LEAF DISPLAY, CANOPY STRUCTURE, AND LIGHT INTERCEPTION OF TWO UNDERSTORY PALM SPECIES1

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ABSTRACT

The implications of leaf size, leaf display, and crown size for whole-plant light interception were investigated in Geonoma cuneata and Asterogyne martiana, two understory palm species native to Central American rain forests. Adults of A. martiana had longer leaves, more leaves per plant, and greater total leaf area than G. cuneata adults. Geometric measurements within whole crowns were used to calculate light interception efficiency, a leaf-based measure of the proportion of total incident light that is intercepted by a crown. Light interception efficiency was higher in adult G. cuneata than in adult A. martiana; seedlings of the two species did not differ significantly in light interception efficiency. Decreased efficiency of adult A. martiana crowns was largely due to an increased proportion of pendent leaves. Compared to G. cuneata, adults of A. martiana had greater light interception capacity (the product of light interception efficiency and total leaf area), but they also had higher biomass costs of light interception. Lower biomass costs of light interception in adult G. cuneata enable this species to exploit successfully the most deeply shaded microsites in the rain forest understory.

PLANTS growing in low light conditions often experience levels of photosynthetically active radiation (PAR) close to their light compensation point. Under these conditions, light interception by individual leaves is maximized when leaves are unshaded and are oriented perpendicular to the direction of incident radiation (deWit, 1965; Horn, 1971). If these conditions are met for all leaves within a plant crown, the light interception capacity of the entire crown is simply the sum of the area of all leaves within it. However, if leaves overlap within the crown, and/or if foliage is oriented at angles other than horizontal, whole-plant light interception capacity is not equivalent to total leaf area. To what extent do shaded plants achieve maximum light interception, and what factors constrain the efficiency of light interception?

The purpose of this study was to describe quantitatively the implications of leaf size, leaf display, and crown size for whole-plant light interception in two species of rain forest understory palms. Asterogyne martiana H. Wendl. ex Burrett and Geonoma cuneata H. Wendl. ex Spruce are shade tolerant dwarf palms that reach heights of 1-2 m. They are abundant in lowland rain forests from Nicaragua through Panama (Wessels Boer, 1968). Because of the extremely low light levels characteristic of their understory habitats (Chazdon and Fetcher, 1984), the leaf display and canopy structure of these palms should reflect selection pressures to maximize whole-plant light interception per unit of crown biomass. Quantitative studies of the relationship between light interception capacity and crown biomass may provide insights into the adaptive significance of leaf display and canopy structure in rain forest understory palms.

These palms have no aboveground branching; leaves are produced continuously throughout the year from a single growing point (Halle, Oldeman and Tomlinson, 1978). As individual plants grow from seedling stages to reproductive maturity, increases in both leaf size and leaf number contribute to the developing canopy area. Internodal elongation occurs following leaf abscission, so that leaves within the

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greater investments in leaf-support structures. Consequently, leaf orientation varies with leaf age; as new leaves are produced, older leaves are displaced outward and downward.

In this study I evaluate the significance of this pattern of canopy development to whole-plant light interception at different stages of growth. Increases in total leaf area may raise the probability of foliage overlap within the crown, thereby reducing the proportion of incident light that is intercepted. As crowns produce new leaves, the displacement of older leaves may also reduce light interception. Furthermore, increases in total leaf area require greater investments in leaf-support structures (Chazdon, 1984). In this paper, I describe the degree of foliage overlap within crowns, the distribution of leaf angles, and the total amount of light intercepted per biomass investment in crown structures from seedling to reproductive stages.

**Light interception efficiency**—The actual amount of light intercepted by a plant crown at any one point in time is a function of 1) the angular distribution of light intensity around the crown (light directionality), and 2) the spatial distribution of leaves within the crown. Therefore, light interception by individual crowns changes with time of day, atmospheric conditions, and season.

