

LEAF DEVELOPMENT AND CROWN GEOMETRY OF TWO IRIARTEOID PALMS¹

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We examined changes in pinnately compound leaf morphology and crown geometry that occur during height growth of the iriarteoid palms *Socratea exorrhiza* and *Iriartea deltoidea* in tropical wet forest of Costa Rica. Although light availability increased with height, the number of leaves per plant was relatively constant. Total leaf area, however, was much larger in taller individuals. Increases in linear dimensions of leaves (length and width) was responsible for less than half of this greater surface area. More important was the transition from a basically dorsiventral display of leaflets in small individuals to a more radial display in taller plants. Production of leaflets in more than one plane resulted in leaves whose surface area was more than twice the horizontally projected area and whose lateral light interception was greatly enhanced. *S. exorrhiza*, a faster-growing and more light-demanding species, undergoes this transformation in leaf morphology at heights between 3 and 6 m; whereas in the slower-growing and more shade-tolerant *I. deltoidea* this occurs at heights between 10 and 20 m. Pinnate leaves, with dense radial packing of leaflets along the rachis, are functionally comparable to branches of dicotyledonous trees and may have been important for the evolution of arborescence in palms.

Palms exhibit morphological and developmental features that limit their ability to adjust foliar display as resource availability changes throughout their life cycle. Most palms are monopodial and thus unable to increase their crown size by branching (Tomlinson, 1961, 1970, 1990; Hallé, Oldeman, and Tomlinson, 1978). Yet among palms there is considerable diversity in crown size and form (Dransfield, 1978; Uhl and Dransfield, 1987). Palm crowns are generally comprised of relatively few, large leaves, the largest of which are pinnately compound (Hallé, 1977). In terms of function, pinnately compound leaves have been compared to branches because they distribute photosynthetic surfaces away from the central axis (Givnish, 1978). Palms may augment their photosynthetic area either by producing more leaves or by producing larger leaves. Leaf overlap and self shading limits the number of leaves that can be efficiently displayed within a crown; whereas without change in shape, larger leaves require more than linear increases in support tissue (McMahon and Kronauer, 1976; Chazdon, 1985a, 1986; Niklas, 1992). As crown size increases, the most efficient display of photosynthetic tissue may require changes in leaf shape, as well as increases in leaf number and size (Chazdon, 1985a, 1991; Givnish, 1986). Ontogenetic changes in leaf form, with production of distinct juvenile vs. mature leaf morphologies (Tomlinson, 1960, 1990), may enable palms to build efficient crowns and respond to changes in crown microclimate during growth. Forest species of arborescent

palms experience radical changes in microclimate as they grow up through the understory; in particular, light levels often increase dramatically. This study examines changes in leaf and crown morphology that accompany height growth of two iriarteoid palms in a wet, tropical forest.

We have a basic understanding of leaf development in palms (Kaplan, 1973, 1983; Dengler, Dengler, and Kaplan, 1982; Kaplan, Dengler, and Dengler, 1982a, b; Dengler and Dengler, 1984; Tomlinson, 1990). However, little is known about consequences of leaf geometry for building efficient crowns. Nor is it known whether ontogenetic changes in leaf form result from fixed developmental patterns or more plastic responses to changes in environmental conditions. Iriarteoid palms typically have crowns that consist of five to eight pinnately compound leaves, and for mature plants each leaf contains several distinct classes of leaflets that differ in shape and orientation (Henderson, 1990). While it has been reported that juvenile leaves of iriarteoid palms are very different from the leaves of mature plants (Henderson, 1990; Rich, 1985), the progression of ontogenetic changes has not been described from a functional perspective. How do changes in the development of successive leaves lead to changes in three-dimensional crown geometry among iriarteoid palms? Does the variable presence and disposition of different leaflet types correspond to changes in resource availability that may occur during the life of the plant? Is the timing of ontogenetic changes in leaf form related to differences between species in life history characteristics?

MATERIALS AND METHODS

Research site, study species, and sampling design—Research was conducted at the Organization for Tropical Studies La Selva Biological Station in the Atlantic lowlands of northern Costa Rica, a tropical premontane wet forest with a mean rainfall of approximately 4,000 mm (see Holdridge et al., 1971; Hartshorn, 1983, for detailed site descriptions). La Selva has a high diversity of palm species, with 29 species in 16 genera (Chazdon, 1985b; Moore and Chazdon, 1985). We examined changes in leaf

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TABLE 1. Stem, crown, and leaf characteristics of plants sampled for leaf morphology. The numbers 1 through 5 across the top refer to the height classes. For each characteristic, the mean value and standard error (italics) are provided. Leaf length, width, depth, area, and mass are mean values for sample consisting of a single leaf per plant. Leaf length and width were measured with the excised leaf laid on a flat surface. Leaf depth, however, was measured with the leaf held horizontal and thus allowed to arch naturally under its own weight. Note that the leaf length is defined here as the length of the rachis and does not include the sheathing leaf base; the leaf length exceeds the diameter of the crown in intact crowns.

