

**ALLOMETRY AND STILT ROOT STRUCTURE OF THE NEOTROPICAL  
PALM *EUTERPE PRECATORIA* (ARECACEAE) ACROSS SITES  
AND SUCCESSIONAL STAGES<sup>1</sup>**

GERARDO AVALOS<sup>2–4</sup> AND MAURICIO FERNÁNDEZ OTÁROLA<sup>2,5</sup>

<sup>2</sup>Escuela de Biología, Universidad de Costa Rica, 2060 San Pedro, San José, Costa Rica; and <sup>3</sup>The School for Field Studies, Center for Sustainable Development Studies, 10 Federal St., Salem, Massachusetts 01970 USA

The lack of secondary meristems shapes allometric relationships of the palms, influencing species segregation according to their capacity to adjust form and function to spatial and temporal changes in environmental conditions. We examined the stem height vs. diameter allometry of *Euterpe precatoria* across environmental gradients and measured how terrain inclination and palm size affected stilt root structure at two sites in Costa Rica. We dissected the root cone into eight variables and used principal component analysis to summarize their correlation structure. The fit of the stem diameter–height relationship to the stress, elastic, and geometric similarity models was examined using data from 438 palms. Terrain inclination did not affect stilt roots, whose structure was determined by palm size. Palms under 1 m showed geometric similarity, whereas palms above 1 m had slope values that were one and a half times higher, independent of successional stage, and did not adjust to any mechanical model. Taller palms departed from these models when they were large because they had stilt root support. We conclude that height in *E. precatoria* is constrained by structural support at the base and that diameter at the base of the stem and stilt roots balances height increments over all the size ranges examined.

**Key words:** allometry; Arecaceae; Costa Rica; *Euterpe precatoria*; mechanical stability; palm growth; stilt root structure; tree architecture.

The analysis of the adaptive significance of size-correlated variation in plant structure remains an essential tool for understanding the physiological and ecological basis of plant performance because structure is intrinsically coupled with function. Allometric analyses examine size-correlated variations in plant form and processes, projecting the structure–function relationship over time as the different parts of an organism modify its performance through growth and development (Niklas, 1994). Different allometric strategies have strong ecological and evolutionary impacts because growth and competitive ability are clearly related to changes in allometric relationships (Küppers, 1994; Valladares and Niinemets, 2007).

In palms, the lack of secondary meristems shapes allometric relationships, influencing their strategies for habitat colonization and resource access (Tomlinson, 1979, 1990, 2006). The

distribution and abundance of palms are indicative of fine shifts in environmental heterogeneity (Kahn and de Castro, 1985; Clark et al., 1995; Svenning, 1999, 2001, 2002; Vormisto, 2002; Vormisto et al., 2004). In arborescent palms, adaptation to environmental gradients is constrained by their ability to adjust their allometric relationships to increase in height and provide crown support while maintaining structural stability (Lieberman et al., 1988; de Carvalho et al., 1999; Terborgh and Davenport, 2001). Niche differences in habitat selection should be reflected in distinctive allometric strategies, segregating species according to their flexibility to respond to current environmental conditions while adjusting form and function in the face of temporal changes in resource distribution (Kohyama, 1987; Canham, 1988; King, 1990). It is critical to understand how an allometric strategy integrates the overall adjustment of palms to different spatial and temporal changes in resource conditions.

Here, we analyze the allometry of stem diameter and stem height in the neotropical palm *Euterpe precatoria* Mart. (Arecaceae) by examining its adjustment to the three scaling models proposed by McMahon and Kronauer (1976) and discussed by Rich et al. (1986) and Niklas (1994): stress, elastic, and geometric similarity. These models assume that the properties of the material (such as wood density and Young's modulus of elasticity) are independent of size and isometric in nature because mass and volume maintain a constant relationship along the height of the stem. This assumption is not necessarily true because the mechanical properties of woody plants change with age and size, as do the scaling relationships of diameter and height. Our primary goals were (1) to determine how closely the structure of *E. precatoria* matches the assumptions of these models, (2) whether it transitions between models as it increases in size, presuming an isometric relationship between mass and volume across different ontogenetic stages, and (3) to establish whether the adjustment is affected by environmental

<sup>1</sup> Manuscript received 25 May 2009; revision accepted 30 November 2009.

The authors thank A. Williams, L. Glockner, and the students and staff of the School for Field Studies for their help during fieldwork and the park rangers of Quebrada González (C. Mora, P. Ezeta-Salicetti, and S. Barquero) and the staff of La Selva for logistical support. Comments by J. Fisher significantly improved the manuscript. M.F.O. was supported by the REU Scholarship Program of the Organization for Tropical Studies (OTS) with CRUSA Foundation financial support and by an OTS Research Fellowship (Don and Beverly Stone Fund). This research was supported by the Directorate of Research of the University of Costa Rica project number 111-A3-129 and the School for Field Studies. Ideawild provided part of the field equipment. The authors thank G. Jiménez (Ministry of the Environment) for endorsing fieldwork in Braulio Carrillo.

<sup>4</sup> Author for correspondence (e-mail: faetornis@yahoo.com)

<sup>5</sup> Present address: Departamento de Genética e Evolução, Instituto de Biologia, Universidade Estadual de Campinas (UNICAMP) 13083-970, CP 6109, Campinas, São Paulo, Brazil

conditions. Because mechanical properties change with age, neighborhood effects, and light conditions (Henry and Aarssen, 1999), it is reasonable to expect *E. precatoria* to traverse a series of models as it goes from different ontogenetic stages and environmental conditions. Previous studies on the height–diameter relationships of tropical canopy trees have shown that most species adjust to the geometric similarity model (i.e., O'Brien et al., 1995; Osunkoya et al., 2007), but data on palm species is still limited (see Rich, 1986, 1987; Rich et al., 1986).

