Mechanical Architecture of Arborescent Rain Forest Palms

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ABSTRACT

Mechanical architecture refers to the morphological basis of mechanical support in plants. Ecological and developmental studies of arborescent palms in the lowland rain forest of Costa Rica were focused on the mechanical architecture that enables palms to grow to tree stature and changes in stem structure that accompany height growth. Work centered primarily on *Iriartea gigantea* and *Welfia georgii*, but also included comparisons with other subcanopy and canopy level species: *Socratea durissima, Euterpe macrospadix, Prestoea decurrens,* and *Cryosophila albida*. The project included studies of 1) inter- and intraspecific allometry of stem diameter and height, 2) distribution of specific gravity and elastic modulus within individual stems, 3) developmental anatomy of the stem, 4) biomass distribution, and 5) leaf production and height extension growth rates. Palms have evolved a means for attaining tree stature that is distinct from that of arborescent dicotyledons and conifers. Arborescent palms maintain a margin of safety against elastic buckling during height growth by various combinations of 1) initiation of height growth with a stem diameter that is sufficient for future support requirements, 2) increase in stem diameter by means of sustained cell expansion, and 3) increase in stiffness and strength of stem tissue by means of sustained lignification. *Welfia, Prestoea,* and *Cryosophila* begin height growth with a stem girth that is sufficient to support their maximum heights. *Iriartea, Socratea,* and *Euterpe* have pronounced abilities to increase stem girth by means of sustained cell expansion. All six palm species show dramatic increases in stem strength and stiffness during height growth.

All taxa in the Palmae have woody stems and many palms are arborescent and unbranched above the ground (Moore 1973, Dransfield 1978, Tomlinson 1979, Hallé et al. 1978). Unlike most monocotyledons, many palms are capable of growing to tree stature—to maximum heights of 20, 30, and even greater than 40 meters. How do arborescent palms grow to heights that are comparable with arborescent dicotyledons and conifers? What are the fundamental features of palm stem development and mechanical structure that enable this height growth? I use the term "mechanical architecture" to refer to the morphological basis of mechanical support in plants. The work described here focused on the mechanical architecture of arborescent palms, and particularly on rain forest palms in Costa Rica.

Stem Function and Resource Allocation

At each developmental stage of a plant there are "trade-offs" involving allocation of photosynthates to leaves, roots, stem, and reproductive structures. Cost-benefit models of plants generally assume that photosynthesis, and ultimately reproductive fitness, is maximized over the life of the plant (Givnish 1982, 1984). In this paper I consider stem function and potential costs and benefits of allocation of resources to stem maintenance and growth.

The stem serves the basic functions of mechanical support, and transport and storage of water, nutrients, and photosynthates. Potential benefits of height growth include increased light availability for photosynthesis, overshading of neighboring plants, increased pollination, increased dispersal, positioning of leaves out of reach of ground-dwelling herbivores, reduced risk

of damage by falling branches and large palm leaves, and growth away from festooning vines and lianas. Furthermore, some minimal amount of extension growth may be necessary because of intrinsic morphological constraints. For instance, palms must produce at least some new stem tissue to accommodate leaf attachment and vascular connections, and this in vertical stem axes results in height growth. Concurrent with any benefits of height growth are costs of resources that must be devoted to structural support but do not contribute directly to photosynthesis or reproduction. Increased support requirements during height growth can be met by 1) increases in stem diameter as the result of increase in cell number and/or size and 2) internal increases in stem strength and stiffness. In the absence of increases in stem diameter or increases in tissue strength and stiffness, the margin of safety against mechanical failure will progressively decrease with height growth. At a critical height, a stem without secondary changes will collapse under its own weight. Thus, without secondary changes, stems must be overbuilt initially to provide a sufficient margin of safety.

Developmental Morphology of Palms

New stem and leaf tissue of palms originates from an apical meristem located within the leaf crown. The apical meristem initiates each new leaf within the sheathing leaf base of the next older leaf. A large number of leaf primordia are enclosed within the crown. Each leaf expands in turn at the top of the crown. A single stem internode is associated with each leaf. In general, cell division and differentiation continue in the crown region. Leaves shift in position from the top to the bottom of the crown as new leaves are produced. Thus, tissue is youngest toward the top of the stem and oldest toward the base. Where the leaves abscise cleanly,

leaf scars constitute a record of past leaf production (Corner 1966). Palms lack a vascular cambium in the stem, so the original set of vascular bundles is used for supply and support throughout the life of a palm (Tomlinson 1961, 1964, Tomlinson and Zimmermann 1967). Palm stems consist of a central cylinder of woody tissue and a narrow cortical region. Vascular bundles are distributed throughout the central cylinder, but usually concentrated toward the periphery. Each bundle has a fibrous mechanical sheath, but bundles toward the stem periphery have the most extensive sheaths. Consequently, strength and stiffness are concentrated toward the outer portion of the stem.