	<i>Socratea exorrhiza</i>					<i>Iriartea deltoidea</i>				
	1	2	3	4	5	1	2	3	4	5
Sample size	4	4	4	4	1	4	4	4	4	1
Height (m)	1.95 <i>0.12</i>	2.95 <i>0.19</i>	7.81 <i>0.44</i>	11.36 <i>2.34</i>	17.00 —	1.47 <i>0.09</i>	3.43 <i>0.19</i>	8.10 <i>0.40</i>	15.17 <i>0.53</i>	25.70 —
Height to base of crown (m)	0.54 <i>0.09</i>	1.00 <i>0.09</i>	3.28 <i>0.30</i>	6.51 <i>1.55</i>	14.10 —	0.19 <i>0.04</i>	1.25 <i>0.02</i>	4.30 <i>0.99</i>	9.72 <i>0.30</i>	23.90 —
DBH (cm)	2.1 <i>0.3</i>	3.9 <i>0.2</i>	9.5 <i>0.5</i>	12.5 <i>2.5</i>	14.6 —	3.2 <i>0.2</i>	5.4 <i>0.5</i>	9.9 <i>0.5</i>	18.4 <i>0.8</i>	20.4 —
Crown diameter (m)	0.94 <i>0.06</i>	1.59 <i>0.11</i>	2.50 <i>0.06</i>	2.33 <i>0.31</i>	2.80 —	1.06 <i>0.06</i>	1.60 <i>0.04</i>	2.51 <i>0.20</i>	3.30 <i>0.15</i>	2.60 —
Crown depth (m)	1.01 <i>0.12</i>	1.35 <i>0.07</i>	3.26 <i>0.20</i>	5.03 <i>0.95</i>	3.20 —	1.02 <i>0.14</i>	2.07 <i>0.26</i>	3.26 <i>0.37</i>	5.35 <i>0.51</i>	3.50 —
Number of leaves	5.0 <i>0.0</i>	4.8 <i>0.2</i>	6.3 <i>0.2</i>	7.2 <i>0.6</i>	7.0 —	5.0 <i>0.4</i>	5.8 <i>0.2</i>	6.0 <i>0.4</i>	8.0 <i>0.4</i>	5.0 —
Leaf length (m)	1.33 <i>0.07</i>	2.07 <i>0.15</i>	2.98 <i>0.09</i>	3.18 <i>0.44</i>	3.16 —	1.40 <i>0.09</i>	2.35 <i>0.12</i>	3.14 <i>0.28</i>	3.89 <i>0.15</i>	3.16 —
Leaf width (m)	0.66 <i>0.04</i>	0.94 <i>0.06</i>	1.16 <i>0.04</i>	1.32 <i>0.16</i>	1.11 —	0.68 <i>0.03</i>	1.07 <i>0.10</i>	1.47 <i>0.08</i>	2.37 <i>0.24</i>	1.64 —
Leaf depth (m)	0.17 <i>0.02</i>	0.38 <i>0.02</i>	0.85 <i>0.02</i>	1.04 <i>0.21</i>	0.67 —	0.22 <i>0.01</i>	0.38 <i>0.02</i>	0.65 <i>0.06</i>	1.04 <i>0.05</i>	1.18 —
Leaf area (m ² /lf)	0.2673 <i>0.0428</i>	0.7264 <i>0.1051</i>	2.0909 <i>0.0774</i>	3.7915 <i>0.9129</i>	3.9600 —	0.2902 <i>0.0296</i>	0.8925 <i>0.1546</i>	2.1813 <i>0.2687</i>	5.7205 <i>0.7825</i>	7.6839 —
Leaf mass (g/lf)	19.4 <i>3.3</i>	76.0 <i>3.3</i>	261.9 <i>20.6</i>	574.0 <i>152.5</i>	—	30.6 <i>3.4</i>	110.5 <i>20.1</i>	325.1 <i>53.0</i>	974.1 <i>138.1</i>	2,035.1 —

and crown form that occur during development for the iriarteoid palms *Socratea exorrhiza* and *Iriartea deltoidea*. *Socratea* and *Iriartea* are closely related genera of the subfamily Arecoideae, Iriarteinae group (Uhl and Dransfield, 1987; Henderson, 1990). Both species are characterized by the presence of stilt roots and commonly grow taller than 30 m (Rich, 1986; Rich et al., 1986).

We examined leaf morphology of four individuals from each of four height classes, ranging in height from 2 to 15 m, for a total of 16 individuals sampled per species (Table 1). Data for an additional tall individual of each species (> 15 m tall) was obtained from studies of palms felled with a chain saw (Rich, 1986, 1987a, b). For each individual we recorded height to the highest portion of the highest expanded leaf, height to the bottom of the lowest leafbase, stem diameter and internode length (at breast height when possible, just above the stilt roots for tall individuals, or just below the lowest leafbase for very short individuals), crown radius (measured in each of two orthogonal directions), crown depth (distance between the lowest and highest expanded leaves), and total number of leaves. The second or third fully expanded leaf was excised at the base of the petiole, using a 10-m pole saw from atop a step ladder for the tallest size class.

Leaf morphology—We made detailed morphological measurements of each leaf collected, including length (exclusive of leafbase), petiole length, blade width, and blade depth (distance between highest and lowest foliage while sustaining the leaf horizontally). Shorter individuals produce leaflets displayed in a dorsiventral pattern, essentially in a single layer, hereafter referred to as monolayer

leaves; whereas leaves of taller individuals have two or more morphologically distinct leaflet types arrayed radially about the rachis in several tiers, hereafter referred to as multilayer leaves. Leaflets were divided into three categories according to morphological and developmental criteria: 1) broad, wedge-shaped leaflets, which we call fins; 2) narrower, linear leaflets, which we call straps; and 3) smaller, wedge-shaped leaflets, which we call secondary fins. We determined the total number of each leaflet type and measured the length and width of five leaflets in each of the leaflet categories. Dry biomass was determined for all categories of leaf tissue after drying to constant weight at 70 C. Total leaf nitrogen and phosphorous content was determined for each leaflet category. Representative subsamples were ground through a 20 mesh, digested in sulfuric acid heated to 400 C with a vanadium pentoxide catalyst to convert N to ammonia and P to phosphate, and duplicate measurements were made using an Alpchem RFA/2 autoanalyzer (Bran+ Luebbe Analyzing Technologies, Inc., Elmsford, NY).

Leaf and crown geometry—Leaf and crown geometry was examined with respect to potential light interception. We measured leaf surface area, of the same leaves used for morphological studies, using a Licor LI-3100 leaf area meter (Licor, Inc., Lincoln, NE). Leaf areas were determined separately by leaflet type. We estimated projected area of individual leaves in horizontal and vertical dimensions by photographing leaves sustained horizontally against a white background, with photographs taken from above and from the side using black-and-white film (Kodak Tri-X). The leaves were held at the base of the petiole