We also analyze the distribution and size of the stilt root cone in *E. precatoria* as influenced by the inclination of the terrain and palm size. Stilt roots facilitate further height increases, enabling resprouting when the palm has been knocked down by falling trees, allowing to grow out of debris accumulation or after a disturbance (Bodley and Benson, 1980; Avalos, 2004). Relatively few palm species have been explored in terms of their stilt root structure (Dransfield, 1978; Schatz et al., 1985; Avalos et al., 2005; Goldsmith and Zahawi, 2007). Because palms are morphologically constrained to increase in height, we expect the structure of stilt roots in *E. precatoria* to scale with palm size, matching stem height, rather than local conditions of topography over a wide range of slope conditions. In this manner, taller palms will have more and taller stilt roots independent of the slope. Understanding the architectural strategy and allometric relations of *E. precatoria* will provide insight for determining how physical limits to morphological diversity influence the distribution, abundance, and evolutionary diversification of tropical plants.

## MATERIALS AND METHODS

**Study sites**—This study was conducted in 2004 and 2005 at Quebrada González in Braulio Carrillo National Park (BCNP) and at La Selva Biological Station, Costa Rica (LSBS). BCNP is situated on the Caribbean side of the Central Mountain Slope (48 000 ha, 10°13'N, 84°37'W, 400–500 m a.s.l. for Quebrada González), at an elevation range of 30–3000 m a.s.l. The forest at this site receives an average of 4095 mm of rain per year and is considered a tropical, premontane rain forest (Holdridge et al., 1971). LSBS is located in Puerto Viejo de Sarapiquí, in the NE Caribbean lowlands of Costa Rica (1600 ha, 10°25'N, 84°00'W, 30–150 m a.s.l.). The area is weakly seasonal, with a mean annual precipitation of 3962 mm and at least 100 mm of rain per month (Sanford et al., 1994).

**Study species**—The neotropical palm *Euterpe precatoria* (Arecaceae) is distributed from sea level to 1150 m a.s.l. from Belize to Bolivia (Henderson et al., 1995), being common in low- and mid-elevation neotropical forests. The solitary stem reaches up to 25 m in height and a diameter at breast height (DBH) of 23 cm. This monoecious species has protandrous inflorescences and is mostly pollinated by beetles and bees (Küchmeister et al., 1997) and dispersed by birds (Galetti and Aleixo, 1998; Henderson, 2002). It benefits from forest disturbances, as well as by intermediate light levels (Poorter, 1999). The density of this species, especially their seedling density, reflects the disturbance level (natural or human-induced), with higher seedling density in places of higher disturbance (Fernández Otárola 2007). In Costa Rica, *E. precatoria* constitutes the major source of illegally harvested heart of palm, with poachers removing up to 300 palms in extraction bouts lasting 2–3 d. The structural disturbance created by the extraction process favors seedling and juvenile growth, increasing the overall abundance of *E. precatoria* at extracted sites (Avalos, 2007).

**General morphology**—*Euterpe precatoria* is commonly described as a single-stemmed, solitary subcanopy palm (Grayum, 2003). Only occasionally is it referred to as rarely clustered or cespitose (Henderson et al., 1995). We have observed that the production of ramets (i.e., new sprouting shoots connected to the genet or mother palm, sensu Harper, 1977), emerging from the base of the stem or from established, mature stilt roots (similar to the related species *E. oleracea*), is relatively common. This is congruent with the phylogenetic relationships of the *Euterpe* clade in which clonality is frequent (Henderson, 2002). *Euterpe precatoria* shows a high degree of morphological plasticity in

the structure and distribution of stilt roots and the types of substrata it can colonize. Tall palms are often rooted on fallen, decomposing logs, as well as the buttresses of dead, snapped-off canopy trees up to 3 m above the ground. Under these conditions, the stilt root cone reaches over 2 m, and the roots that are usually clustered, separate, as in the case of *S. exorrhiza*. Although the phylogeny and classification of palms has experienced recent progress (Asmussen et al., 2006) and the *Euterpe* clade is well known (i.e., Henderson, 2002), a more comprehensive study of this species across its latitudinal range is likely to produce a classification that better reflects this morphological plasticity.

**Measurement of stilt root structure**—For the analysis of stilt root structure, 31 individuals of *E. precatoria* were randomly selected in BCNP, ranging from 0.34 to 20.52 m in stem height. These individuals were located over a wide variety of topographic slope conditions (range = 0°–60°, mean = 12.98° ± 12.14 SD). Congruent with Svenning (1999), we have found that at BCNP *E. precatoria* prefers hill tops and relatively flat topography, in contrast with the results reported by Clark et al. (1995) for LSBS. Therefore, individuals located on very steep sites were less abundant in BCNP (35% were located above moderate inclinations 15° and only 10% were located on steep sites above 24°).

To characterize the structure of the cone of stilt roots, we followed the general methods described by Avalos et al. (2005). For each individual palm, stem height from the ground until the first frond was measured with a Suunto (Vantaa, Finland) clinometer. Stem height was then corrected by subtracting the height of the cone of stilt roots. Stem diameter was measured immediately above the stilt roots in all individuals. The prevalent terrain inclination was measured within a 3-m radius around the trunk. In *E. precatoria*, the trunk is not cylindrical, and diameter decreases gently from the base of the trunk above the stilt roots toward the tip of the stem and the site of production of the first frond in taller individuals.

To measure the structure of the stilt root cone and determine how it was distributed along the terrain inclination, we dissected the cone into eight morphological variables: (a) the width of the root cone perpendicular to the prevalent terrain inclination; (b) the stem diameter immediately above the stilt roots; (c) the horizontal projection of the cone base downhill, and (d) uphill; (e) the height of the tallest root downhill and (f) uphill; and (g) the length of the farthest root downhill (h) and uphill.

