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Morphology and architecture of the threatened Florida palm Acoelorrhaphe wrightii (Arecaceae: Coryphoideae)

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Abstract

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Rhizomatous palms are economically and ecologically important, but few studies on their growth and architecture have been published. The purpose of this study was to describe morphology, growth and architecture of *Acoelorrhaphe wrightii* (Griseb. & H. Wendl.) Becc. *(Arecaceae: Coryphoideae),* a rhizomatous circum-Caribbean wetland palm. The study was conducted on cultivated individuals at two botanical gardens in Florida, USA. Leaf morphology, stem height and circumference, lamina length, width and pinna number, and petiole length and width were measured on 2 ramets of 16 genets. Ramet growth rates were determined by recording leaf production per ramet every 3 months for 2 years on 2 ramets of 38 genets. Genet circumference, diameter, and number of ramet tiers, plus number of living ramets > 0.5 m, were measured on 41 genets. Ramets have an establishment period from inception to 0.3 m ramet height. This establishment phase is reflected in leaf morphology, leaf production and rhizome growth. Plant growth varies seasonally, with greater leaf production in the warmer wet season and less in the cooler dry season. Clonal architecture was consistent across gardens and populations. This study quantifies growth and the architectural potential for this species and highlights the importance of botanical gardens for research on long-lived, slow-growing species such as many palms.

Keywords

ARECACEAE – *Acoelorrhaphe* – Clonal growth – Leaf production – Ramet – Genet

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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 et al., 2004; Rodríguez-Buriticá et al., 2005; Endress et al., 2006; Portela et al., 2010). Slow growing plants are a permanent challege for structural biological studies and the use of living collections are an important resource in order to explore developmental questions. As a result, the diversity of palm morphology and architecture is not well understood.

The architecture of multi-stemmed palm individuals, in particular, is not well described, even though the multi-stemmed habit is present in many palm genera (Dransfield et al., 2008; Edelman & Richards, submitted). There are two commonly-used architectural models that describe the multi-stemmed palm habit (Tomlinson, 1990; Henderson et al., 1995; Henderson, 2002; Dransfield et al., 2008): (1) the caespitose habit is created from basal node branching where new ramets immediately grow upward, producing closely-spaced vertical stems; and (2) the colonial habit 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 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.) Becc., paurotis palm, is a clonal coryphoid palm that grows in wetland habits around the coastal Caribbean basin (southern Florida, western Cuba, Caribbean coast from Mexico to northern Costa Rica, and Andros and New Providence islands in the Bahamas) (Henderson et al., 1995). Paurotis is economically important in Central America, where its stems are used for timber and its fruits for medicines, similar to the closely-related species *Serenoa repens* (W. Bartram) Small (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 due to changes in water level and habitat loss (USDA, 2017).

Acoelorrhaphe wrightii has a combination of basal node branching and rhizomatous growth that produces an unusual palm architecture of rounded clonal stands (Henderson et al., 1995). Despite this morphological complexity and its economic and ecological importance, no morphological or demographic studies have been conducted on *A. wrightii*, and only a handful of horticultural studies have been published (Broschat, 2005, 2011). The goal of this 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 close to its natural habitat, 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

This 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 and experience similar weather conditions.

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 (MBC: 2001-1198, 2001-1199, 2001-1200, 99717, 99722, RM1395; FTBG: 2001-0485, 2001-0486, 84384). 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 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 (November 2012 to November 2014) on two ramets per genet for 38 genets (76 ramets total) from Belize (24 plants) and Florida (14 plants); genets 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 3 months for 2 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 most recently matured leaf was tagged so that measurements could be repeated three months later. Internode length the length between leaf nodes, was calculated as the difference 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. This 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; 2 or 3 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 leaf blade 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. Leaf blade length was measured from the point of petiole attachment (*A. wrightii* has a reduced leaf sheath) 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 this 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 we designated 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 (4 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. 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 with a BQM Apogee quantum meter (Apogee Instruments, Inc., Logan, UT). Four light measurements were taken at cardinal directions on the outside perimeter of each individual at around noon and averaged. Individuals with average measurements < 500 μmol $m^{-2}s^{-2}$ were classified as growing in shade, while those with > 500 μmol $m^{-2}s^{-2}$ were classified as growing in sun.