Schoute (1912), enlarging on the work of earlier authors, demonstrated that in many palms, stem tissue beneath the crown continues to grow by means of sustained cell expansion. Schoute found wide variation in secondary increase of stem diameter below the crown. Some species show little or no increase and others show marked increases (Table 1). Of 90 species in 9 of the major palm groups, 70% had at least some diameter growth and 14% had very strong growth. No distinct taxonomic trends are apparent from Schoute's data. In Schoute's study, Arecoid, Cocosoid, Caryotoid, and Phoenicoid palms include species across the full range of increase in diameter, from no growth to pronounced growth. On the other hand, species sampled in the Borassoid, Chamaedoreoid, Geonomoid, and Lepidocaryoid groups showed little or no diameter growth. Waterhouse and Quinn (1978) found greater stem girth in taller individuals of *Archontophoenix cunninghamiana*, which they attribute in part to sustained cell expansion during the early stages of height growth and in part to higher survivorship of individuals with bigger stem diameters. Schatz et al. (1985) showed that *Socratea durissima* and *Iriartea gigantea* have marked increases in stem diameter with height, while *Welfia*

Table 1. *Taxonomic distribution of sustained stem thickening in palms.*[a]

Major Group	Number Species Examined	Number Genera Examined	Number of Species by Growth Category (0 = No Growth to 6 = Strong Growth)						
			0	1	2	3	4	5	6
Arecoid	50	24	11	5	5	5	3	9	12
Borassoid	2	1	2	0	0	0	0	0	0
Caryotoid	6	3	0	1	1	1	2	1	0
Chamaedoroid	2	1	2	0	0	0	0	0	0
Cocosoid	10	3	3	6	0	0	1	0	0
Coryphoid	11	7	5	3	1	0	1	0	1
Geonomoid	1	1	1	0	0	0	0	0	0
Lepidocaryoid	5	3	3	2	0	0	0	0	0
Phoenicoid	3	1	0	2	0	0	1	0	0
Total	90	44	27	19	7	6	8	10	13

[a] Adapted from Schoute (1912). Major groups after Moore (1973).

georgii has little or no increase. Sustained cell expansion is the predominant mechanism for stem diameter increase (Schoute 1912, Tomlinson 1961, Wessels Boer 1968, Waterhouse and Quinn 1978), although there may be some cell division in expanding ground parenchyma cells. In addition to sustained cell expansion, cell wall thickness and degree of lignification increase with tissue age, especially in fiber cells (Schoute 1912, Tomlinson 1961).

Mechanical Structure of Palms

Arborescent dicotyledons and conifers are able to compensate for increased structural demands during height growth primarily by increase in diameter as the result of cell division in a lateral cambium. Dicotyledonous trees generally follow a 3/2 power law in which diameter increases with the 3/2 power of height (d $\propto$ h$^{3/2}$) (Greenhill 1881, McMahon 1973, 1975, McMahon and Kronauer 1976, McMahon and Bonner 1983, Rich et al. in press). The 3/2 power law implies that elastic similarity is maintained, meaning that the relative margin of safety against mechanical failure remains constant. To maintain elastic similarity, tall trees have relatively bigger stem diameters for their height than do small trees. By contrast, geometric similarity would be maintained if shape did not change with increase in size. Stem diameter growth is regulated by the ability of trees to modify the rate of cambial cell production, to a certain extent, in response to stress stimuli, with increased stress leading to increased cell division and changes in cell properties (Wilson and Archer 1979). In addition, arborescent dicotyledons and conifers have the ability to reorient and maintain axis orientation by producing reaction wood in response to gravity (Wilson and Archer 1977). Similar mechanisms are not known for arborescent palms. Reaction fibers are known in monocotyledons only for *Xanthorrhoea* (Staff 1974).

The mechanical structure of palms has been little studied, with the exception of stem properties and leaf support in *Cocos nucifera* (Richolson and Swarup 1977, Wainwright et al. 1976, Sudo 1980, Killmann 1983) and leaf support and resource allocation in *Geonoma cuneata* and *Asterogyne martiana* (Chazdon 1984, 1986). Findings for coconut indicate that density, rigidity, and strength of stem tissue increase with age and are greatest at the stem periphery and toward the stem base. These studies suggest that palms undergo appreciable secondary changes in stem mechanical architecture.

Arborescent palms must maintain a margin of safety against mechanical failure of the stem under its own weight, the weight of the crown and reproductive structures, and transient loads from wind and other sources. My research concerned the mechanical architecture that enables palms to grow to tree stature, developmental changes in stem structure that accompany height growth, and the cost of height growth in terms of the stem tissue required to support leaf crowns at different heights. I tested the hypothesis that palms avoid decreases in the margin of safety against elastic buckling during height growth by increasing stem diameter and/or stem tissue strength. Also, I explored whether palms of maximum height and stem diameter are elastically similar and obey the 3/2 power law (McMahon 1973). I characterized changes in the margin of safety against elastic buckling that result from 1) initial development of a stem that is sufficient for future support requirements, 2) changes in stem girth that result from sustained cell expansion, and 3) changes in stem tissue rigidity and strength that result from sustained lignification. I utilized five major approaches in the study of arborescent palms: 1) study of the allometry of stem diameter with height; 2) study of internal physical and mechanical properties of the stem; 3) study of developmental anatomy of the stem; 4) study of weight distribution in the stem and crown; and 5) study of growth rates in natural populations.