Following Warren Wilson (1981), I adopt a simplified approach to empirical measurement of whole-plant light interception under rain forest canopy conditions. In closed-canopy understory sites, most of the radiation available to the ground layer vegetation comes from directly above. Measurements of photosynthetically active radiation (PAR) at different angles in closed-canopy understory sites showed that horizontally oriented sensors received greater total daily quantum flux than sensors at other orientations (Chazdon, unpubl. data). Furthermore, sunflecks, which may contribute over 50% of total daily PAR (Chazdon and Fetcher, 1984), usually occur at midday. These data support the assumption that a horizontal orientation of leaf surfaces maximizes light interception of rain forest understory palms.

The light interception efficiency of a plant crown is defined as the ratio of total intercepted light flux to total incident light flux (Warren Wilson, 1981). Light interception efficiency (on a leaf-area basis) is composed of two independent components: the effect of leaf angles and the effect of foliage overlap. For the purposes of this study, I made the simplifying assumption that, under closed-canopy conditions, light interception efficiency is 100% when all leaf surface area is oriented horizontally and no leaves overlap within a crown. This assumption is the basis for the methods I adopt to estimate the light interception capacity of rain forest understory palms.

**Study site**—I conducted this study at La Selva Field Station of the Organization for Tropical Studies in the Caribbean lowlands of Costa Rica (10°26'N). The vegetation is classified as tropical premontane wet forest by Holdridge et al. (1971). Mean annual rainfall is approximately 4 m and mean daily temperature is 24 C. Details of the light environments in understory and gap habitats at La Selva are described by Chazdon and Fetcher (1984) and Chazdon (1984). More information on the climate and composition of the vegetation can be found in Holdridge et al. (1971) and Hartshorn (1972).

*Geonoma cuneata* and *Asterogyne martiana* are among the most common understory plants at La Selva. Densities of reproductive individuals in study sites were 306 and 256 per hectare, respectively (Chazdon, 1984). Although the two species are similar in habitat and bifid leaf morphology, reproductive individuals of *A. martiana* often exceed 1.5 m in height, whereas *G. cuneata* plants rarely reach this height (Chazdon, 1984).

**Methods**—**Crown size**—Leaf size and leaf number were measured during a growth census of plants in four 400 m² understory plots. Sampling areas included extremely shaded, gap edge, and gap interior microenvironments, thus spanning the range of environmental variation experienced by populations of these species at La Selva. All individuals having reproductive structures present were considered to be reproductively mature. Individuals of *A. martiana* were classified as seedlings if the midrib length of the most recently produced leaf was <25.0 cm; larger, nonreproductive plants were classified as juveniles. Individuals of *G. cuneata* were classified as seedlings if the midrib length of the most recently produced leaf was <20 cm; juveniles were classified as in *A. martiana*. Dead leaves were not included in leaf number measurements. The midrib length of the newest expanded leaf of each plant was measured as an index of leaf size. Data on leaf size and leaf number were used to create frequency distributions of crown size for seedling, juvenile, and reproductively mature plants of the two species.

**Leaf display**—Leaves were first numbered consecutively according to leaf age (Leaf 1 being the most recently produced). For each leaf, the following measurements were taken: compass
direction at the base of the lamina, petiole length, leaf length and width (W), midrib length (M), leaf height at the widest point, and petiole angle just below the lamina (P; Fig. 1A, B). Leaf angles from vertical were measured at four standard positions along the lamina; at the basal third of the lamina (V), the middle third (\(\frac{2}{3}\)), the bifid split (V), and the leaf tips (T; Fig. 1B). The percentage of total leaf area corresponding to these four locations was calculated based on a sample of four leaves of each species. From these data, a weighted average leaf angle was calculated for each leaf.

I used two methods to describe leaf curvature; both enable a description of leaf curvature that is independent of leaf size. I defined the arch length (A) of each leaf to be the straight-line distance between the base of the lamina and the bifid split (Fig. 1B). I then calculated percent extension as the ratio of arch length to midrib length \(\times 100\). By this definition, a high percent extension would be characteristic of a relatively flat leaf, whereas a curved leaf would have a relatively lower percent extension. For a second measure, the total degrees curvature of each leaf (\(\theta\)) was computed as the difference between the angle at the bifid split (V) and the angle at the base of the leaf (P) (Fig. 1B). Degrees curvature indicates the extent of bending that occurs along the lamina; a flat leaf has 0 degrees curvature, while a leaf that bends through a 90° angle has 90 degrees curvature.