**Measurement of the stem allometry**—For analyses of stem allometry, we used morphological data from 192 palms from 30 permanent plots of 15 × 15 m established in BCNP in April 2004 in a primary forest without extraction (Las Palmas trail, 10 plots), a primary forest where illegal extraction took place in 2000 (La Botella trail, 10 plots), and a secondary forest without extraction (El Ceibo trail, 10 plots). Plots were separated by at least 50 m. At Las Palmas, we found only 8 individuals in 10 plots, and thus, we excluded this site from further comparisons of sites differences in stem height vs. diameter relationships. At LSBS, we obtained data from 263 palms established in primary (20 plots) and secondary forests (10 plots) in June 2004. All measured individuals had at least one leaf with a minimum length (from the leaf base to the leaf apex) of 50 cm. Stem height and diameter were measured following the methods described for the stilt root structure. Stem diameter immediately above the stilt roots (DASR), as well as DBH for individuals taller than 1.3 m, were highly correlated ( $r = 0.96$  for BCNP and  $r = 0.88$  for LSBS). Therefore, we used DASR for allometric analyses instead of DBH because this applied to all palms, including those below 1.3 m.

**Analysis of stilt root structure**—We used a principal component analysis (PCA) to summarize the correlation structure of the morphological variables describing stilt root structure (variables a, c, d, e, f, g, and h explained above). These morphological variables were highly correlated (mean  $r = 0.80 \pm 0.13$  SD; Table 1). The scores of the first principal component (the projection of the original variables on the principal component axis) were used as response variables summarizing overall changes in stilt root structure as a function of terrain inclination and stem height using the following stepwise regression:

$$(\text{Prin}_{ijk})^T = \mu + \text{INCLINATION}_i + \text{STEM HEIGHT}_j + \text{DASR}_k + e_{ijk},$$

where  $\text{Prin}_{ijk}$  is the vector of the first principal component transposed (T),  $\mu$  is the grand mean of the scores from all measured palms,  $\text{INCLINATION}_i$  is the deviation from the grand mean due to the effect of the terrain inclination,  $\text{STEM HEIGHT}_j$  is the deviation due to the effect of stem height,  $\text{DASR}_k$  is the deviation due to the effect of DASR, and  $e_{ijk}$  is the deviation due to random error. The scores of the first principal component were transformed following the Box–Cox procedure (Quinn and Keough, 2002) to accommodate for normality and equality of variances before running the stepwise regression. Only one principal component was used because it explained a significant proportion

TABLE 1. Correlation matrix of morphological characters describing stilt root structure in *Euterpe precatoria*.

Morphological character	(a)	(c)	(d)	(e)	(f)	(g)	(h)
Width of cone perpendicular to the prevalent slope (a)	1.00						
Horizontal projection of the base of the cone down the slope (c)	0.93	1.00					
Horizontal projection of the base of the cone up the slope (d)	0.93	0.93	1.00				
Height of roots down the slope (e)	0.87	0.80	0.79	1.00			
Height of roots up the slope (f)	0.64	0.57	0.59	0.84	1.00		
Length of roots down the slope (g)	0.95	0.92	0.89	0.85	0.54	1.00	
Length of roots up the slope (h)	0.89	0.85	0.82	0.84	0.66	0.83	1.00

of the variation (83.8%, eigenvalue = 5.86) in contrast to only 9.5% (eigenvalue < 1; Quinn and Keough, 2002) explained by the second principal component. The loadings of every variable onto the first principal component were very similar (Table 2), and thus, we concluded that this component satisfactorily summarized the relationships among the variables in terms of their effect on the structure of stilt roots.

**Mechanical scaling of palm height**—We examined the adjustment of the allometry of stem diameter and stem height to the three scaling models (stress, elastic, and geometric similarity) proposed by McMahon and Kronauer (1976). These models derive from the observation that the height of record-sized trees is about one-fourth of the height that would cause a uniform cylinder of the same diameter to buckle under its own weight (McMahon, 1973). The stress similarity model assumes that the stem undergoes a constant maximum bending stress throughout its entire height. This assumption requires the height of the stem to scale to the square root of the diameter ( $H \propto D^{1/2}$ ). The elastic similarity model indicates that structures of different sizes have the same margin of safety against mechanical failure (in this case,  $H \propto D^{2/3}$ ). The geometric similarity model represents an alternative hypothesis to the aforementioned models and assumes that structures of different sizes have the same shape, with stem height changing as a simple function of diameter ( $H \propto D$ ). In this case, the scaling component (the slope coefficient in the log-transformed models for the regression between diameter and height) for the three allometric models is 0.5 (stress similarity), 0.67 (elastic similarity), or 1.0 (geometric similarity), respectively. We estimated the value of the slope for the logarithmic regression between diameter and height for palms of different size across sites and successional stages, using ordinary least squares regression (OLS), whose slope estimates were compared to those generated after standardized major axis estimation (SMA), considering that both the predictor (diameter) and the response variables (height) are random and, thus, subject to natural variation and measurement error (Warton et al., 2006). The SMA minimizes the sums of squares of the areas of the triangles formed by the vertical and horizontal lines from each observation point to the line of best fit. SMAs are recommended by Niklas (1994), Legendre and Legendre (1998), Quinn and Keough (2002), and Warton et al. (2006) for the scaling of random allometric variables not under the strict control of the experimenter (i.e., the base 10 logarithm of diameter and height). Seim and Saether (1983) described small differences among OLS and SMA and concluded that the choice depends on the nature of the data and the magnitude of the error variances of the predictor and response variables. The most accurate slope estimate is obtained throughout the SMA, which is less sensitive to extreme observations, differences in scale, and differences in the magnitude of the variables even when the same unit of measurement is used. We used the program PAST PAleontological STatistics, version 1.90 (downloadable at website <http://folk.uio.no/ohammer/past/>) to calculate the SMA coefficients and 95% confidence intervals and JMP 7.0 Statistical Software (SAS Institute, Cary, North Carolina, USA) for all other statistical analyses.