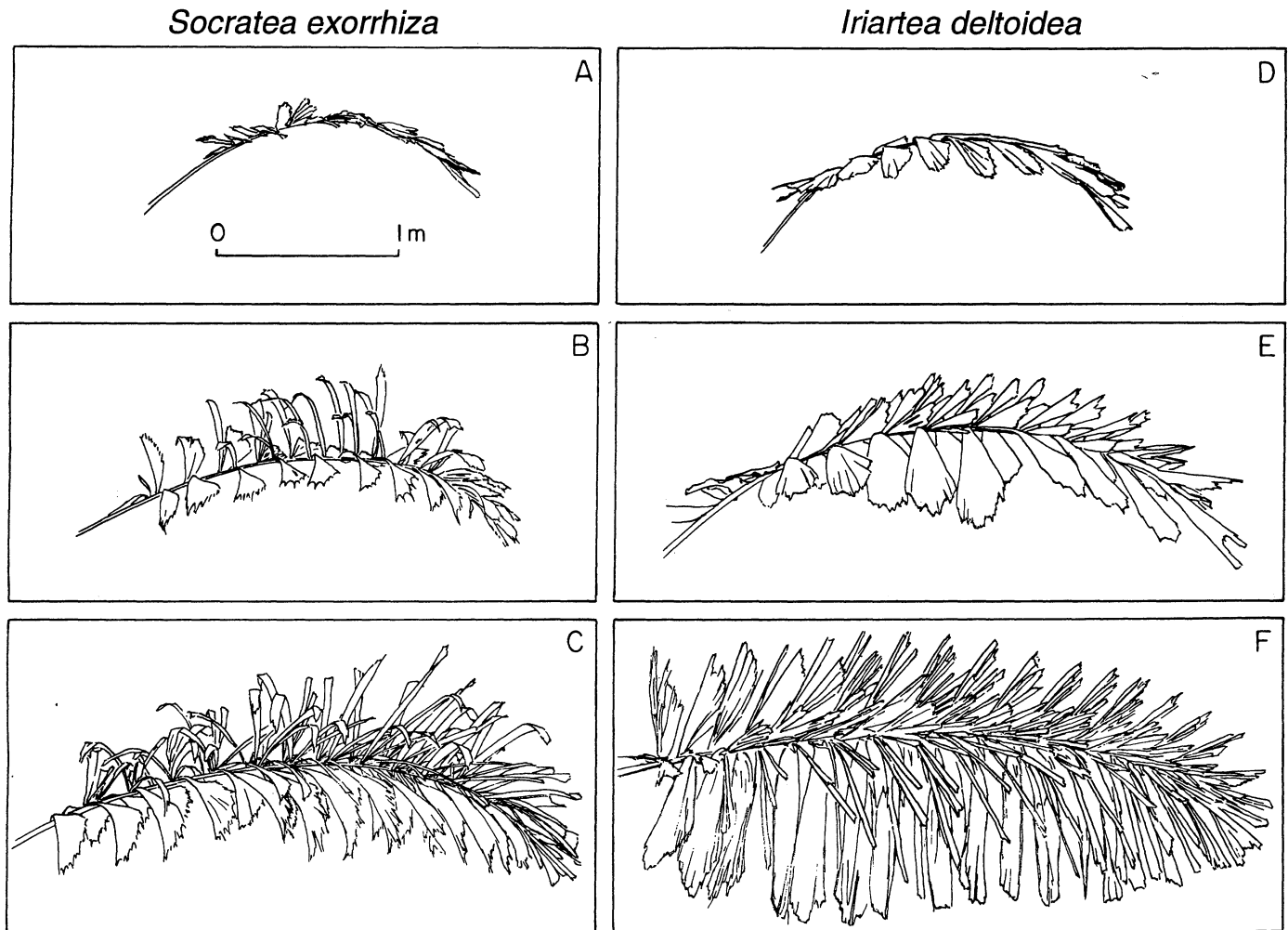


Fig. 1. Lateral view of *S. exorrhiza* and *I. deltoidea* leaves showing monolayer (A, D), early multilayer (B, E), and more developed multilayer (C, F) morphologies. Each panel represents a mature leaf taken from 2-m-, 8-m-, and 14-m-tall plants of *S. exorrhiza*, respectively (A, B, C), and from 2-m-, 12-m-, and >20-m-tall plants of *I. deltoidea*, respectively (panels D, E, F). Note that in *I. deltoidea* the first leaves to show the multilayer morphology consist primarily of fins and secondary fins (E). More dissected leaves from taller individuals (panel F) have fins, straps, and secondary fins.

and allowed to arch naturally such that the tip of the terminal leaflet was in the same horizontal plane as the point of attachment of the most basal leaflets. Projected leaf area was measured from negatives using the image analysis system IMAGE (Rich, Ranken, and George, 1989).

Leaf area index (LAI) of individual leaves was calculated by dividing total area of a leaf, including all leaflets, by its circumscribed horizontally projected area. Circumscribed horizontally projected area was determined by laying the intact leaf flat on a large piece of paper and then tracing a smooth curve connecting the outermost tips of the leaflets in contact with the paper. This shape was then cut out and its area determined using the leaf area meter. LAI of entire crowns (LAI_{cr}) was calculated based on the leaf area (L_a) of the sampled leaf, the number of leaves (L_n) within the crown, and the horizontally projected crown area:

$$LAI_{cr} = L_a \cdot L_n / (R^2),$$

where R is crown radius.

Developmental changes with respect to size and light environment—Leaf morphology (monolayer vs. multilayer) and light environment (estimated using hemispherical photographs) were recorded for 75 individuals of *S. exorrhiza* and 100 individuals of *I. deltoidea* ranging in height from 0.5 to 12 m tall. These individual palms were the subject of long-term leaf demography and growth studies (Rich, 1986). Hemispherical photographs were taken above crowns following Rich (1989) and analyzed using the program CANOPY (Rich, 1989, 1990). Because the transformation from monolayer to multilayer leaf morphology in *I. deltoidea* generally occurred in individuals taller than 12 m, an additional 25 individuals between 10 and 25 m were visually scored in four classes of leaf morphology and four classes of light environment. The leaf morphology classes corresponded to 1) monolayer (as in Fig. 1D), 2) low multilayer (as in Fig. 1E), 3) medium multilayer, and 4) high multilayer (as in Fig. 1F). Light environment was scored according to surrounding canopy characteristics: 1) densely overtopped; 2) sparsely overtopped; 3) small gap or with significant side lighting; and 4) large gap.