Study Site

Research was conducted at La Selva Biological Station in the Atlantic lowlands of northern Costa Rica (10°26′N, 83°59′W). La Selva has a mean rainfall of approximately 4,000 mm and a mean daily temperature of 24° C, and according to the Holdridge Life Zone system is tropical premontane wet forest (Holdridge 1967). La Selva is situated at the confluence of the Rio Sarapiqui and the Rio Puerto Viejo in the rugged foothills of the Cordillera Central (35–200 m elevation). Detailed site descriptions are provided elsewhere for climate, vegetation, and soils (Hartshorn 1983, Lieberman et al. 1985). The La Selva forest, with an estimated flora of more than 1,800 species, is dominated by Pentaclethra macroloba (Leguminosae). Palms, both arborescent and dwarf, are a major component of the forest, with 29 species in 16 genera (Chazdon 1985, Moore and Chazdon 1985). In 12 ha of mapped forest at La Selva, 25% of stems greater than 10 cm DBH were arborescent palms (Lieberman et al. 1985).
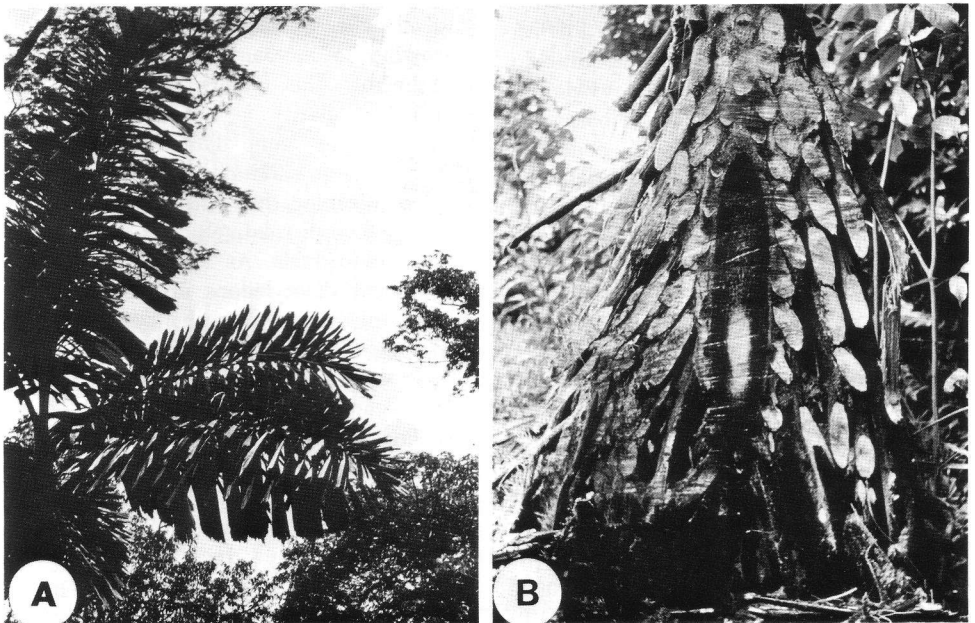
Study Species

Research was focused primarily on two arborescent palm species: Welfia georgii H. A. Wendl. ex Burret (Fig. 1) and Iriartea gigantea H. A. Wendl. ex Burret (Fig. 2). Work also included comparisons with four other sympatric arborescent palms: Socratea durissima (Oerst.) H. A. Wendl. (Fig. 3), Euterpe macrospadix Oerst. (Fig. 4), Prestoea decurrens (H. A. Wendl.) H. E. Moore (Fig. 5), and Cryosophila albida Bartlett (Fig. 6). Table 2 summarizes characteristics of the six species.

Welfia georgii (Fig. 1), a monoecious geonomoid palm, is distributed from Colombia to Costa Rica (Standley 1937). Welfia has a long period of establishment growth in which it remains as a large-leaved rosette with no above-ground stem while a bulbous underground stem is produced (Schatz et al. 1985). Later, Welfia develops a single columnar above-ground stem that supports a massive crown. The ecology of Welfia was studied by Vandermeer and co-workers (Vandermeer et al. 1974, 1979, Vandermeer 1977, 1979). Iriartea gigantea (Fig. 2) is a monoecious iriarteoid palm of Costa Rica and possibly Nicaragua (Standley 1937). Iriartea begins producing a single columnar above-ground stem immediately after germinat-
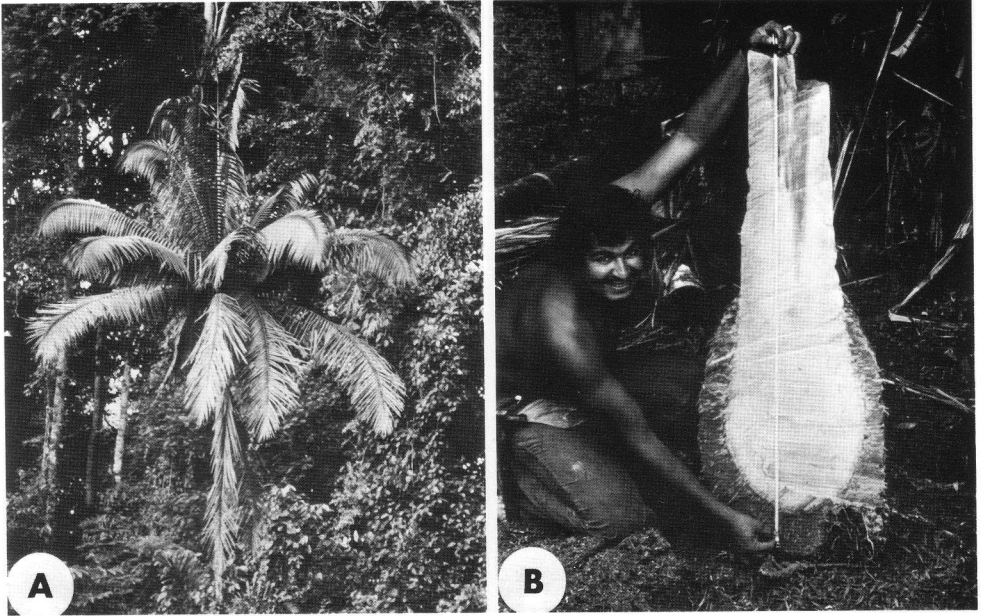
1. *Welfia georgii*, A) the general habit, and B) the bulbous undergound stem.