Circumference, number of ramets, and number of tiers were found 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 correlations were examined for each genet growing in full sun aged 13-15 years: circumference versus number of ramets; circumference versus number of tiers; and number of tiers versus number of ramets.

Statistical analyses were done in the R statistical environment (RStudio, 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). ANOVA tests were used to analyze 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). T-tests were used to analyze differences in growth rates and architectural relationships between populations. Exponential regressions were reported instead of linear regression based on higher R^2 values for the exponential models.

Modeling clonal growth

Given the clonal growth and tiered architecture of *A. wrightii* individuals, we developed an exponential architectural model in order to better understand the effect of growth rate on number of ramets in a genet and determine growth rate of *A. wrightii* under garden conditions. We started with a basic model of exponential growth to predict number of ramets in a genet by manipulating growth rate, $N_t = N(0) \times R^t$, where N_t = total number of established ramets in a genet with t tiers, N(0) = the number of ramets at initiation and R = growth rate. The variable t = number of tiers, which was equivalent to the number of generations. We set N(0) = one, and t, number of tiers, varied from 1 to 6. We assumed the growth rate (R), was a function of (1) the number of offspring ramets each ramet produced (r), and (2) the survivorship of the offspring ramets (s) (Tilman, 1988). Thus, $R = r \times s$. We also assumed, based on observations of ramet production in the garden clones, 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.

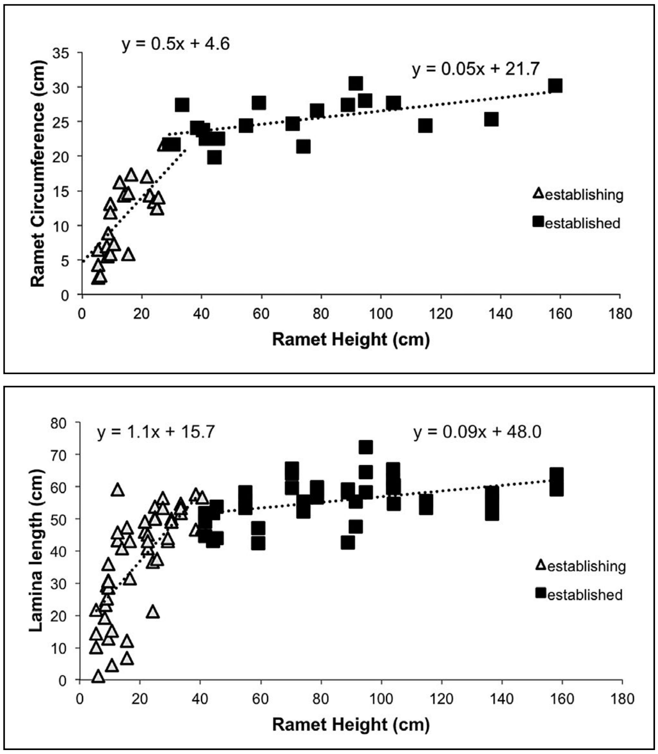

Fig. 1. - *Acoelorrhaphe wrightii* ramet height vs. ramet circumference (**A**) and lamina length (**B**). Left regression equations are for establishing phase (ramet height ≤ 0.3 m), while right regression equations are for established phase (ramet height > 0.3 m).

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

Characters	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)

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 this difference was more dramatic in the summer, as indicated by a significant interaction term (mixed within-between ANOVA, $P < 0.01$).

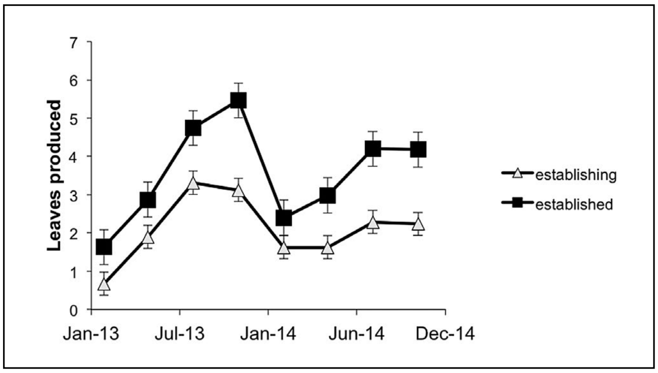

Fig. 2. - *Acoelorrhaphe wrightii* leaf production on ramets of different heights in Fairchild Tropical Botanic Garden and Montgomery Botanical Center plants in Miami FL, measured from Nov. 2012 through Dec. 2014. Data divided into leaves from establishing ramets (ramet height ≤ 0.3 m) and established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