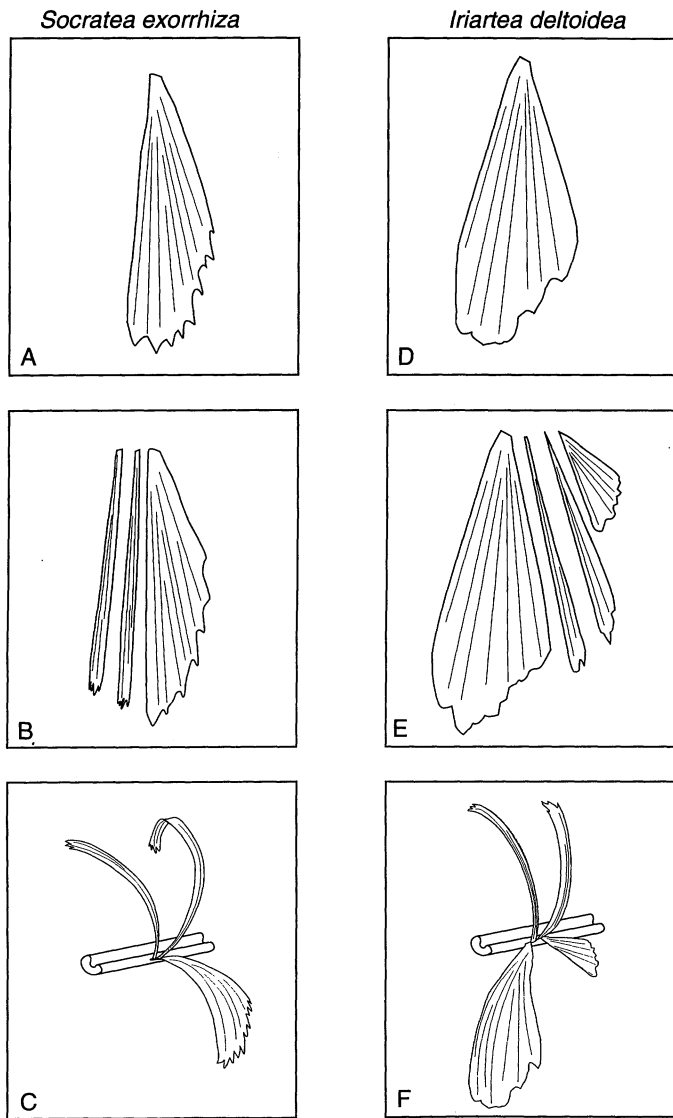


Fig. 2. Diagram showing leaflet form and development in *S. exorrhiza* (left panels) and *I. deltoidea* (right panels). Wedge-shaped leaflets (A, D) are the elementary form in both species. The lamina bases are compressed and twisted at the proximal side of *S. exorrhiza*, producing strap-shaped leaflets (straps) on the proximal side and wedge-shaped leaflets (fins) on the distal side of each leaflet group (B, C). In contrast, lamina bases are compressed and twisted on the distal edge of *I. deltoidea*, producing wedge-shaped leaflets (fins) on the proximal side, strap-shaped leaflets (straps) in the middle, and small wedge-shaped leaflets (secondary fins) on the distal side (E, F).

RESULTS

Leaf morphology—All individuals of *S. exorrhiza* and *I. deltoidea* produce wedge-shaped fin leaflets (Figs. 1, 2). Fins are regularly arranged along the rachis, asymmetrically deltoid to elliptic in shape, and have praemorse (fish-tailed) tips (Fig. 2). Each fin contains numerous ribs that diverge from the base to the margin. The basic shape of the fin leaflets differs in the two species. In short (monolayer) *S. exorrhiza*, most of the proximal margin of each fin leaflet is entire, while the distal margin is entire for only a short length, after which the margin is praemorse (Fig. 2A). In fin leaflets of short (monolayer) *I. deltoidea*,

TABLE 2. Foliar characteristics of individual leaflet types of *S. exorrhiza* and *I. deltoidea*. Numbers across the top of the table refer to different height classes (Table 1). For each characteristic, the mean value and standard error (italics) are provided. LSW refers to leaf specific weight (cm^2/g).

	<i>Socratea exorrhiza</i>				<i>Iriartea deltoidea</i>			
	1	2	3	4	1	2	3	4
Sample size	4	4	4	4	4	4	4	4
----- Fins -----								
Number/leaf	14.3	20.3	30.3	33.6	10.8	17.0	24.8	33.5
	<i>1.4</i>	<i>0.7</i>	<i>0.6</i>	<i>4.1</i>	<i>0.6</i>	<i>0.9</i>	<i>0.2</i>	<i>1.3</i>
Length (cm)	30.8	35.9	55.5	59.5	33.1	38.1	65.8	89.0
	<i>1.7</i>	<i>2.3</i>	<i>1.6</i>	<i>7.6</i>	<i>1.4</i>	<i>3.2</i>	<i>3.0</i>	<i>2.6</i>
Width (cm)	7.5	10.2	13.1	13.3	10.5	13.1	20.5	21.9
	<i>0.5</i>	<i>1.1</i>	<i>0.4</i>	<i>1.6</i>	<i>0.6</i>	<i>1.1</i>	<i>2.1</i>	<i>0.2</i>
LSW (cm^2/g)	48.9	58.1	76.0	82.7	72.7	81.1	97.0	119.7
	<i>1.8</i>	<i>2.3</i>	<i>3.3</i>	<i>8.6</i>	<i>0.5</i>	<i>2.5</i>	<i>6.0</i>	<i>1.4</i>
----- Straps -----								
Number/leaf	0.0	0.0	35.0	70.8	0.0	0.0	0.0	70.5
			<i>3.3</i>	<i>19.5</i>				<i>21.4</i>
Length (cm)	—	—	56.5	57.6	—	—	—	59.0
			<i>1.7</i>	<i>14.7</i>				<i>0.8</i>
Width (cm)	—	—	6.1	3.9	—	—	—	5.4
			<i>0.4</i>	<i>1.0</i>				<i>0.4</i>
LSW (cm^2/g)	—	—	83.2	85.2	—	—	—	117.5
			<i>4.5</i>	<i>21.9</i>				<i>2.8</i>
----- 2° Fins -----								
Number/leaf	—	—	—	—	0.0	0.0	0.0	22.0
								<i>2.1</i>
Length (cm)	—	—	—	—	—	—	—	43.3
								<i>1.3</i>
Width (cm)	—	—	—	—	—	—	—	13.1
								<i>1.9</i>
LSW (cm^2/g)	—	—	—	—	—	—	—	102.3
								<i>2.1</i>

both the proximal and distal margins are typically entire for a shorter length after which the margin is praemorse (Fig. 2D). Fins are displayed roughly in a single layer forming a smoothly arching plane that contains the rachis along its apex (Fig. 1).

More highly dissected, multilayer leaves are produced in taller plants (Table 2). In both species, longitudinal separations between ribs produce narrow strap leaflets. In *I. deltoidea*, smaller wedge-shaped leaflets (secondary fins) also occur. These leaflets (straps and secondary fins) are displayed along many radii above the fins, giving the leaf a plumose appearance (Uhl and Dransfield, 1987; Figs. 1, 2). Whereas monolayer leaves consist of a regular arrangement of entire leaflets, multilayer leaves have distinct groups of leaflets (Figs. 1, 2). In *S. exorrhiza* each group consists of a single fin and a variable number of straps located proximal to the fin. *I. deltoidea* leaflets also consist of leaflet groups containing a single fin, a variable number of straps, and a single secondary fin. In contrast to *S. exorrhiza*, fins occupy the basal position of each leaflet grouping in *I. deltoidea*, straps occur in the middle, and secondary fins occur on the distal side. The orientation of straps and secondary fins above the fins is reflected in their attachment to the rachis. The basal portion of fins parallels the axis of the rachis. Groups of straps (and secondary fins), on the other hand, are attached above the central axis of the rachis, leading to the three-dimensional, multiseriate character of these leaves (Figs. 1, 2).