2. *Iriartea gigantea*, A) the crown, and B) a longitudinal cut through the stilt roots and lower stem.
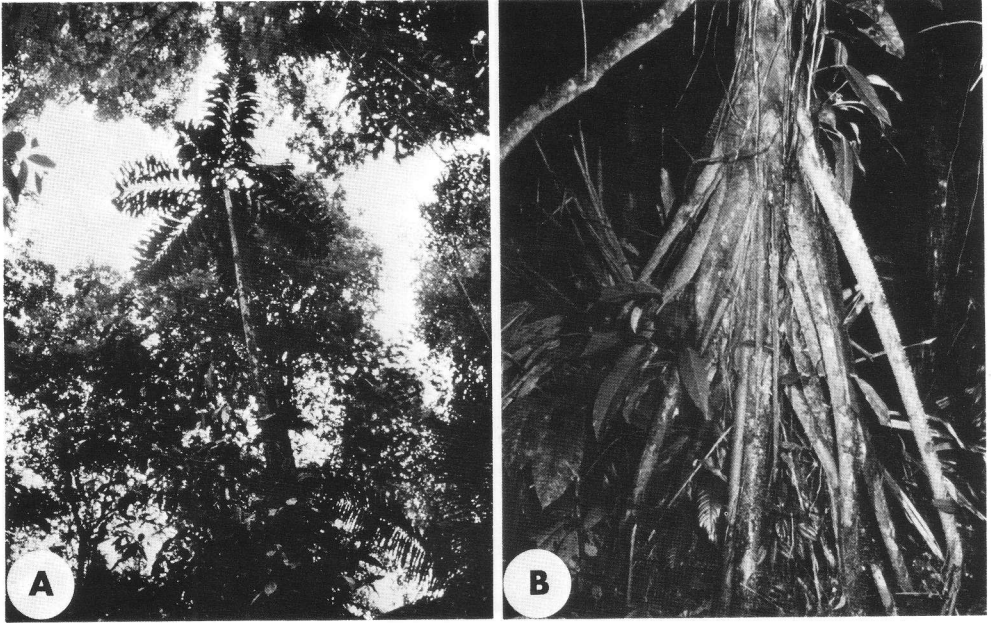
3.   *Socratea durissima*, A) the crown, and B) the stilt roots.

ing and develops a dense cone of stilt roots (Schatz et al. 1985). Though *Iriartea* crowns contain few leaves (5–7), pinnae become markedly dissected and multi-layered in individuals taller than 15 m.

Allometry of Palm Height and Stem Diameter

Allometry of stem diameter and height was studied for each of the six main study species and among maximum height individuals of 25 palm species (Rich 1985, Rich et al. in press). Some arborescent palm species, such as *Welfia georgii*, *Prestoea decurrens*, and *Cryosophila albida*, showed little or no capacity for sustained stem diameter growth (Fig. 7a). Other palms, *Socratea durissima*, *Iriartea gigantea*, and *Euterpe macrospadix*, had a pronounced ability to increase their stem diameter (Fig. 7b). Sustained increase in stem diameter is one means by which many palm species avoid decreases in the margin of safety against mechanical failure during height growth. During growth of all palm species observed, stem diameter did not increase with the 3/2 power of height. This implies that, for palms, elastic similarity is not maintained by increases in stem diameter. No palm species even maintained geometric similarity, meaning that during growth shape changed, with relatively thinner stems in taller individuals. As compared with arborescent dicotyledons and conifers, all palm species were overbuilt with respect to stem diameter when short and underbuilt when near their maximum height. Palms appeared to follow a 3/2 power scaling law for maximum height individuals, such that stem diameter varied with the 3/2 power of height (Rich 1985). This is in accordance with the 3/2 power law for dicotyledonous trees. Variance about the interspecific allometric curve for palms was partially explained by differences in internal stem properties, crown size, and life history (Rich 1985).
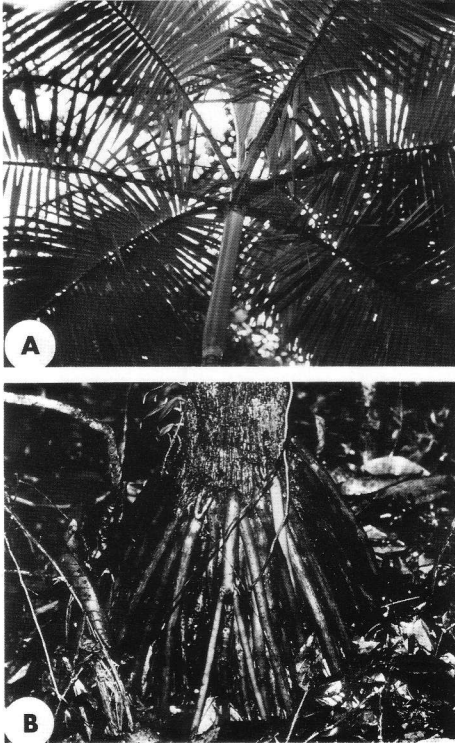
4. *Euterpe macrospadix*, A) the crown, and B) the above-ground roots.

5. *Prestoea decurrens*.