## RESULTS

**Analysis of stilt root structure**—Most *E. precatoria* palms were located on topographic slopes under 30°. Few individuals were found on steeper terrains. There was no relationship between palm height and terrain inclination ( $r^2 = 0.0008$ ,  $N = 57$ ,  $P = 0.83$ ). Accordingly, DASR did not vary with the terrain inclination ( $r^2 = 0.021$ ,  $N = 31$ ,  $P = 0.43$ ). Therefore, inclination did not influence the magnitude of stem height and diameter over the range of topographic slopes considered.

We defined only one principal component, which accounted for 83.8% of the total variation in the data. This component had an almost identical contribution to the seven stilt root variables, and was termed “root cone structure” (Table 2). Results of the stepwise regression showed a strong significant effect of stem height and DASR on the structure of stilt roots (Table 3). The inclusion of terrain inclination did not significantly increase the fit of the model. Stilt root structure was determined by the size of the palm (DASR and stem height), and not by the inclination of the terrain.

**Stem allometry**—Preliminary scatter plots between stem diameter and stem height indicated a major change in the slope of the line of best fit after 1 m in height across all sites and disturbance stages (i.e., proportion of the slope for palms under 1 m relative to that of palms above 1 m; Fig. 1, Table 4). Therefore, we estimated the value of the slope for juveniles (palms under 1 m) and palms above 1 m. These scatter plots indicated relatively homogeneous trend lines within these two groups, with palms taller than 1 m having slope values one and a half times higher than palms below 1 m (Table 4). This pattern was maintained across sites and successional stages (significant differences in the magnitude of the slopes for palms above and below 1 m, one-way ANOVA,  $r^2 = 0.69$ ,  $F_{3,12} = 9.05$ ,  $P < 0.002$ ). We could not distinguish any more groups based on stem vs. diameter relationships for palms above 1 m.

Palms under 1 m approached the geometric similarity model across all sites and successional stages, independently of the method used to estimate the slope (average magnitude of the slope = 1.05, SD = 0.13; Wilcoxon signed rank test showed that the slope was not different from 1,  $P = 0.40$ ; Fig. 1, Table 4). Therefore, height scaled in direct proportion to diameter in palms below 1 m. Slope estimates for palms above 1 m were more variable, but were in general above 1 (average magnitude

TABLE 2. Summary of morphological characters describing stilt root structure measured on 31 individuals of *Euterpe precatoria* in Braulio Carrillo National Park, Costa Rica, and coefficients of the principal component (PC) analysis done on these variables.

Morphological character	Mean (range; SD)	PC 1
Width of cone perpendicular to the prevalent slope, cm (a)	57.32 (9–139.5; 34.26)	0.40
Horizontal projection of the base of the cone down the slope, cm (c)	23.03 (4–63; 16.18)	0.38
Horizontal projection of the base of the cone up the slope, cm (d)	22.74 (1–59; 16.24)	0.38
Height of roots down the slope, cm (e)	43.84 (5–134.5; 33.3)	0.30
Height of roots up the slope, cm (f)	30.26 (5–122; 24.02)	0.38
Length of roots down the slope, cm (g)	24.90 (4–90.5; 18.70)	0.38
Length of roots up the slope, cm (h)	19.51 (11.7–46; 11.7)	0.38
Proportion of variation explained (%)		83.8

TABLE 3. Effects of slope inclination, palm height, and diameter above stilt roots (DASR) on the scores of the first principal component summarizing the variation of seven morphological variables describing the structure of the stilt root cone in *Euterpe precatoria* ( $N = 31$  individuals) in Braulio Carrillo National Park.

Variable	$r^2$	F ratio	P
Slope inclination	0.06	22.31	0.16
Height of stem	0.69	62.88	<0.0001
DASR	0.66	58.13	<0.0001
Slope inclination and height of stem	0.71	33.22	<0.0001
Slope inclination and DASR	0.68	29.68	<0.0001
Height of stem and DASR	0.74	38.99	<0.0001
Slope inclination, height of stem, and DASR	0.75	26.34	<0.0001

of the slope = 1.46, SD = 0.20; Table 4). In this case, the OLS and SMA estimates did not fit any of the similarity models. The slope values obtained from the two methods were in all cases above the values expected from these models, indicating a faster than expected change in stem height per unit of change in diameter for palms above 1 m. We can thus conclude that palms under 1 m adjusted to the geometric similarity model, whereas palms above 1 m did not adjust to the stability models proposed for other woody plants.

DISCUSSION

**Stilt root structure**—Stilt roots provide better support under steep conditions and waterlogged soils (Dransfield, 1978), facilitating root respiration at the same time. They also favor resprouting and palm recovery from mechanical damage after tree falls (Bodley and Benson, 1980), and a rapid elongation of stems and attainment of canopy height (Swaine, 1983). The support provided by stilt roots, combined with the mechanical stability of the trunk in *I. deltoidea*, determines that the main mode of death in this species is to die while still standing. Only 8% of 51 individuals were uprooted, and 45% were snapped off (Gale and Barfod, 1999). Palms that were snapped off were killed by the fall of large canopy trees, indicating that *I. deltoidea* is very strong and has great stability. Massive aerial stilt root cones, developed above the ground at variable heights over the functional set of stilt roots, have been observed in *S. exorrhiza* and *I. deltoidea* (Avalos, 2004), as well as in *E. precatoria* (G. Avalos, personal observation). The capacity to generate a second set of stilt roots reflects the adaptive importance of stilt roots facilitating palm re-emergence out of high detritus accumulation after a physical disturbance.