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 (n° pinnae = 0.67 × lamina width + 13.65) than established ramets (n° 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 a single stem that branched rhizomatously to form a clump. 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

Fig. 3. - *Acoelorrhaphe wrightii*. **A.** Absence of the protoclone, which results in empty-centered ring of ramets; **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 through horizontal elongation before turning upward; **D.** Tiers are present in all observed *A. wrightii* individuals and decrease in height from inner to outer tiers. [Photos: S. Edelman]

Table 2. - Parameters for models of clonal growth in *Acoelorrhaphe wrightii*. The model is $N_t = N(0) \times R^t$, 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	81
6	high veg. reprod., high, surv.	6	0.8	4.8	531
	Measured genets				10

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 (d2/d1 = 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, $F_{1\,35} = 53.5$, $P << 0.01$).

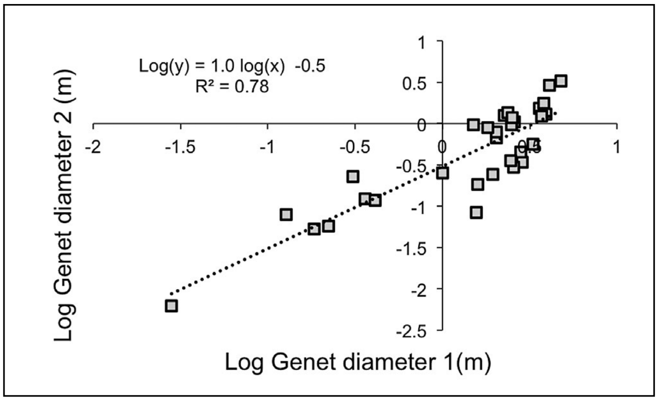

Fig. 4. - Two perpendicular diameters (diam. 1 and 2) for 31 genets of *Acoelorrhaphe wrightii* of different sizes at Fairchild Tropical Botanic Garden and Montgomery Botanical Center plants in Miami FL; data from plants measured in Nov. 2013.

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 that 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 was predicted by the exponential model (Fig. 5C), which predicted 19 ramets for a clone with five tiers.

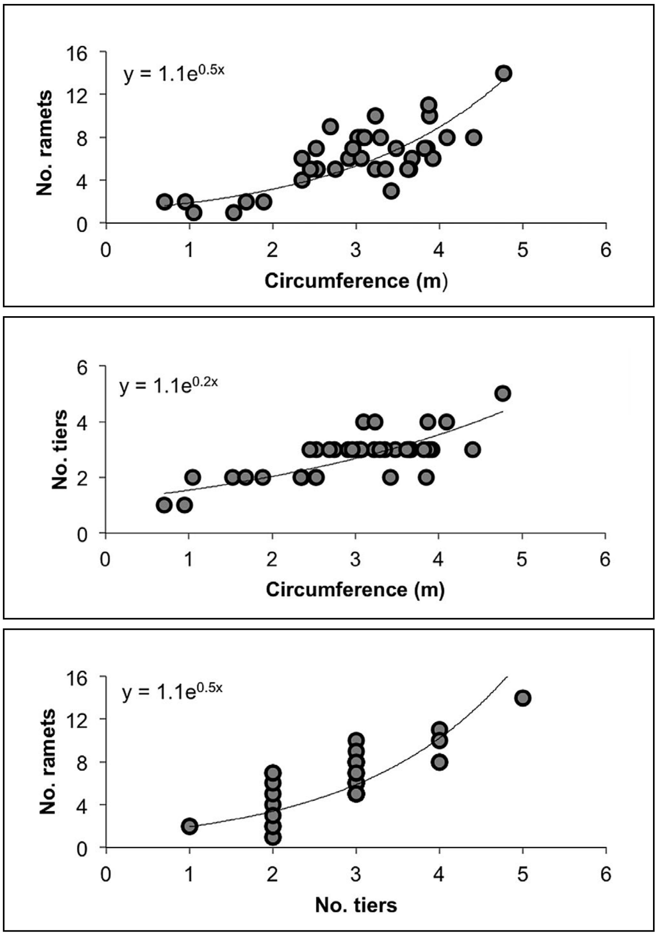

Fig. 5. - Architectural relationships in *Acoelorrhaphe wrightii*. **A.** Number of ramets vs. genet circumference; **B.** Number of tiers vs. circumference; **C.** Number of tiers vs. number of ramets in 31 genets of *A. wrightii* in Fairchild Tropical Botanic Garden and Montgomery Botanical Center plants in Miami FL; data from plants growing in full sun and measured in Nov. 2013.