Mechanical Structure of the Palm Stem

Internal properties of palm stems were studied for the six main study species, with detailed analyses of developmental changes in *Welfia georgii* and *Iriartea gigantea* (Rich 1985). Dry density, or specific gravity, and elastic modulus, a measure of stiffness, were greatest toward the stem periphery and base. These properties increased markedly with inferred age in sequences of individuals with different overall heights (Fig. 8). Even though palms were overbuilt with respect to diameter when young and underbuilt when near

Table 2. *Characteristics of arborescent palm species studied at La Selva Biological Station, Costa Rica.*[a]

Species	Major Group	Ht m	DBH m	C m	LL m	LN #	RT m
Welfia georgii	geonomoid	22.9	0.195	5.6	6.3	25	0.0
Iriartea gigantea	iriarteoid	36.6	0.229	2.7	3.3	5	2.0
Socratea durissima	iriarteoid	34.2	0.157	2.5	3.1	5	2.6
Euterpe macrospadix	arecoid	24.0	0.145	2.4	3.0	8	0.8
Prestoea decurrens	arecoid	12.8	0.069	2.3	2.5	7	0.0
Cryosophila albida	coryphoid	11.2	0.078	2.1	2.6	18	1.0

[a] Overall height (Ht) and stem diameter at breast height (DBH) are from maximum height individuals. Average crown radius (C), average leaf length (LL), number of leaves in the crown (LN), and height of above-ground roots (RT) are composite estimates.

PRINCIPES

6.   *Cryosophila albida.*

their maximum height, there was a tendency to maintain a constant margin of safety against mechanical failure by means of changes in stiffness and strength, with initial low values increasing to exceptionally high values. The capacity to increase stem rigidity and strength is the major means by which arborescent palms compensate for increased structural demands during height growth.

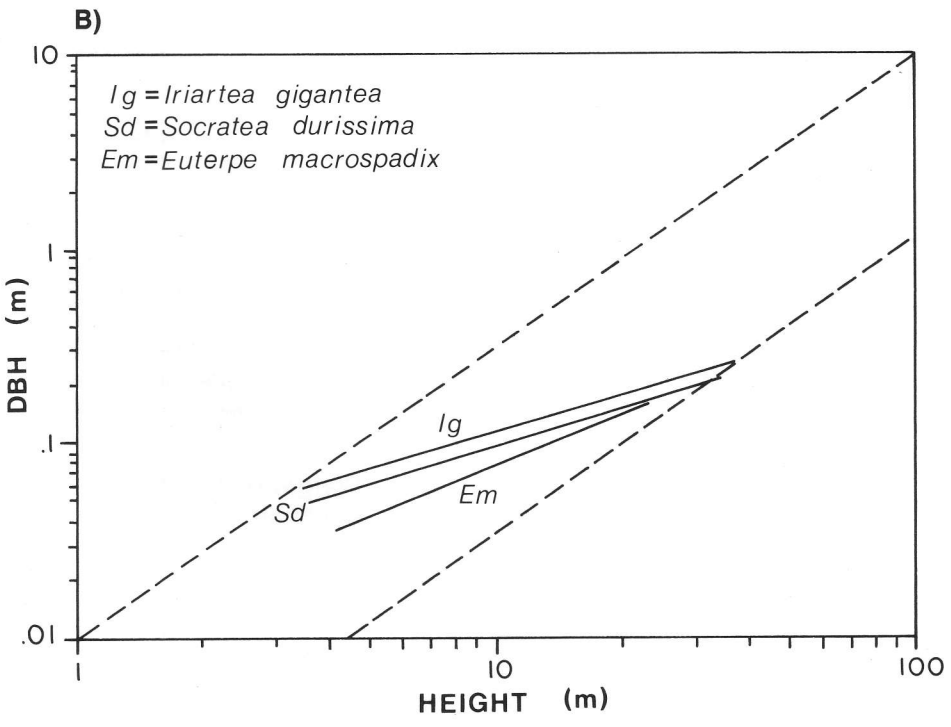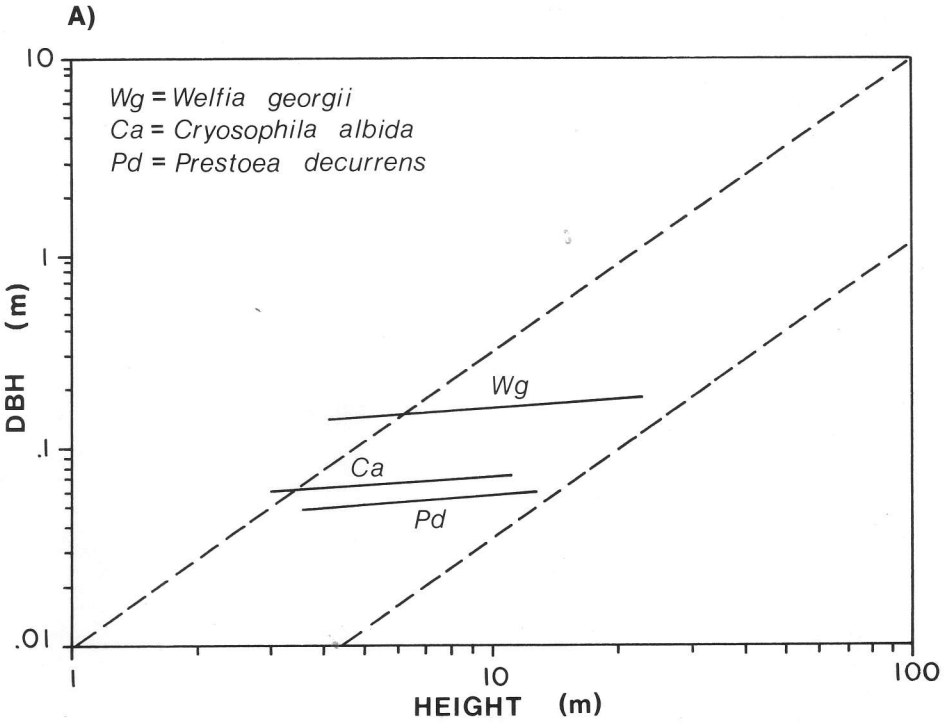### Developmental Anatomy of the Palm Stem