Similar to what was found by Avalos et al. (2005), the structure and distribution of stilt roots in *E. precatoria* were determined by palm size, not by slope conditions. There was a strong, positive scaling between the morphological characters composing the stilt root cone and palm size. In *E. precatoria*, tissues around the stem periphery increase in strength and stiffness with age and height (Rich et al., 1986; Rich, 1987). It is clear that palms develop complex internal ontogenetic changes in stem mechanical properties as compared to dicotyledonous and conifer trees (Rich, 1987). It is likely that the timing of expression of developmental changes in the stem is affected by resource heterogeneity, as suggested by the diameter vs. height relationship observed in this study, as well as in other palms such as *I. deltoidea* and *S. exorrhiza* (Homeier et al., 2002; Avalos et al., 2005), for which similar heights were achieved by

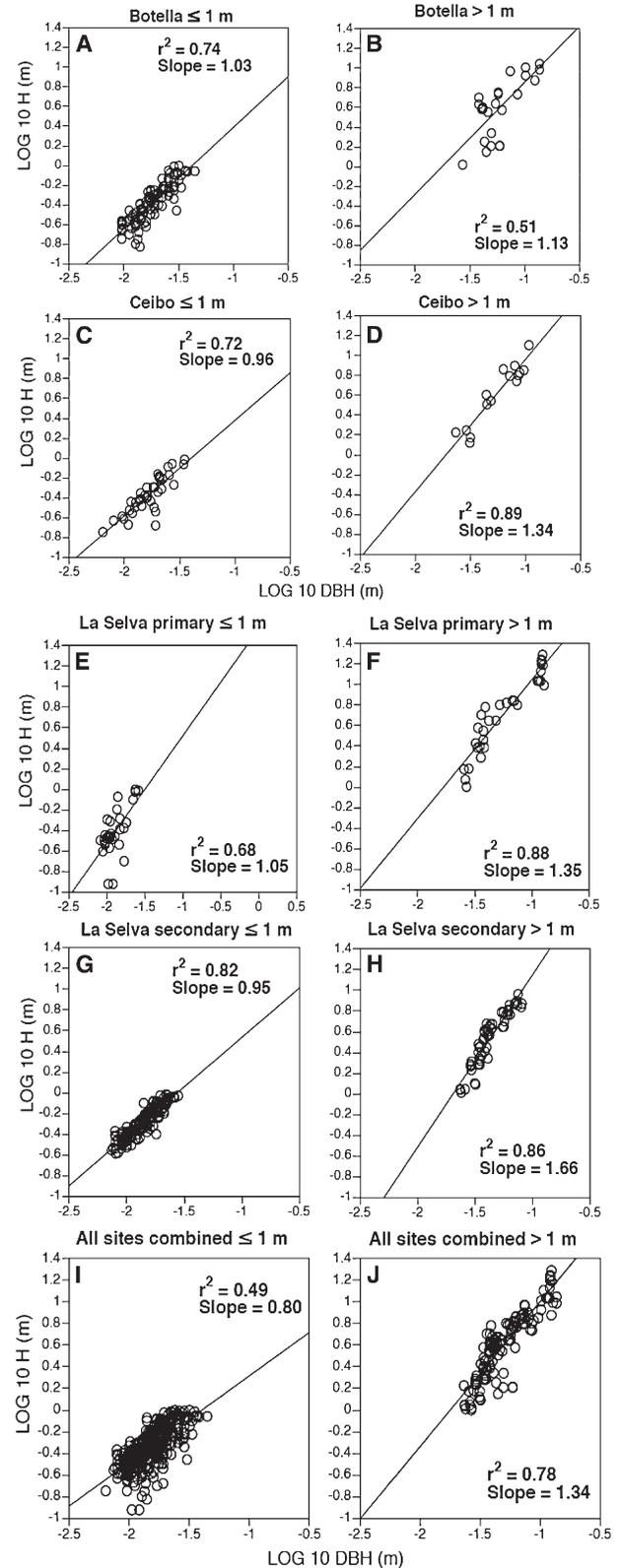


Fig. 1. Scatter plots of the OLS regression analysis of  $\text{Log}_{10}(\text{height})$  vs.  $\text{Log}_{10}(\text{diameter})$  for *Euterpe precatoria* at Braulio Carrillo National Park (Botella and Ceibo trails, A–D), and La Selva Biological Station (Primary and Secondary forests, E–H), and all sites combined (I, J). Diameter for individuals below 1 m was measured above the stilt roots.

TABLE 4. Logarithmic (base 10) ordinary least squares (OLS) regression and standardized major axis (SMA) coefficients (95% confidence interval in parentheses,) obtained for the relationship between palm height and stem diameter in *Euterpe precatoria* for palms above and below 1 m in height at different sites and successional stages.

Site	<i>n</i>	Size (m)	<i>r</i> <sup>2</sup>	OLS slope	SMA slope	SE
Botella (primary forest)	99	≤1	0.74	1.03 (0.91–1.15)	1.2 (1.08–1.33)	0.06
	24	>1	0.51	1.13(0.77–1.47)	1.56 (1.22–2.02)	0.23
Ceibo (secondary forest)	38	≤1	0.72	0.96 (0.54–0.92)	0.88 (0.74–1.00)	0.08
	15	>1	0.89	1.34 (1.09–1.60)	1.41 (1.16–1.67)	0.13
La Selva primary	28	≤1	0.68	1.05 (0.78–1.22)	1.28 (1.08–1.52)	0.14
	32	>1	0.88	1.35 (1.16–1.51)	1.44 (1.26–1.60)	0.08
La Selva secondary	143	≤1	0.82	0.95 (0.88–1.02)	1.05 (0.98–1.12)	0.04
	56	>1	0.86	1.66 (1.51–1.83)	1.8 (1.62–1.97)	0.08
All sites combined	311	≤1	0.49	0.80 (0.73–0.88)	1.14 (1.05–1.25)	0.04
	127	>1	0.78	1.34 (1.22–1.45)	1.51 (1.40–1.63)	0.06

Notes: Expected slope values according to three mechanical stability models: geometric similarity = 1, elastic similarity = 0.67, stress similarity = 0.5; SE = standard error for OLS and SMA estimates

a wide range of diameters. The heterogeneity in resource availability is affecting the mechanical structure of palms at different life stages.