All intact, living leaves of each plant were measured. I measured plants in situ, except for seedlings that were too small to measure in the field. These plants were uprooted carefully and brought to the laboratory, where they were repositioned with a pinch clamp at the base of the crown.

Leaf display measurements were taken on a sample of 19 and 21 individuals of G. cuneata and A. martiana, respectively, including at least five seedlings and five reproductive plants.

Leaf area and crown biomass—Following leaf display measurements, 15 individuals of each species were harvested for measurements of total leaf area and biomass distribution. Leaf areas were measured to the nearest square centimeter using a Licor 3100 leaf area meter. Fresh and dry weights of all crown structures, including petioles and leaf bases, were obtained using an electronic top-loading balance. In calculations of mean individual leaf area, I excluded leaves that had greater than 10% of the area removed. Whole-plant leaf areas include all leaves, regardless of condition.

Whole-plant light interception—Leaf display measurements were used to calculate two independent components of light interception efficiency, each with a maximum value of 1.0 (or 100%). The first component accounted for the angular distribution of leaf surfaces within the crown; this was termed angular efficiency. The second component accounted for the degree of superposition of leaves within the crown; this was termed exposure efficiency.

Angular efficiency was determined for each crown by calculating the horizontally projected area of each leaf, based on measurements of total leaf area, leaf angles at four positions along the leaf, and the proportion of total leaf area at these four angles. The leaf area in each of these four sections was multiplied by the sine of the angle at that position to obtain projected leaf area. This projected area was summed for all the leaves of each plant and divided by the total measured leaf area. Thus, if all the leaf tissue were horizontally oriented (90° from vertical), the projected area would be equal to the total area, and the angular efficiency would be 1.0 or 100%.

Exposure efficiency was calculated from drawings of two-dimensional \(\frac{1}{100}\) scale horizontal crown projections (top view) of each plant (Fig. 1C). Measurements of petiole and midrib lengths were multiplied by the sine of the petiole angle and the \(\frac{2}{3}\) leaf angle, respectively (Fig. 1B), to obtain horizontally projected petiole and midrib lengths. Leaf width was then drawn to scale perpendicular to the midrib (Fig. 1B). The leaf tips were drawn last, based on measured lengths and leaf angle T (Fig. 1B). Projected crown area was then measured by cutting out the area, weighing the paper, and then converting the weight to an area measure. Total unexposed (shaded) area was measured in the same manner (Fig. 1C). The exposure efficiency was calculated as the ratio of projected crown area to total area (projected + unexposed). In a crown with no overlapping leaf area, the exposure efficiency would be 1.0 or 100%.

The two measures of light interception efficiency described above are independent measures. Angular efficiency estimates the angular distribution of leaves regardless of spatial relationships among leaves. Exposure efficiency estimates the degree of within-crown shading regardless of leaf angles. It is possible for a crown to have all leaf tissue horizontal (an angular efficiency of 1.0) and half of the total leaf area shaded from above (an exposure efficiency of 0.50) and vice versa. Total light interception efficiency of each plant was obtained by multiplying both efficiency measures together, following Warren Wilson (1981).

Light interception capacity (Warren Wilson, 1981) was calculated as the product of total
Fig. 1. Projection of an idealized leaf of Asterogyne martiana from A) above, and B) side, showing locations of measurements; M = midrib length; W = width; $\theta$ = degrees curvature; A = arch length; P = petiole angle; $\frac{1}{3}$ = angle at basal third; $\frac{2}{3}$ = angle at middle third; V = angle at split; T = angle at leaf tips. C) Crown projection (top view) of a reproductive individual of Asterogyne martiana, drawn from leaf display measurements. Leaves are numbered from youngest (=1) to oldest.
measured leaf area and light interception efficiency. This definition of light interception capacity is equivalent to the "effective leaf area" of Honda and Fisher (1978) and to the "projected surface area" of Niklas and Kerchner (1984).

The allometric relationship between crown biomass and light interception capacity was then determined for both palm species using natural log-transformed data.