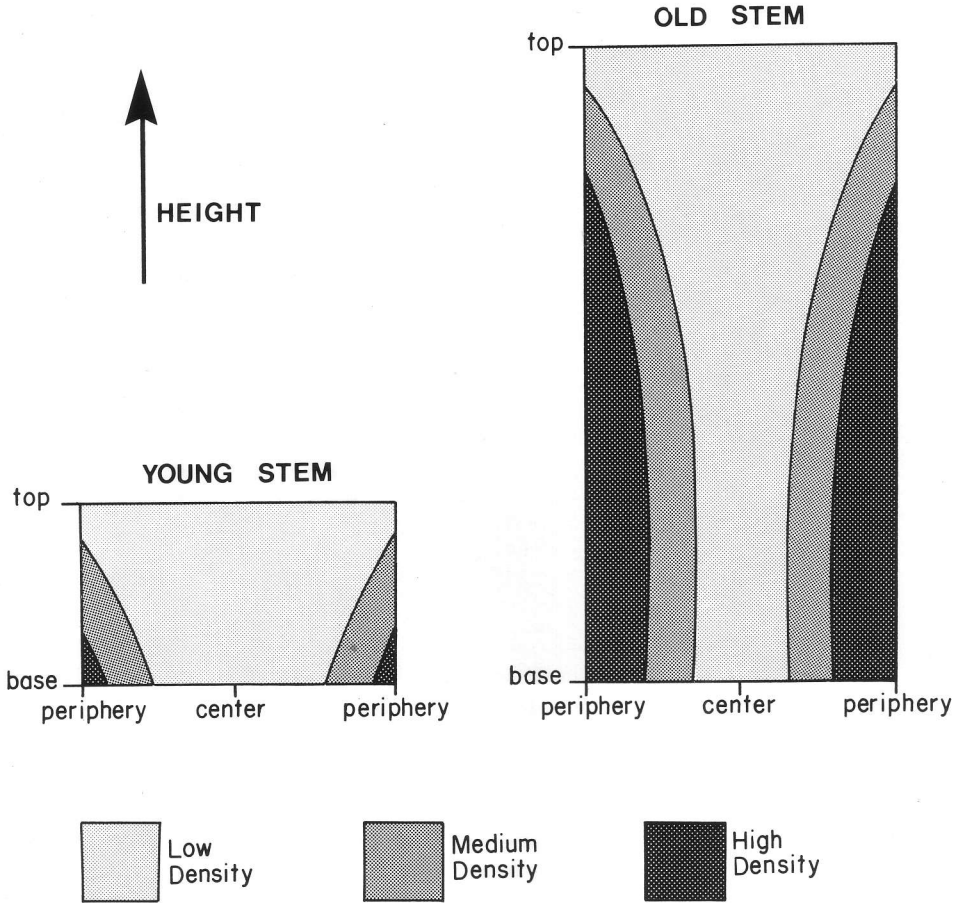Developmental anatomy was studied within the stems of each of the six main study species, with detailed studies for stems of *Welfia georgii* and *Iriartea gigantea* (Rich 1985). Vascular bundles were concentrated toward the stem periphery and peripheral bundles contained more fibers than central bundles. On the basis of comparison of stem tissue from the same level in individuals differing in height, *Welfia* showed a small increase in vascular bundle size in peripheral stem tissue during height growth, in keeping with its limited growth in stem diameter. Pronounced sustained cell expansion in *Iriartea* accounted for larger stem diameters of taller individuals. In *Iriartea*, sus-

$\longrightarrow$

7.   Allometry of stem diameter (DBH) and height for six species of arborescent palms in tropical wet forest of Costa Rica. Allometric curves are shown for A) palms with little or no stem diameter increase with height and B) palms with marked increase in stem diameter with height. The line for each species represents the regression line for 50 measurements across a full range of heights. The upper dashed line is the allometric curve for record-size North American trees and the lower dashed line a theoretical buckling limit for an "average" tree, beyond which the tree will buckle under its own weight (McMahon 1973). Both reference lines have a slope of 3/2, which implies that elastic similarity is maintained.

A)

Wg = *Welfia georgii*
Ca = *Cryosophila albida*
Pd = *Prestoea decurrens*

B)

Ig = *Iriartea gigantea*
Sd = *Socratea durissima*
Em = *Euterpe macrospadix*

HEIGHT

OLD STEM

top

base
periphery   center   periphery

YOUNG STEM

top

base
periphery   center   periphery

☐ Low Density   ▨ Medium Density   ■ High Density

8. Schematic representation of the distribution of stem tissue dry density, or specific gravity, within a young palm stem (left) and an old palm stem (right). Dry density is highest toward the stem periphery and base. Dry density increases during height growth. An increase in stiffness and strength accompanies the increase in dry density. This general distribution of density, stiffness, and strength characterizes all palm species.

tained expansion occurred in both fibers and ground parenchyma cells and large lacunae formed between cells in the central stem. Sustained sclerification, with major thickening of cell walls of fiber cells, accounted for dramatic increases in stem stiffness and strength for both species. Studies of developmental anatomy of the palm stem demonstrated the importance of secondary changes in the stem below the crown. Sustained cell expansion allows limited but significant stem diameter increase in many palm species. Sustained

sclerification, however, results in major increases in stem stiffness and strength in all arborescent palms.