**Stem allometry**—Palm height is limited by the development of enough support for the stem and crown (Waterhouse and Quinn, 1978; Rich et al., 1986; Rich, 1987; Terborgh and Davenport, 2001). Differences in the structure of stems and distribution of tissues are reflected in different diameter vs. height relationships and growth rates (Rich et al., 1986; Rich, 1987). For instance, there was a difference of four orders of magnitude between the diameter of small and very tall palms in *Socratea exorrhiza*, a relatively fast-growing, stilt-rooted palm, in contrast to *Welfia georgii*, a slow-growing palm without stilt roots (Rich et al., 1986).

In contrast to woody plants, which increase their girth through secondary growth, palms increase their mechanical support by maintaining proportionally small-diameter stems composed of schlerenchyma, primary xylem fibers, and parenchyma cells with thick primary walls, which once combined, have very high Young's moduli and density-specific stiffness (Niklas, 1994). Height increases are achieved through developmental changes in tissue composition and distribution (Young's modulus strategy). Further increases in palm height are limited by the ability to accommodate more biomass with limited increases in girth, either by increasing stem diameter, modifying the weight distribution of aerial parts, or exceeding their theoretical buckling heights, assuming that the changes with height in Young's modulus and density-specific stiffness are constant. The final result is a rapid increase in height with relatively small changes in diameter, as observed in the present case.

In *E. precatoria*, palms above 1 m had about one and a half times higher rates of change in height relative to diameter than palms under 1 m, independently of whether the relationship was linear or logarithmic. When all sites were combined, the slope for the log-transformed model for palms above 1 m was one and a half times higher than the slope of palms under 1 m. This relationship was maintained across sites and successional stages, suggesting that the shape of the diameter–height relationship for juveniles and individuals above 1 m is relatively constant, and what varies with the successional gradient is the rate at which a specific height–diameter combination is attained. We observed significantly faster growth rates in individuals above 1 m at BCNP relative to individuals under 1 m over 1 year, especially for individuals established in sites exposed to increased light conditions (Fernández Otárola, 2007). The significant increase in

slope observed after 1 m for both, the OLS and SMA analyses, reflects the overbuilt nature of the stem base (the stem is wider at the base, with the magnitude of stem diameter decreasing gently along the stem as height increases) combined with support provided by stilt roots. The height of *Euterpe precatoria* increases faster than expected relative to its diameter during the adult stages once support at the base of the stem has been secured. When the relationship between stilt roots, stem height, and DASR is considered, it is clear that taller palms depart from these mechanical models when they get large because they have stilt root support. Height in small palms increases slowly relative to diameter. After a height of 1 m, both variables scale in linear fashion one and a half times faster. Similar results have been observed in *E. edulis*, where a shift in diameter vs. height takes place at 1.25 m in height (Alves et al., 2004) and, in *Chamaedorea tepejilote*, between number of leaf scars and height (Oyama, 1993). In this latter case, palms close to 45 cm in height had a smaller slope relative to the number of leaf scars than taller palms, which grew faster despite a significant variation in the number of scars for palms of a wide range of sizes. This evidence suggests an important influence of differences in habitat quality.

Because the quality of the tissues and their distribution changes with height and size over the life span of a plant (Waterhouse and Quinn, 1978; Niklas, 1993, 1995), a population with a varied size class distribution is unlikely to conform to only one mechanical stability model or to the theoretical buckling limit predicted by McMahon (1973). Niklas (1994) criticizes McMahon (1973) on statistical and theoretical grounds. McMahon's analyses of the height–diameter relationship for angiosperms and conifers considered only the maximum height of individuals of a diverse assemblage of species, as reported in the literature. Assumptions about the theoretical buckling limit were limited by the lack of experimental data on the elastic and density properties of the wood tissues in the species considered by McMahon (1973), apart from the lack of information on the ontogenetic changes in material properties, making his analyses merely exploratory. Still, there is a dearth of research on the physical properties and distribution of the tissues that make up the stem of arborescent palms and how these properties change with habitat conditions and stem dimensions, relative to other life forms such as trees, for which data are more comprehensive (see Chave et al., 2005). Since the seminal papers of McMahon (1973) and Rich (1986, 1987), we have progressed little in exploring and extending the answers to this question to other arborescent palm species. A better analysis of the height scaling

in palms must consider the whole span of sizes at all stages represented in a population, along with an examination of the physical strength, stiffness, and distribution of tissues.

In this study, we have shown that in *E. precatoria* palms under 1 m adjusted to the geometric similarity model, whereas palms above 1 m did not fit similarity models developed for other angiosperm groups and conifers. The slopes of the OLS and SMA analyses for palms above 1 m were higher than any of these models could predict. Tall palms are released from the biomechanical constraints considered in these models because they develop secondary thickening growth and have additional support provided by stilt roots. Similarly in an analysis of the height–diameter scaling of *E. edulis*, Alves et al. (2004) did not find a match with the same mechanical stability models considered here. They did not partition their analysis according to differences in slope for palms of different heights, although their data suggests a significant change in slope around a height value of 1 m. The same authors acknowledge a shift in the height vs. diameter relationship after 1.25 m, but did not explore this relationship further. We have observed secondary thickening growth in a range of arborescent palm species, including *Euterpe edulis*, *Prestoea decurrens*, *P. acuminata*, *Iriarteia deltoidea*, and *Socratea exorrhiza*, all stilt-rooted species.

The results observed in this study indicate that growth toward the canopy in arborescent palms is constrained by structural support. Although palms may eventually reach the canopy at variable speed, they will maintain a basic size–shape relationship determined by the support structures that sustain the stem, as well as the crown. Future lines of inquiry should focus on an analysis of the physical properties of tissues along the stem and how they influence diameter–height relationships. The old paradigm of McMahon's buckling limit must be replaced by experimental data specific to plant groups such as palms across different ontogenetic stages. In addition, the ontogenetic development of stilt roots (both below and above the ground) and its relationship with topography, soil characteristics, mycorrhizal associations, and light conditions, still deserves further exploration. Considering the essential structural and functional role of palms in tropical rainforests, the answers to such research questions are long overdue.

