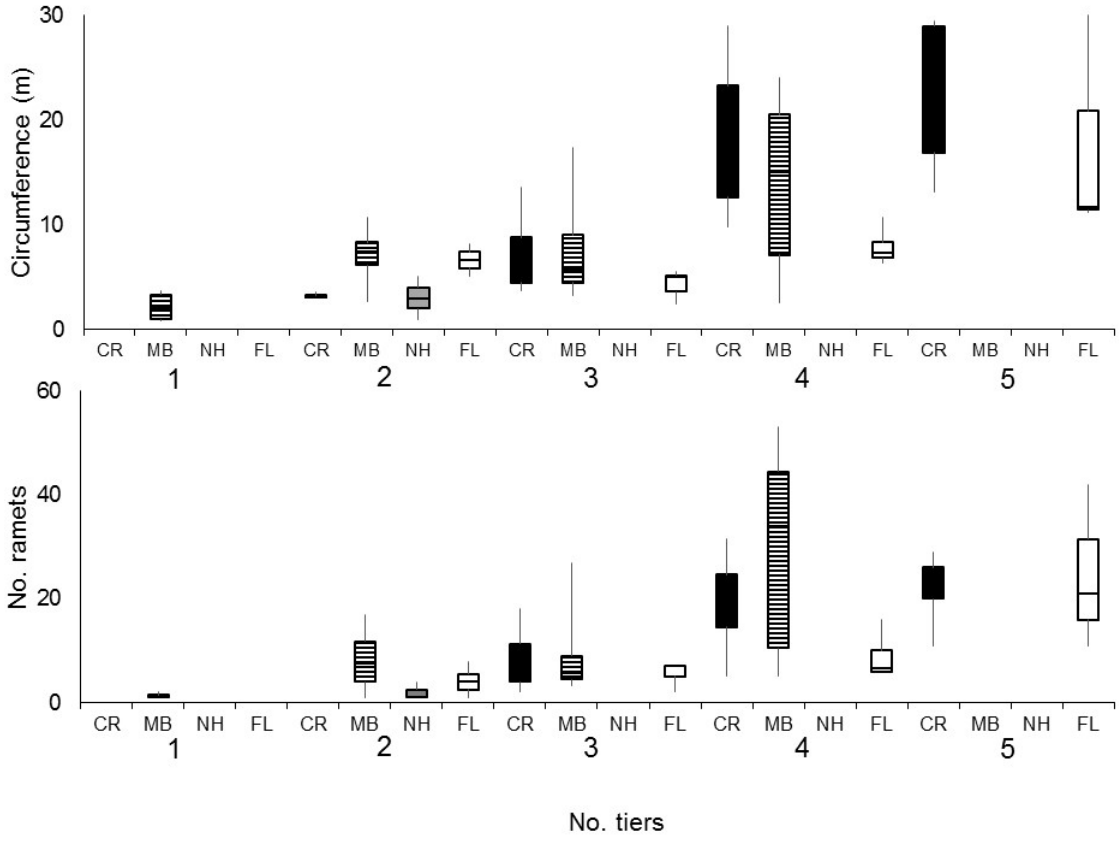
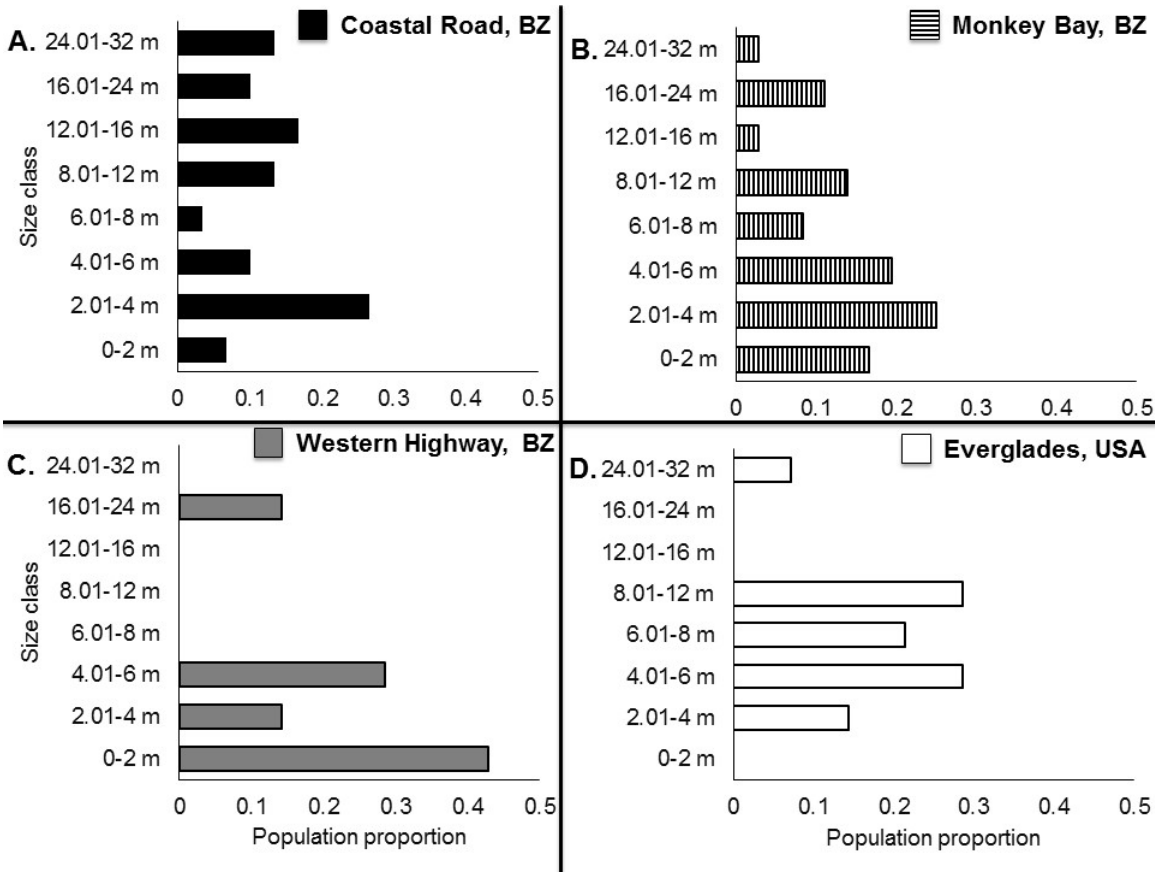