Weight Distribution and Mechanical Architecture

Crown radius relative to stem diameter was examined for 16 species of arborescent palms and weight distribution was measured for the six main study species (Rich 1985) (Table 3). Species with relatively small stem diameters tended to have

Table 3. Distribution of weight in collected palms.[a]

Species	Ht m	Wst kg	Wcr kg	Wrep kg	Wtot kg
Welfia georgii	6.7	55.8	62.7	0.0	118.5
W. georgii	13.0	184.9	246.3	14.6	445.8
W. georgii	19.0	279.6	91.3	0.0	370.9
Iriartea gigantea	6.7	10.6	22.2	0.0	32.8
I. gigantea	9.0	13.6	29.8	0.0	43.4
I. gigantea	17.2	226.3	38.4	38.7	303.4
I. gigantea	26.5	378.8	44.2	10.5	433.5
Socratea durissima	17.3	32.1	26.3	2.6	61.0
Euterpe macrospadix	20.6	114.7	4.3	0.0	119.0
Prestoea decurrens	10.2	33.3	14.7	0.5	48.5
Cryosophila albida	4.5	8.8	10.3	0.0	19.1

[a] Key to symbols: Ht = height to top of crown (to highest expanded leaf); Wst = weight of above-ground stem; Wcr = weight of crown (includes leaves and stem within leafbases); Wrep = weight of reproductive structures; Wtot = total above-ground weight (above-ground roots not included).

relatively small crown radii and species with relatively large stem diameters tended to have relatively large crown radii. For short individuals of both *Welfia* and *Iriartea*, weight per unit length, in both the stem and crown, decreases as a function of height within an individual, essentially cone-shape weight distributions. Taller *Welfia* had nearly constant weight per unit length within the stem and a much greater weight per unit length within the massive crowns, essentially parasol-shape weight distributions. Taller *Iriartea* had small crowns relative to *Welfia*, and approximately a constant weight per unit length within both the stem and crown, essentially cylinder-shape weight distributions. *Iriartea* and *Welfia* had similar maximum stem diameters and internal stem properties. In the case of *Iriartea*, the stem supported a tall maximum height (up to 37 meters), but a small crown. In the case of *Welfia*, the stem supported a shorter maximum height (up to 23 meters), but a massive crown.

Growth Rates and Mechanical Architecture

Measurements of leaf production rates and internode lengths allow the calculation of height extension rates in palms. Leaf production rates over relatively short periods must include a correction for the length of the unexpanded spear leaf to account for partial leaf production. Leaf production rates of palms are being monitored for individuals up to 13 m tall in a continuing study of growth within natural populations of the six main study species (Rich 1985). On the basis of preliminary data from the first year of monitored growth, leaf production rates for the six study species displayed wide variance and increased significantly with height (Table 4). Height extension rates showed even broader variance and increased significantly with height for all species, except *Euterpe* and *Prestoea* (Table 5). *Cryosophila* had the fastest leaf production rate, but a slow height extension rate. *Socratea* and *Euterpe* had the highest rates of height extension and produced weaker stems, presumably because of "trade-offs" in resource allocation. *Welfia* produced leaves and grew in height faster than *Iriartea*, while at the same time producing a more substantial stem. This probably resulted because early allocation of resources to leaf production and enlargement of the meristem allowed later rapid height growth. Two major factors contrib-

Table 4. Linear regressions and statistical tests of significance of regressions of leaf turnover rate (#/year) as a function of height for palms less than 13 m tall, based on one year of growth data.[a] Leaf turnover rates for 5 and 10 m tall individuals, based on the regressions, are shown for comparison.

Species	n	b	a	r^2	Test[b] of $b = 0$	Leaf Turnover[c] 5 m	10 m
Welfia georgii	100	0.411	0.343	0.516	$p < 0.01$	2.40	4.45
Iriartea gigantea	99	0.110	1.033	0.367	$p < 0.01$	1.58	2.13
Socratea durissima	45	0.300	1.717	0.636	$p < 0.01$	3.21	4.71
S. durissima OF[d]	15	0.315	1.781	0.523	$p < 0.01$	3.36	4.93
S. durissima AC[e]	30	0.291	1.682	0.673	$p < 0.01$	3.14	4.59
Euterpe macrospadix	19	0.168	1.779	0.310	$p < 0.05$	2.62	3.46
Prestoea decurrens	20	0.241	1.935	0.231	$p < 0.05$	3.14	4.35
Cryosophila albida	23	1.075	1.412	0.373	$p < 0.01$	6.79	12.16

[a] Key to symbols: n = sample size, b = slope, a = Y intercept, r^2 = coefficient of determination.

[b] Statistical test with null hypothesis of b = 0 is a two-tailed Student's t test.

[c] Leaf turnover rate (#/yr) is calculated using the regression equation calculated for 5 and 10 m tall individuals.

[d] *S. durissima* in old growth forest.

[e] *S. durissima* in abandoned cacao forest.

ute to the production of less substantial stems in the fastest growing species: 1) limited resources are allocated to height extension and there is a "trade-off" between durability and rate of extension; and 2) shorter-lived species do not require a margin of safety against mechanical failure as high as that of a longer-lived species.