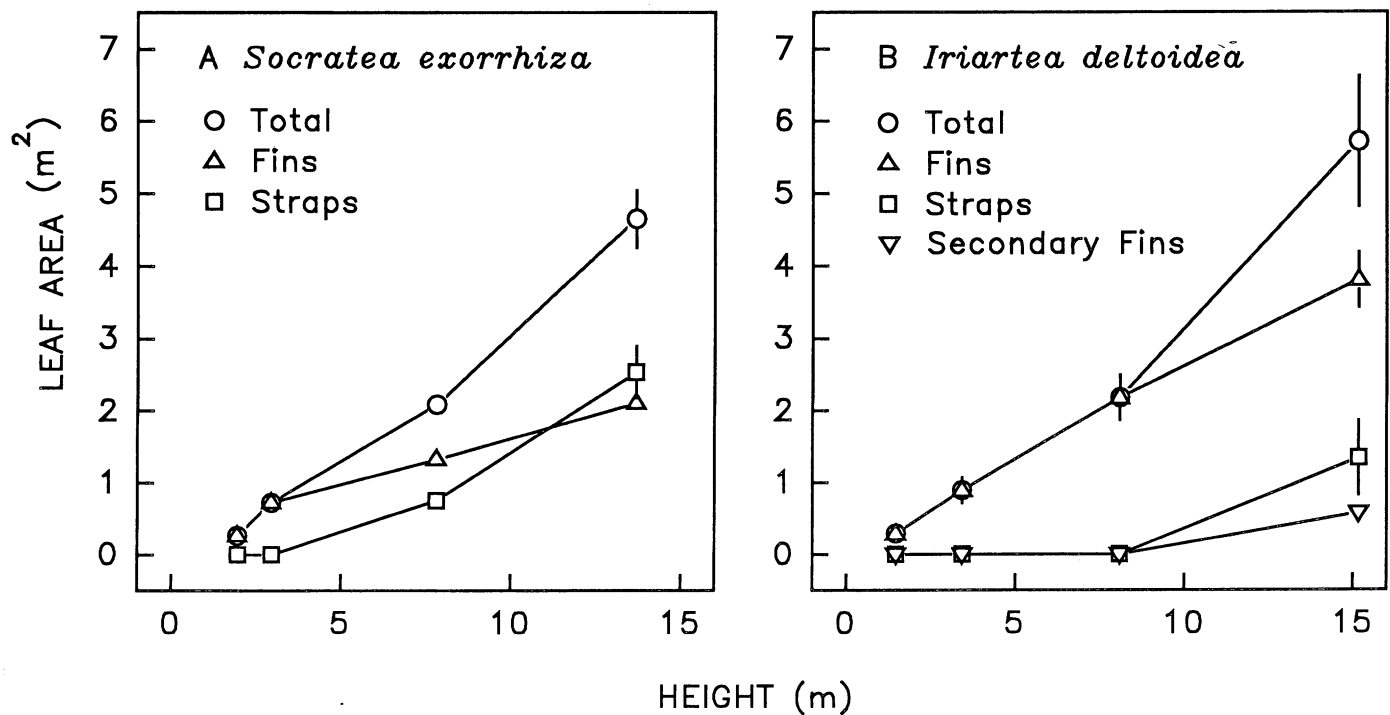


Fig. 3. Surface area of individual leaves of *S. exorrhiza* (A) and *I. deltoidea* (B). Open circles denote the total area of the leaf. Other symbols represent the contribution of the various leaflet types.

Although leaflet types differ in shape and orientation, they were not distinguishable in terms of leaf specific weight (Table 2) or foliar concentrations of nitrogen and phosphorous. Leaves of *S. exorrhiza* ($N = 16$ individuals) had a mean total nitrogen concentration of 17.800 mg/g (SE = 0.378) and a mean total phosphorous concentration of 1.228 mg/g (SE = 0.069); whereas *I. deltoidea* ($N = 16$ individuals) had a mean total nitrogen concentration of 15.733 mg/g (SE = 0.224) and a mean total phosphorous concentration of 1.259 mg/g (SE = 0.103).

Leaf and crown geometry—Taller individuals of *S. exorrhiza* and *I. deltoidea* have larger crowns than do plants in the smaller height classes (Table 1). A greater than eightfold increase in estimated crown leaf area in the two species was primarily due to greater surface area per leaf rather than to greater numbers of leaves. The average number of leaves per individual *S. exorrhiza* increased from five in the smallest height class to slightly more than seven in the largest group (Table 1). Even the tallest *S. exorrhiza* had only seven leaves. The average number of leaves in *I. deltoidea* increased from five to eight, with the tallest individual supporting a crown of only five leaves. Although both leaf length and width increased by severalfold, this was not enough to account for the increases in the surface area of individual leaves (about 13- and 19-fold increase for *S. exorrhiza* and *I. deltoidea*, respectively) (Fig. 3). Leaf depth, on the other hand, increased approximately five times in both species. The larger volume exploited by individual leaves was paralleled at the whole crown level. Crown depth increased more markedly than did crown diameter as a function of height.

Straps accounted for an increasing proportion of leaf

area with increasing height (Fig. 3). Straps constituted roughly 50% of the total leaf area for the 13-m-tall group of *S. exorrhiza*; whereas, straps constituted roughly 20% for the 15-m-tall group of *I. deltoidea*. Visual inspection of tall individuals of both species, for which leaves were not readily accessible, suggested that both total leaf area per leaf and the proportion of leaf area in strap leaflets continues to increase with height. Similarly, projected area, in both vertical and horizontal planes, increased markedly over the height classes examined (Fig. 4). LAI, calculated both on a leaf and a crown basis, also showed a dramatic increase with height (Fig. 5). Individual leaf LAI values above 2 were observed for tall individuals of both *S. exorrhiza* and *I. deltoidea*.

Developmental changes with respect to size and light environment

—Individuals of *S. exorrhiza* shorter than 5 m tended to have monolayer leaves, whereas taller individuals had multilayer leaves (Fig. 6a). Commonly, individuals in the 3- to 6-m-tall transitional size range had older leaves with monolayer morphology and younger leaves with multilayer morphology. For *S. exorrhiza*, estimated light environment, expressed as proportion photosynthetic photon flux density (PPFD) relative to that in the open, was observed to increase significantly with height (Fig. 6a, $P < 0.05$).