#### LITERATURE CITED

- ALVES, L. F., F. R. MARTINS, AND F. A. M. SANTOS. 2004. Allometry of a neotropical palm, *Euterpe edulis* Mart. *Acta Botanica Brasileira* 18: 369–374.
- ASMUSSEN, C. B., J. DRANSFIELD, V. DEICKMANN, A. S. BARFOD, J. C. PINTAUD, AND W. J. BAKER. 2006. A new subfamily classification of the palm family (Arecaceae): evidence from plastid DNA phylogeny. *Botanical Journal of the Linnean Society* 151: 15–38.
- AVALOS, G. 2004. Production of second set of stilt roots in Iriarteoid palms: A solution to the puzzle. *Palms* 48: 83–85.
- AVALOS, G. 2007. Changes in size preference of illegally extracted heart of palm from *Euterpe precatoria* (Arecaceae) in Braulio Carrillo National Park, Costa Rica. *Economic Botany* 61: 96–98.
- AVALOS, G., D. SALAZAR, AND A. ARAYA. 2005. Stilt root structure in the neotropical palms *Iriarteia deltoidea* and *Socratea exorrhiza*. *Biotropica* 37: 44–53.
- BODLEY, J. H., AND F. C. BENSON. 1980. Stilt-root walking by an Iriarteoid palm in the Peruvian Amazon. *Biotropica* 12: 67–71.
- CANHAM, C. D. 1988. Growth and canopy architecture of shade-tolerant trees: Response to canopy gaps. *Ecology* 69: 786–795.
- CHAVE, J., C. ANDALO, S. BROWN, M. A. CAIRNS, J. Q. CHAMBERS, D. EAMUS, H. FOSTER, ET AL. 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* 145: 87–99.
- CLARK, D. A., D. B. CLARK, M. R. SANDOVAL, AND C. M. V. CASTRO. 1995. Edaphic and human effects on landscape-scale distributions of tropical rain forest palms. *Ecology* 76: 2581–2594.
- DE CARVALHO, R. M., F. R. MARTINS, AND F. A. M. SANTOS. 1999. Leaf ecology of pre-reproductive ontogenetic stages of the palm tree *Euterpe edulis* Mart. (Arecaceae). *Annals of Botany* 83: 225–233.
- DRANSFIELD, J. 1978. Growth forms of rain forest palms. In P. T. Tomlinson and M. H. Zimmermann [eds.], *Tropical trees as living systems*, 247–268. Cambridge University Press, New York, New York, USA.
- FERNÁNDEZ OTÁROLA, M. 2007. Análisis demográfico de la palma *Euterpe precatoria* Mart. en la vertiente atlántica de Costa Rica: Efecto de la extracción ilegal en la dinámica poblacional. Master's thesis, Universidad de Costa Rica, San José, Costa Rica.
- GALE, N., AND A. S. BARFOD. 1999. Canopy tree mode of death in a western Ecuadorian rainforest. *Journal of Tropical Ecology* 15: 415–436.
- GALETTI, M., AND A. ALEIXO. 1998. Effects of palm heart harvesting on avian frugivores in the Atlantic rain forest of Brazil. *Journal of Applied Ecology* 35: 286–293.
- GOLDSMITH, G. R., AND R. A. ZAHAWI. 2007. The function of stilt roots in the growth strategy of *Socratea exorrhiza* (Arecaceae) at two neotropical sites. *Revista de Biología Tropical* 55: 787–793.
- GRAYUM, M. H. 2003. Arecaceae. In B. F. Hammel, M. H. Grayum, and N. Zamora [eds.], *Manual de plantas de Costa Rica*, vol. II, 201–293. Missouri Botanical Garden Press, St. Louis, Missouri, USA.
- HARPER, J. L. 1977. *Population biology of plants*. Academic Press, London, UK.
- HENDERSON, A. 2002. *Evolution and ecology of palms*. New York Botanical Garden Press, Bronx, New York, USA.
- HENDERSON, A., G. GALEANO, AND R. BERNAL. 1995. *Field guide to the palms of the Americas*. Princeton University Press, Princeton, New Jersey, USA.
- HENRY, H., AND L. W. AARSEN. 1999. The interpretation of stem diameter–height allometry in trees: Biomechanical constraints, neighbor effects, or biased regressions? *Ecology Letters* 2: 89–97.
- HOLDRIDGE, L. R., W. C. GRECKE, W. H. HATHEWAY, T. LIANG, AND J. A. TOSI. 1971. *Forest environments in tropical life zones: A pilot study*. Oxford University Press, Oxford, UK.
- HOMEIER, J., S. W. BRECKLE, H. DALITZ, C. LEYERS, AND R. ORTIZ. 2002. Demography, spatial distribution, and growth of three arborescent palm species in a tropical premontane rain forest in Costa Rica. *Ecotropica* 8: 239–247.
- KAHN, F., AND A. DE CASTRO. 1985. The palm community in a forest of Central Amazonia, Brazil. *Biotropica* 17: 210–216.
- KING, D. A. 1990. Allometry of saplings and understory trees of a Panamanian rainforest. *Functional Ecology* 4: 27–32.
- KOHYAMA, T. 1987. Significance of architecture and allometry of saplings. *Functional Ecology* 1: 399–404.
- KÜCHMEISTER, H., I. SILBERBAUER-GOTTSBERGER, AND G. GOTTSBERGER. 1997. Flowering, pollination, nectar standing crop, and nectaries of *Euterpe precatoria* (Arecaceae), an Amazonian rain forest palm. *Plant Systematics and Evolution* 206: 71–97.
- KÜPPERS, M. 1994. Canopy gaps: Competitive light interception and economic space filling—A matter of whole-plant allocation. In M. M. Caldwell and R. W. Pearcy [eds.], *Exploitation of environmental heterogeneity by plants: Ecophysiological processes above- and below-ground*, 111–144. Academic Press, New York, New York, USA.
- LEGENDRE, P., AND L. LEGENDRE. 1998. *Numerical ecology*. Elsevier, Amsterdam, Netherlands.
- LIEBERMAN, M., D. LIEBERMAN, AND J. H. VANDERMEER. 1988. Age-size relationships and growth behavior of the palm *Welfia georgii*. *Biotropica* 20: 270–273.
- MCMAHON, T. A. 1973. Size and shape in biology. *Science* 179: 1201–1204.
- MCMAHON, T. A., AND R. E. KRONAUER. 1976. Tree structures: Deducing the principle of mechanical design. *Journal of Theoretical Biology* 59: 443–466.