Conclusion and Perspective

Palms have evolved an effective means for attaining tree stature that is quite distinct from the means evolved among dicotyledonous trees and conifers. Dicotyledonous trees and conifers increase stem diameter by cell division in a lateral cambium, and are thereby able to compensate for increased structural demands during height growth by replacing conducting tissues and adding strengthening tissues. Palms lack a lateral cambium, but rather by primary thickening growth they produce sufficient stem cells to serve permanent functions of supply and support. Hydraulic architecture of palms, the basis of water transport, has received recent

attention (Zimmermann 1983, Sperry 1985); however, mechanical architecture has been neglected.

Sustained cell expansion and sclerification enable palms to meet increased structural demands during height growth. Some palms are able to grow exceedingly tall by producing extremely stiff and strong tissue at the stem periphery, and by developing narrow crowns. For instance, *Socratea durissima* is able to grow taller than 30 m and *Iriartea gigantea* is able to grow taller than 35 m. Other species are able to grow to more modest heights, but produce massive crowns by virtue of similar stem characteristics. For instance, *Welfia georgii* is able to support a massive crown, weighing 50 to 250 kg, at heights of 10 to 20 m.

Palms tend to maintain elastic similarity during height growth. Within a palm species, short individuals have stems that are overbuilt with respect to diameter but underbuilt with respect to stem stiffness and strength, relative to dicotyledonous trees of similar height; tall individuals have stems that are underbuilt with respect to

Table 5. *Linear regressions and statistical tests of significance of regressions of height extension growth rates (m/year) as a function of height for palms less than 13 m tall, based on one year of growth data.[a] Height extension rates for 5 and 10 m tall individuals, based on the regressions, are shown for comparison.*

Species	n	b	a	r^2	Test[b] of $b = 0$	Height Growth[c]	
						5 m	10 m
Welfia georgii	34	0.059	−0.056	0.185	p < 0.05	0.24	0.54
Iriartea gigantea	99	0.021	0.064	0.120	p < 0.01	0.17	0.27
Socratea durissima	45	0.121	−0.215	0.560	p < 0.01	0.39	1.00
S. durissima OF[d]	15	0.094	−0.207	0.560	p < 0.01	0.26	0.73
S. durissima AC[e]	30	0.132	−0.198	0.591	p < 0.01	0.46	1.12
Euterpe macrospadix	13	0.047	0.087	0.257	NS	0.32	0.56
Prestoea decurrens	19	0.018	0.127	0.036	NS	0.22	0.31
Cryosophila albida	23	0.021	0.012	0.322	p < 0.01	0.12	0.22

[a] Key to symbols: n = sample size, b = slope, a = Y intercept, r^2 = coefficient of determination.

[b] Statistical test with null hypothesis of b = 0 is a two-tailed Student's t test.

[c] Height growth rate is calculated using the regression equation calculated for 5 and 10 m tall individuals.

[d] *S. durissima* in old growth forest.

[e] *S. durissima* in abandoned cacao forest.

diameter but overbuilt with respect to stem stiffness and strength. A rigorous test of whether elastic similarity is maintained is lacking and requires direct measurements of intact stems.

Mechanical models of palms must take into account the heterogeneity of the stem, as well as changing geometry and material properties during height growth. Existing models that assume homogeneous materials are not sufficient. Elastic modulus and other mechanical properties vary as a function of radial position and height. Elastic modulus is greatest toward the stem periphery, decreases markedly toward the stem center, and decreases with height. The upper trunk is quite flexible and the lower trunk is quite stiff. The crown can be viewed as a mass at the top of the trunk, a mass that can vary greatly both within and between species.

Mechanical models are important for understanding the ecology and evolution of palms. The margin of safety against mechanical failure would be expected to vary depending upon the risk of mechanical failure, which is a function of the environment where the palm grows. For

instance, palms that grow in the open are subjected to a higher risk of breakage by wind as compared to palms growing in the shelter of a forest. The risk of mechanical failure changes as an individual palm grows in height, both because the individual's geometry and structural properties change and because aspects of the environment that the individual experiences change. The margin of safety would also be expected to vary depending upon "trade-offs" in the allocation of resources to stem reinforcement versus other functions. For instance, less durable stems may be produced in species where allocation of resources to rapid height extension allows more favorable positioning of the crown for photosynthesis. Patterns of resource allocation to support versus other functions are best viewed in terms of whole life histories.

The work described herein employed studies of biomechanics, developmental morphology, and ecology to characterize the basic mechanical architecture of palms. Future work will involve direct measurements of intact palm stem properties, chemical analysis of structural stem tis-

sue, development of formal models of the relationship between mechanical structure and life history, and long-term study of the growth and ecology of selected palm species.

Acknowledgments

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Panama Collecting Trip

I am organizing a group of up to 12 people to go on a guided collecting trip to Panama next year. We will visit Chiriqui and Cocle areas. For more information, write and send a S.A.S.E. to JOHN O. WILD, 1123 15th Ave. S.E., Minneapolis, Minn. 55414.

IMPORTANT NOTICE

Change in Address of Seed Bank

On April 14th 1986 the management of The Seed Bank changed from Lois Rossten to David Sylvia, 36279 Christine St., Newark, CA 94560 and Inge Hoffman, 695 Joaquin Ave., San Leandro, CA 94577. October *Principes* will give a full report on the change. Meanwhile requests to The Seed Bank should be addressed to one of the new managers.