By contrast, all of the 75 long-term study individuals of *I. deltoidea* had monolayer morphology, except one 9.5-m-tall individual that had some early multilayer leaves. Light environment, expressed as proportion PPFD, showed a low r^2 but significant increase with height (Fig. 6b, $P < 0.10$). Based on examination of the additional 25 taller individuals of *I. deltoidea*, multilayer leaves were

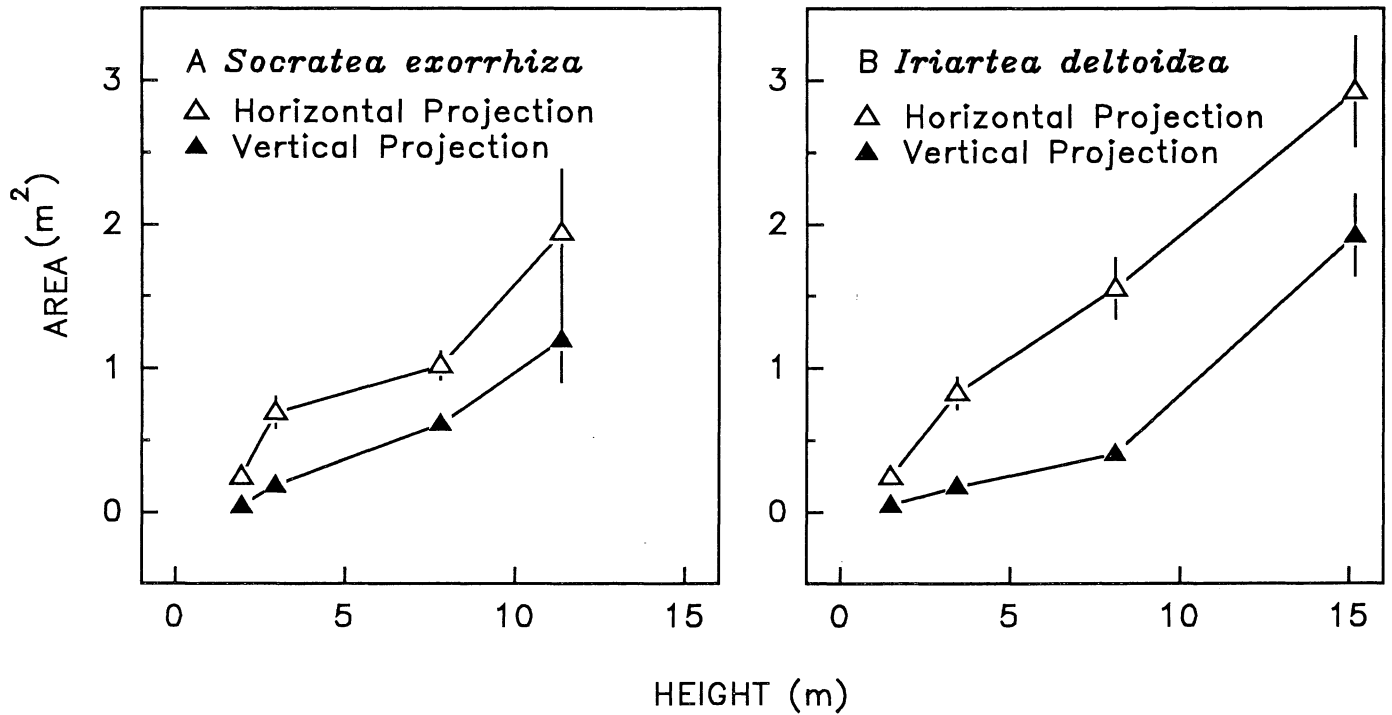


Fig. 4. The area of individual *S. exorrhiza* (A) and *I. deltoidea* (B) leaves projected on a horizontal plane (i.e., viewed from above, open symbols) and projected on a vertical plane (i.e., viewed laterally, closed symbols).

present in 40% of individuals with heights between 10 and 15 m, in 90% of individuals with heights between 15 and 20 m, and in all individuals taller than 20 m (Fig. 7a). The degree of multilayer character increased mark-

edly with height, such that leaves of taller individuals were more highly dissected and had their narrow fin leaflets displayed in more layers than shorter individuals. Increasing degree of multilayer leaf character was asso-

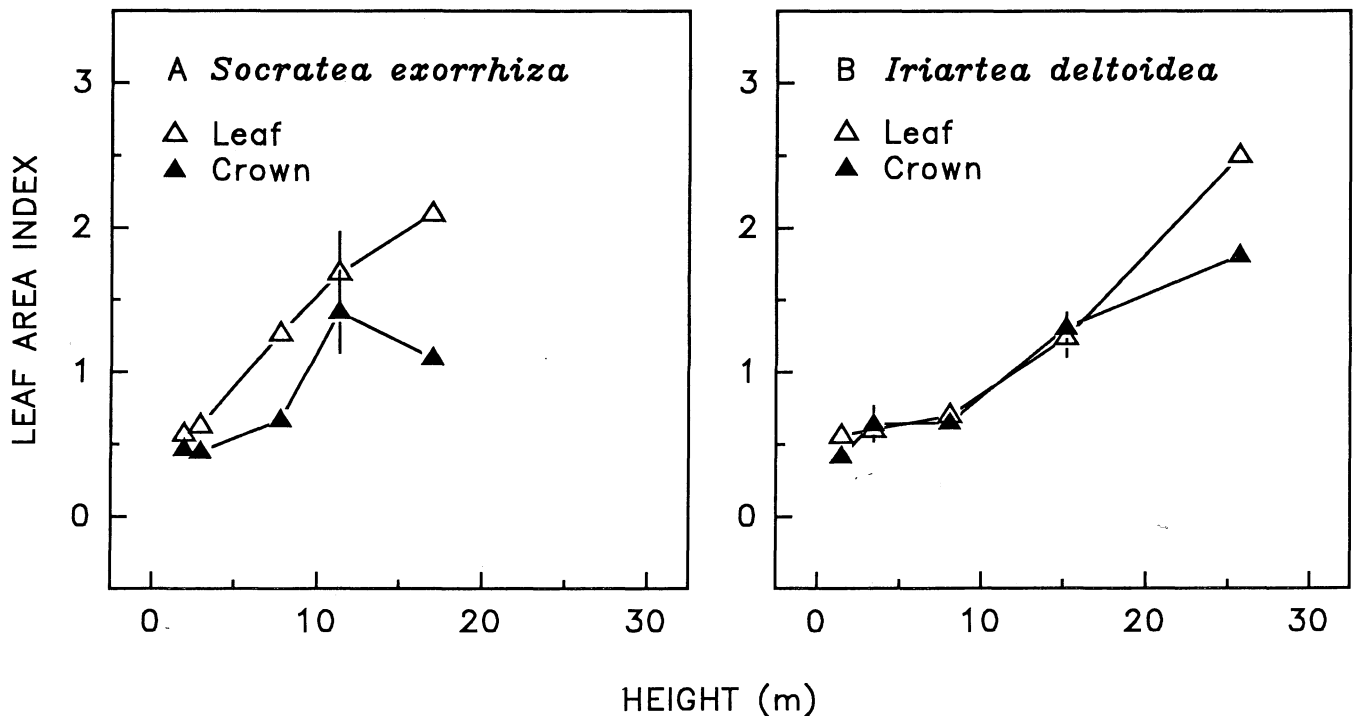


Fig. 5. Leaf area index (LAI) of individual leaves (open symbols) and the entire crown (closed symbols) of *S. exorrhiza* (A) and *I. deltoidea* (B). See text for details.