RESULTS—Crown characteristics—Sixty-five and 72% of the seedlings of G. cuneata and A. martiana, respectively, had 5–8 leaves (Fig. 2A). Crown sizes increased dramatically in A. martiana; 51% of reproductive individuals had 17 or more leaves. In contrast, 55% of the reproductive individuals of G. cuneata had between 9–12 leaves (Fig. 2C). Frequency distributions of different stages within each species and between species were significantly different (Kolmogorov-Smirnov test; \( P < 0.01 \)). A. martiana adults had an average of 17 leaves, compared to 9 in G. cuneata (Table 1). Leaves of A. martiana were significantly larger in length than leaves of G. cuneata but did not differ significantly in area (Student's \( t \)-test, \( P > 0.05 \)). Canopies of A. martiana were deeper and had larger total area (Table 1). On average, A. martiana crowns had 1.7 m\(^2\) total leaf area, and were 64 cm deep. On the other hand, the mean total leaf area of G. cuneata crowns was 0.9 m\(^2\), and crown depth was 50 cm (Table 1). The largest total leaf area for A. martiana and G. cuneata was 1.87 m\(^2\) and 1.19 m\(^2\), respectively.

Leaf display—The frequency distributions of weighted leaf angles and petiole angles differed significantly between species (Fig. 3, Kolmogorov-Smirnov test, \( P < 0.01 \)). In G. cuneata, 40% of all leaves were at angles between 80–100°, compared to only 27% in A. martiana. Thirty percent of A. martiana leaves were at angles greater than 120°, compared to 12% in G. cuneata. In G. cuneata, most of the petioles were oriented between 0–20°, whereas in A. martiana, the greatest proportion were between 21–40° (Fig. 3). In A. martiana, 6% of the petioles were horizontally oriented, whereas no petioles in G. cuneata were above 80°.

In both species, weighted leaf angles and petiole angles varied with crown position (Fig. 4). The uppermost leaves are more vertically oriented; these are also the youngest leaves (Fig. 4A). As new leaves are produced, the younger leaves are displaced horizontally (Fig. 4B) and eventually become pendent (Fig. 4D). The oldest leaves in the crown were oriented at angles above 90° in both species (Fig. 4D). Frequency distributions of weighted leaf angles and petiole angles at each of the four leaf age classes did not differ significantly between the species (Kolmogorov-Smirnov test; \( P > 0.05 \)).

Measurements of divergence angle, the compass angle between successive leaves, showed a high degree of variability within each species. For all plants, the mean divergence angle was between 138–143°; coefficients of variation ranged from 22–32. Fifty percent of A. martiana and 53% of G. cuneata had a clockwise phyllotactic spiral.

In both species, seedling leaves were significantly more curved than leaves from juvenile and reproductive plants, as measured by percent extension and degrees curvature (Table 2; analysis of variance: \( P < 0.001 \)). Leaves from juvenile and reproductive plants did not differ in percent extension in either species, but leaves of reproductive plants had significantly lower de-
Table 1. Crown characteristics of reproductive individuals of A. martiana and G. cuneata. Values are means ± SE. Data for leaf numbers are from plants growing in four 400 m² study plots; data for other characteristics are from a subset of these plants that were used for leaf display and crown biomass determinations. Significant differences between species are indicated by * (P < 0.05) and ** (P < 0.01).

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>G. cuneata</th>
<th>A. martiana</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of leaves</td>
<td>9.10 ± 0.3</td>
<td>17.2 ± 2.8**</td>
</tr>
<tr>
<td>N</td>
<td>58</td>
<td>47</td>
</tr>
<tr>
<td>Rachis length (cm)</td>
<td>49.3 ± 1.26</td>
<td>63.4 ± 0.79*</td>
</tr>
<tr>
<td>N</td>
<td>41</td>
<td>65</td>
</tr>
<tr>
<td>Individual leaf area (cm²)</td>
<td>1,039.6 ± 41.3</td>
<td>1,194.2 ± 29.2</td>
</tr>
<tr>
<td>N</td>
<td>35</td>
<td>60</td>
</tr>
<tr>
<td>Whole-plant leaf area (m²)</td>
<td>0.9 ± 0.11</td>
<td>1.7 ± 0.08**</td>
</tr>
<tr>
<td>N</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Crown depth (cm)</td>
<td>49.6 ± 4.9</td>
<td>63.6 ± 4.3*</td>
</tr>
<tr>
<td>N</td>
<td>5</td>
<td>5</td>
</tr>
</tbody>
</table>

Degrees curvature compared to leaves of juveniles (Student’s t-test: P < 0.05).