- NIKLAS, K. J. 1993. Influence of tissue density-specific mechanical properties on the scaling of plant height. *Annals of Botany* 72: 173–179.
- NIKLAS, K. J. 1994. Plant allometry: The scaling of form and process. University of Chicago Press, Chicago, Illinois, USA.
- NIKLAS, K. J. 1995. Plant height and the properties of some herbaceous stems. *Annals of Botany* 75: 133–142.
- O'BRIEN, S. T., S. P. HUBBELL, P. SPIRO, R. CONDIT, AND R. B. FOSTER. 1995. Diameter, height, crown, and age relationships in eight neotropical tree species. *Ecology* 76: 1926–1939.
- OSUNKOYA, O. O., K. OMAR-ALI, N. AMIT, J. DAYAN, D. S. DAUD, AND T. K. SHENG. 2007. Comparative height–crown allometry and mechanical design in 22 tree species of Kuala Belalong rainforests, Brunei, Borneo. *American Journal of Botany* 94: 1951–1962.
- OYAMA, K. 1993. Are age and height correlated in *Chamaedorea tepejilote* (Palmae)? *Journal of Tropical Ecology* 9: 381–385.
- POORTER, L. 1999. Growth responses of 15 rain-forest tree species to a light gradient: The relative importance of morphological and physiological traits. *Functional Ecology* 13: 396–410.
- POORTER, L., F. BONGERS, F. J. STERCK, AND H. WÖLL. 2003. Architecture of 53 rain forest tree species differing in adult stature and shade tolerance. *Ecology* 84: 602–608.
- QUINN, G. P., AND M. J. KEOUGH. 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, UK.
- RICH, P. M. 1986. Mechanical architecture of arborescent rain forest palms. *Principes* 30: 117–131.
- RICH, P. M. 1987. Mechanical structure of the stem of arborescent palms. *Botanical Gazette* 148: 42–50.
- RICH, P. M., K. HELENURM, D. KEARNS, S. R. MORSE, M. W. PALMER, AND L. SHORT. 1986. Height and stem diameter relationships for dicotyledonous trees and arborescent palms of Costa Rican tropical wet forest. *Bulletin of the Torrey Botanical Club* 113: 241–246.
- SANFORD, R. L., P. PAABY, J. C. LUVALL, AND E. PHILLIPS. 1994. Climate, geomorphology, and aquatic systems. In L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn [eds.], *La selva: Ecology and natural history of a neotropical rain forest*, 19–33. University of Chicago Press, Chicago, Illinois, USA.
- SCHATZ, G. E., G. B. WILLIAMSON, C. M. COGSWELL, AND A. C. STERN. 1985. Stilt roots and growth of arboreal palms. *Biotropica* 17: 206–209.
- SEIM, E., AND B. E. SAETHER. 1983. On rethinking allometry: Which regression model to use? *Journal of Theoretical Biology* 104: 161–168.
- SVENNING, J. C. 1999. Microhabitat specialization in a species-rich palm community in Amazonian Ecuador. *Journal of Ecology* 87: 55–65.
- SVENNING, J. C. 2001. On the role of microenvironmental heterogeneity in the ecology and diversification of neotropical rainforest palms (Arecaceae). *Botanical Review* 67: 1–53.
- SVENNING, J. C. 2002. Crown illumination limits the population growth rate of a neotropical understory palm *Geonoma macrostachys*, Arecaceae. *Plant Ecology* 159: 185–199.
- SWAINE, M. D. 1983. Stilt roots and ephemeral germination sites. *Biotropica* 15: 240.
- TERBORGH, J., AND L. DAVENPORT. 2001. Endogenous and exogenous control of leaf morphology in *Iriartea deltoidea*, Palmae. *Journal of Tropical Ecology* 17: 695–703.
- TOMLINSON, P. B. 1979. Systematics and ecology of the Palmae. *Annual Review of Ecology and Systematics* 10: 85–107.
- TOMLINSON, P. B. 1990. The structural biology of palms. Clarendon Press, Oxford, UK.
- TOMLINSON, P. B. 2006. The uniqueness of palms. *Botanical Journal of the Linnean Society* 151: 5–14.
- VALLADARES, F., AND U. NIINEMETS. 2007. The architecture of plant crowns: From design rules to light capture and performance, 101–149. In F. Pugnaire and F. Valladares [eds.], *Functional plant ecology*, 2nd ed. CRC Press, Boca Raton, Florida, USA.
- VORMISTO, J. 2002. Palms as rainforest resources: How evenly are they distributed in Peruvian Amazonia? *Biodiversity and Conservation* 11: 1025–1045.
- VORMISTO, J., H. TUOMISTO, AND J. OKSANEN. 2004. Palm distribution patterns in Amazonian rainforests: What is the role of topographic variation? *Journal of Vegetation Science* 15: 485–494.
- WARTON, D. I., I. J. WRIGHT, D. S. FALSTER, AND M. WESTOBY. 2006. Bivariate line-fitting methods for allometry. *Biological Reviews of the Cambridge Philosophical Society* 81: 259–291.
- WATERHOUSE, J. T., AND C. J. QUINN. 1978. Growth patterns in the stem of the palm *Archontophoenix cunninghamiana*. *Botanical Journal of the Linnean Society* 77: 73–93.