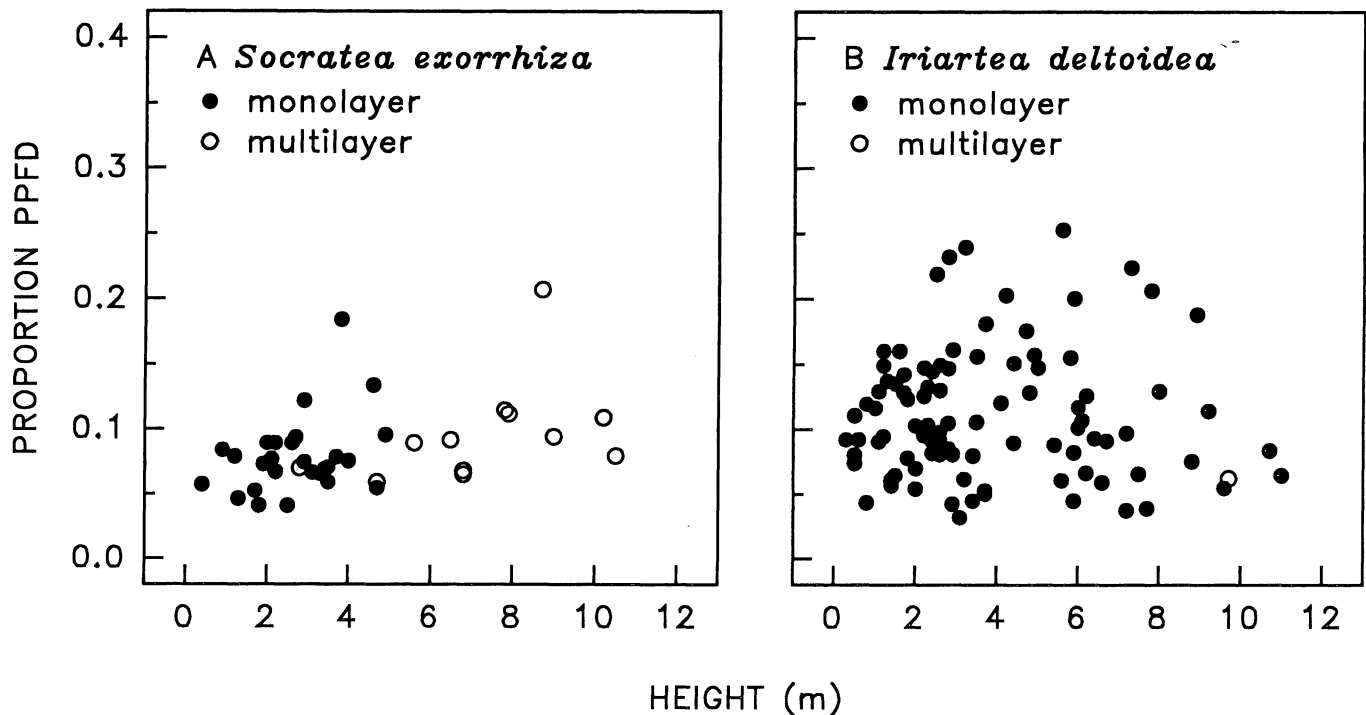


Fig. 6. Estimated photosynthetic photon flux density (PPFD), expressed as a proportion of PPFD in the open, at the tops of individual crowns of *S. exorrhiza* (A) and *I. deltoidea* (B). Closed symbols indicate plants with only monolayer leaves. Open symbols denote plants that have one or more multilayer leaves.

ciated with individuals whose crowns were positioned in or adjacent to light gaps (Fig. 7b).

DISCUSSION

Developmental changes in leaf morphology—The leaf morphology of *S. exorrhiza* and *I. deltoidea* undergoes three categories of developmental changes: 1) increases in size, area, and biomass; 2) production of additional distinct leaflet types; and 3) shift in leaflet arrangement from strictly dorsiventral (monolayer) to more radial (multilayer) display. This three-dimensional packing leads to LAIs greater than one for individual leaves (Fig. 5) and substantial increases in projected area when viewed from the side (Fig. 4). Similar overall form is attained by different means in the two species, in that straps split off on the proximal vs. distal sides of fins, for *S. exorrhiza* and *I. deltoidea*, respectively. While our studies did not examine developmental details of how leaflets are formed, the observation that splits between straps and fins are often incomplete suggests that the leaflets are formed by cell separation along plications. Highly dissected pinnately compound leaves develop in many species of arborescent palms, and functional equivalence may be achieved as the result of modification of the number of splits along plications or by increasing the number of plications. In the two species of iriarteoid palms studied, a combination of both enables a continuum of form in which leaf size and degree of multilayer character increase with height.

Fins constitute the elementary leaflet morphology in *S. exorrhiza* and *I. deltoidea*. All plants, regardless of size,

produce fins. Additional leaflet types are formed in larger individuals by the differential growth of outer lamina tissue relative to the longitudinal expansion of the rachis. This places the lamina in tension, eventually leading to a separation along plications. It is this splitting of an initially intact leaflet that results in the production of different leaflet morphologies. In *S. exorrhiza*, the portion of the leaflet base that is most compressed relative to the attached lamina occurs at its proximal edge such that the stresses are greatest along the basal margin of the leaflet (Fig. 2A). As this is the long, straight side of the praemorse leaflet, strap-shaped leaflets are produced (Fig. 2B). In *I. deltoidea*, the leaflet base is compressed on the distal side (Fig. 2D); thus the first separation results in a wedge-shaped leaflet (secondary fin), with subsequent tears producing strap-shaped leaflets (Fig. 2E). The compressed lamina tissue at the base of the leaflets is also twisted relative to the rest of the leaflet base (Fig. 2C, 2F), such that the straps and secondary fins stick up from the primary plane in which the fins occur (Fig. 1).