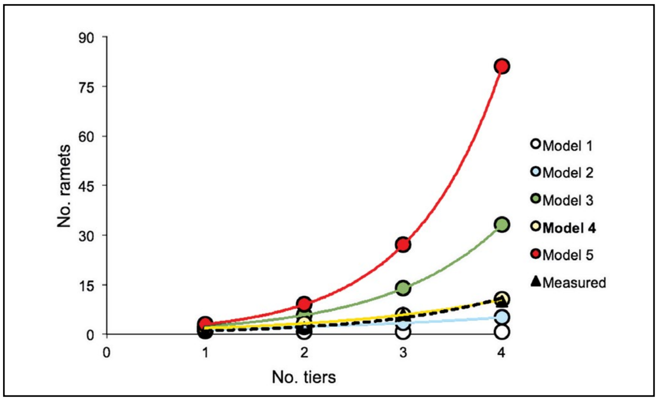

Fig. 6. - Exponential clonal growth model estimations for different growth rates (R), given different levels of reproduction (r) and survival rates (s) for clonal palm, *Acoelorrhaphe wrightii*. Model 1: r = 3, s = 0.3, R = 0.9. Model 2: r = 3, s = 0.5, R = 1.5. Model 3: r = 3, s = 0.8, R = 2.4. Model 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 within 1 ramet.

Discussion

Acoelorrhaphe 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. *Acoelorrhaphe wrightii* ramets have distinct establishing and establishment phases of growth. For this palm, 0.3 m height corresponds with stabilization in leaf scaling, leaf production and ramet circumference; this defines the end of an establishment phase that begins with seed germination or ramet (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 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 establishment phase because prior descriptions of an establishment phase were 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 provides 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 of twelve leaves are produced per year with an average internode length of 2 cm. Therefore we can estimate that a ramet grows about 24 cm a year (12 internodes/year × 2 cm = 24 cm/year). This approximation 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. This is a crude estimation of age since variables used in estimation (leaf production and internode length) were variable by season and height of the ramet. This estimation also does not include the time it takes for a rhizome to begin vertical growth. However, maximum rhizome age can be estimated by the difference between parent and daughter culm age.

The method described above provides a method for estimating integrated annual growth, but we documented differences in growth between seasons. The phenology data show 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 from May to June, fruits develop in July, August and September and fruits mature in October and November in south Florida. 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, while most ramets reproduced vegetatively. This difference suggests 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 in other palms. Deviations from model predictions may give insight into how environmental and field conditions affect clonal growth. Particularly, 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 *A. 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 this palm. 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 (i.e., a 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. While architectural measurements (ramet number, clone size) were not directly related to age, they were related to tier number. In this case, tier number, not age, was a better predictor of the overall size and robustness of the genet.

The architectural model for *A. wrightii*, which uses tier formation as a proxy for time, may be unique to plants such as *A. wrightii* that show episodic growth, but growth of tiers 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; Fisher, 1992; Hill, 1997; Sabatier & Barthelemy, 1999; Tomlinson, 2006; Barthelemy & Caraglio, 2007). The tiers found in these vertical models and architectural analyses are formed by the repeated rotation of aerial branches along a main axis. In Nozeran's architecture model, the apex of the seedling axis produces a tier of horizontally oriented branches and the main shoot apex becomes determinate, then 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).

This study highlights the importance of botanic gardens for studying large, slow-growing species. Having numerous individuals in close proximity and growing under homogeneous ecological conditions 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 this history greatly influences growth and architecture. In the gardens, particularly at MBC and FTBG, careful historical records are kept, so the history of the individual is easily determined and can help in understanding growth. Additionally, the similar "common garden" environment reduces variation. The knowledge gained from this type of study provides a baseline description of growth that can then inform field studies.

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