Fig. 6: Distribution of population size classes for each population sampled, showing the proportion of the population in each size class within populations, and differences of overall population structure among populations: (A) Coastal Road population, (B) Monkey Bay Wildlife population, (C) North Western Highway population and (D) Southern Everglades population.



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CONCLUSIONS

Palms provide valuable commercial resources in the tropics and subtropics and are dominant species in tropical lowland forests. (Stiegel et al., 2011; Svenning et al., 2008). Multi-stemmed palms (clonal palms) are particularly important economically in local communities in the tropics where they are used for palm heart and rattan production (Balick 1990; Dransfield et al., 2008). While general biology and ecology of palms is well studied, there are gaps in the literature on the growth, morphology, and effects of environment on clonal palms (Tomlinson, 1990).

Understanding growth of clonal palms requires knowledge about branching in palms. In chapter I, I developed a comprehensive classification scheme that provides a clear description of branching types present in the palms. Branching types from 1903 species from all 181 genera were described and classified. Five branching types were present in the palms: lateral axillary branching, shoot apical division, false vivipary, abaxial branching and leaf-opposed branching. Most species exhibit no vegetative branching (1043 species) and produce solitary individuals. Lateral axillary branching was the most common branching type, found in 646 species. Lateral axillary branching and shoot apical division were predicted to be the earliest evolved branching types and were distributed throughout the palms. Due to differences in phylogenetic distributions, I concluded that the branching types have different evolutionary histories, and it is likely that the solitary habit is more common now than when the palms initially diverged from commelinid relatives.

In chapter II, I described the morphology and architecture of the Florida threatened clonal palm *A. wrightii*. Ramets displayed an establishment period from inception to 0.3 m ramet height. Plant growth varied seasonally in both establishing and

established phases, with greater leaf production in the warmer, wet season and less in the cooler, dry season. Clonal architectural was modeled as the number of established ramets in a genet, using an exponential model that depends on number of ramet tiers, the number of ramets, and their survivorship.

In chapter III, I analyzed how water and light influence germination and juvenile morphology and branching. I found that full sun and saturated soil yielded juvenile plants with a greater number of leaves, more root mass and more branches. The results of this study suggested that while *A. wrightii* is commonly found in flooded areas, it requires a dry down in order to successfully recruit, and it produces more vegetative branches in environments with high light and low water levels.

In chapter IV, I compared morphology, architecture and population structure of adult individuals in four populations in Belize and Florida. Leaf morphology differed among populations and between fire intervals, light regime and elevation. Clonal architecture differed among populations and elevation. However, differences in average values between populations, light and fire regimes were not great, suggesting that leaf morphology and clonal architecture were not highly variable across the geographic range of *A. wrightii*. Population distributions, measured by size class distribution, differed among populations, suggest that population dynamics can vary greatly among populations.

Combining results from all chapters shows how *A. wrightii* grows throughout its lifestages and how environment influences architecture and morphology of *A. wrightii* through those life stages. Specifically, water level is an important determining factor of growth and architecture in all life stages. Therefore, the distruption of natural water levels, as in the Everglades, threatens growth of *A. wrightii*. These results will guide

Everglades decision makers in water management in order to protect this threatened species.

These results also filled a void in palm literature on palm demography and life history. Palms are long-lived and hard to study because of their slow growth. There are few studies that follow palm species from germination through adult growth. By taking a life stage perspective, in a short time I studied growth from germination, to juvenile, to young adult to mature adult life history stages. This dissertation provides a model for how other palm biologists could do similar demographic work. I captured many stages of life history using botanical garden resources, nursery plants and wild individuals. The life stage approach used here provided new data on *A. wrightii* and palm growth in a relatively short time and established a model for conducting these types of life history studies in large, slow-growing species such as the palms.

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