Horn (1971) argues that under low light levels it may be advantageous for a plant to distribute a fixed amount of photosynthetic tissue in a single layer, while high light levels might be best exploited by placing leaf tissue in multiple layers. Although Horn's discussion of monolayer vs. multilayer leaf arrangements is simplistic, it offers insight into the advantages of producing multilayer leaves in taller palms. In terms of resource allocation, producing additional layers of leaflets along an existing rachis may be the most efficient means for adding photosynthetic tissue while minimizing support and supply costs (Givnish, 1978). Since palms are not generally capable of pro-

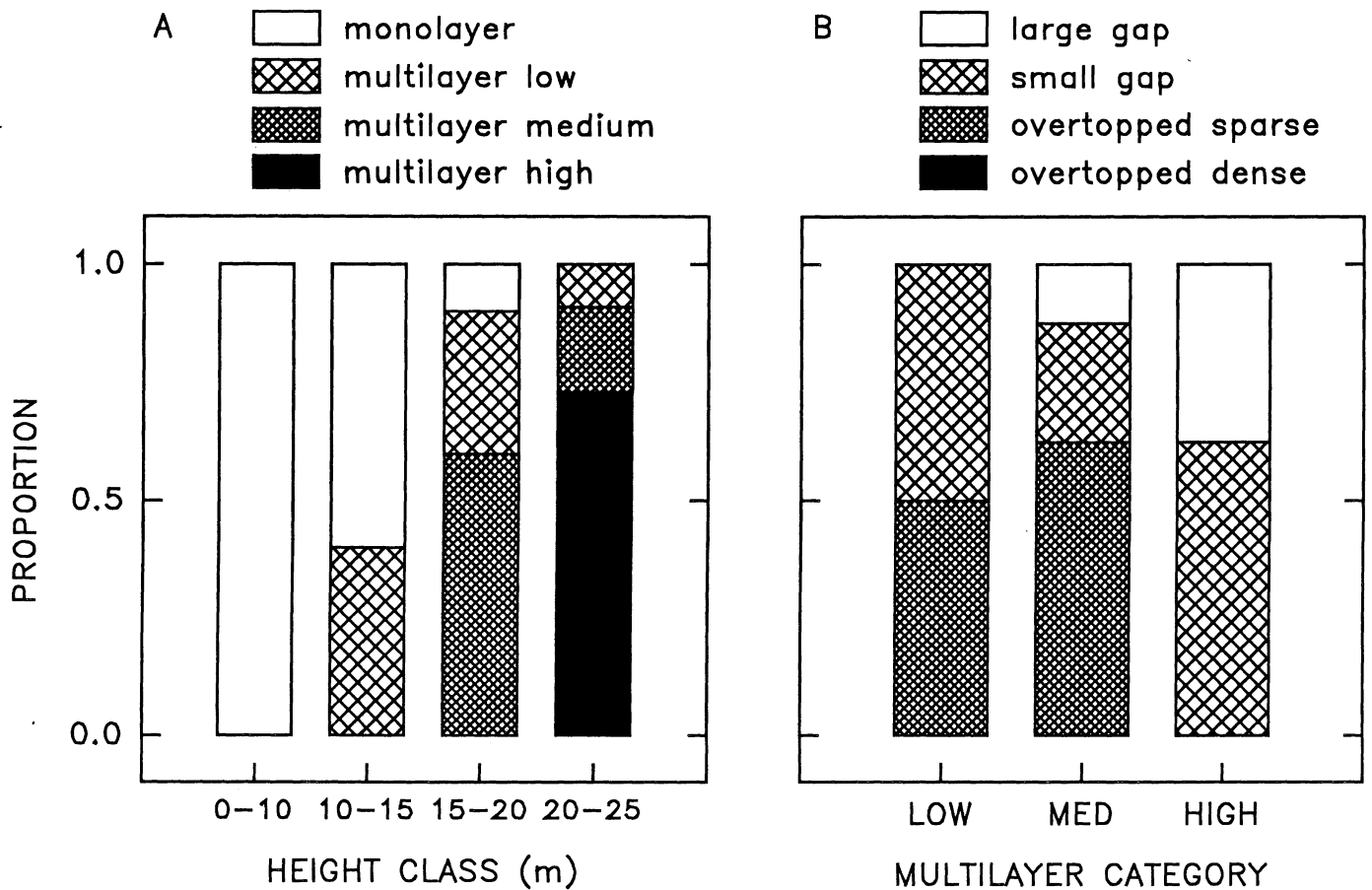


Fig. 7. A. Degree of multilayer character in relation to height for tall *I. deltoidea* ($N = 25$). B. Relationship between canopy light environment and degree of multilayer character for the individuals in panel A that were classified as multilayer.

ducing aboveground branches, production of complex multilayered leaves represents an efficient means for supporting a substantial photosynthetic area, without producing a large number of leaves. In addition, multilayer leaflet distributions enable light interception from many angular directions, not just from above. Even in tropical regions where palms are common, the sun angle is not directly overhead during the majority of time through the day and season, and canopy openings may also not be directly above plants growing in the forest understory (Canham et al., 1990). So lateral light interception may be an important consideration for tropical plants such as palms.

Developmental changes and life history—*S. exorrhiza* and *I. deltoidea* differ markedly in the height at which individuals begin to produce multilayered leaves (3–5 m for *S. exorrhiza* vs. 15–20 m *I. deltoidea*). This is consistent with the observation that *S. exorrhiza* is a fast-growing, light-demanding species, whereas *I. deltoidea* is a slower-growing, mature forest species (Rich, 1986; Rich, unpublished data). This is also in accord with the observation that *S. exorrhiza* places fewer resources in stem tissue per unit height growth and produces more stilt roots than *I. deltoidea* (Rich, 1985, 1986, 1987b). On the other hand, the young *I. deltoidea* sampled in this study oc-

curred in slightly higher light environments than *S. exorrhiza* as measured with photographs (Fig. 6). Further studies are needed to distinguish differences in life history and microclimate that may be related to variation in the height at which leaf morphology transitions occur.

Mechanisms and unanswered questions—Our data suggest that both size and light are important in determining when monolayer vs. multilayer leaves will be produced. The importance of light is further supported by observations that short individuals of *I. deltoidea* growing in light gaps and in areas where the forest has been cleared tend to have multilayer leaves. A mechanistic understanding would require controlled experiments, which are difficult because these palms are long-lived and large, and because the microhabitat is difficult to manipulate. If increased light levels serve as an ontogenetic switch that stimulates development of multilayer leaves, how quickly can individuals respond to changes in light environment? If, on the other hand, changes in leaf morphology are directly tied to leaf size, then conditions that increase resource availability may hasten the onset of the multilayer morphology.

Our study documents developmental changes in leaf morphology that we believe to be important in the ecology of arborescent forest palms. The two taxa of iriarteoid

palms examined undergo a transition from monolayer to multilayer leaf morphology during height growth. *S. exorrhiza* begins to produce multilayer leaves at heights between 3 and 6 m, whereas in *I. deltoidea* this transition occurs in individuals with heights between 10 and 20 m. Size, light environment, and life history patterns all appear to be important in determining when this transition occurs. Changes in leaf form enable palms to adjust foliar display as resource availability increases during height growth. Complex compound leaves in monopodial plants enable the efficient production of massive crowns without branching.

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