Seedling leaves of A. martiana had higher degrees curvature compared to seedling leaves of G. cuneata but were similar in percent extension (Table 2). These results confirm the visual impression that seedling leaves of A. martiana are relatively flat along all but the basal portion of the lamina, where there is a pronounced bend. Larger leaves of A. martiana and G. cuneata are more evenly curved along the lamina. In larger leaves, differences in curvature within and between species are relatively minor. In both species arch length was linearly related to midrib length, indicating that leaf droop was a constant fraction of leaf length (linear regression model; A. martiana: r = 0.99, P < 0.01; G. cuneata: r = 1.00, P < 0.01).

Light interception capacity—In A. martiana, mean light interception capacity increased 47-fold from seedlings to reproductive plants (Table 2). In contrast, the mean light interception capacity of reproductive plants of G. cuneata was only 24 times greater than that of seedlings. The total leaf area of reproductive individuals of A. martiana was, on average, 1.83 times greater than in G. cuneata, whereas light interception capacity was, on average, only 1.66 times greater.

Light interception capacity had a negative allometric relationship with crown biomass; light interception capacity increased at a slower rate than crown biomass (Fig. 6). Both species showed a significant linear relationship (A. martiana: r = 0.99; G. cuneata: r = 0.99, linear regression model). The slopes of the two lines were not significantly different (small sample t-test for parallelism; P < 0.05). Analysis of covariance was done to test for significant differences between the regression lines (Table 3). No significant differences were found (analysis of covariance; F = 0.056; P > 0.10). The slope of the combined regression line was 0.833. Consequently, the ratio of light interception capacity to crown biomass decreased substantially from small to large crown sizes.

Discussion—Increases in leaf size and leaf number during crown development significantly reduced the efficiency of light interception in the largest individuals of A. martiana but not in G. cuneata (Fig. 5A). In reproductive individuals of A. martiana, angular efficiency was substantially lower compared to G. cuneata (Fig. 5A). This difference can be largely attributed to the greater number of pendent leaves in crowns of adult A. martiana. In both species, the tendency for leaves older than Leaf 9 to be pendent is clearly seen in Fig. 4D. Based on the mean number of leaves of adults (Table
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CHAZDON—WHOLE-PLANT LIGHT INTERCEPTION 1499

Weighted Leaf Angle
Petiole Angle

N:248
A. martiana
N:266

Petiole Angle

N:141
G. cuneata
N:141

Fig. 3. Frequency distributions of weighted average leaf angles (*) and petiole angles (**) of Asterogyne martiana and Geonoma cuneata.

1), these older leaves comprise 42% of the leaf population in A. martiana, but only 1% of G. cuneata leaves. A major constraint on light interception efficiency in adult A. martiana is the downward displacement of older leaves resulting from the large number of leaves in the crown. Adult G. cuneata, with an average of only nine leaves, have fewer pendent leaves.

Relatively little self-shading occurred within crowns of the two species; minimum exposure efficiency was 88% for adult A. martiana (Fig. 5B). In seedlings, less than 10% of the total leaf area was shaded from above. This result may be attributed to the even distribution of leaves around the main axis. A divergence angle of 137.5° results in an even distribution of leaves around the main axis and minimizes overlap (Leigh, 1972). The mean divergence angle of both species was very close to this "ideal angle." These palms follow 3/8 phyllotaxy; crowns with more than eight leaves must therefore have some leaf overlap. Crowns of reproductive individuals of G. cuneata have an average of nine leaves, which may explain the slightly

Fig. 4. Frequency distribution of weighted leaf angles and petiole angles in four relative leafage classes. A) Leaves 1-3; B) Leaves 4-6; C) Leaves 7-9; D) Leaves >9 for G. cuneata (□) and A. martiana (□). Leaves are numbered from youngest (=1) to oldest.
**Table 2.** Percent extension (%), curvature (°) of leaves, and light interception capacity (cm$^2$) of crowns of seedlings, juveniles, and reproductive individuals of *G. cuneata* and *A. martiana*. Values are means ± SE for individual leaves and whole crowns.

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Stage</th>
<th><em>G. cuneata</em></th>
<th><em>A. martiana</em></th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Percent extension</td>
<td>Seedling</td>
<td>89.3 ± 1.0</td>
<td>89.7 ± 1.2</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>Juvenile</td>
<td>93.3 ± 1.7</td>
<td>93.8 ± 0.9</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>Reproductive</td>
<td>93.9 ± 0.3</td>
<td>93.1 ± 0.4</td>
<td>88</td>
</tr>
<tr>
<td>Curvature</td>
<td>Seedling</td>
<td>77.7 ± 3.1</td>
<td>94.4 ± 2.4</td>
<td>28</td>
</tr>
<tr>
<td></td>
<td>Juvenile</td>
<td>74.4 ± 3.2</td>
<td>68.5 ± 1.8</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>Reproductive</td>
<td>60.0 ± 1.3</td>
<td>65.1 ± 0.9</td>
<td>88</td>
</tr>
<tr>
<td>Light Interception</td>
<td>Seedling</td>
<td>298 ± 57.5</td>
<td>256.2 ± 162.6</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Juvenile</td>
<td>2,415.2 ± 763.3</td>
<td>4,286.6 ± 1,320.8</td>
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<tr>
<td></td>
<td>Reproductive</td>
<td>7,281.8 ± 918.1</td>
<td>12,114.3 ± 547.2</td>
<td></td>
</tr>
</tbody>
</table>

*Values are means ± SE of five plants. For *G. cuneata* juveniles, where N = 2.*

lower degree of leaf superposition in this species (Table 1; Fig. 5B).

Although the canopy structures of *A. martiana* and *G. cuneata* differ in several important respects, the similarities between the two species underlie their success as shade tolerant rain forest understory plants. One of these similarities is leaf morphology. The plicate lamina provides considerable rigidity of the leaf surface, thereby increasing the projected leaf area. Both species have bifid leaves with a cuneate base, a shape that permits a spiral arrangement of leaves around the main axis with a minimal degree of tissue overlap (Fig. 1C). Leaves of reproductive *A. martiana* are narrower than *G. cuneata* leaves of similar length. This circumstance allows more leaves to be packed in crowns of *A. martiana*, without increasing within-crown shading (Figs. 2C, 5B). Furthermore, in both species, larger leaves are relatively more narrow than small leaves; the width:length ratio decreases are length increases (Chazdon, unpubl. data). This morphological feature serves to reduce the degree of within-crown shading as leaf size and leaf numbers increase during ontogeny (Fig. 2).

The result that leaf curvature was relatively constant over a large range of leaf sizes indicates that these leaves and their mechanical support tissue maintain elastic similarity; leaf droop (as measured by arch length) was linearly related to leaf length (Givnish, 1982; McMahon and Kronauer, 1976). In species where leaf size increases during ontogeny, elastic similarity ensures that leaf orientation is independent of leaf size (although orientation may not be independent of leaf age). The principle of elastic similarity has been demonstrated in tree boles and branches (McMahon and Kronauer, 1976; King and Loucks, 1978). These data provide the first empirical demonstration of its relevance to leaf display.

Although reproductive individuals of *A. martiana* had lower total light interception efficiency compared to *G. cuneata*, these plants possessed greater total leaf area and therefore

**Table 3.** Results of linear regression tests and analysis of covariance for log (light interception capacity) vs. log (crown dry weight) in *G. cuneata* and *A. martiana*.

<table>
<thead>
<tr>
<th>Species</th>
<th>Source of variation</th>
<th>df</th>
<th>Sum of squares</th>
<th>Mean square</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>G. cuneata</em></td>
<td>Regression</td>
<td>1</td>
<td>27.98</td>
<td>27.98</td>
<td>349.1</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>Residual</td>
<td>10</td>
<td>0.801</td>
<td>0.0801</td>
<td></td>
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</tr>
<tr>
<td><em>A. martiana</em></td>
<td>Regression</td>
<td>1</td>
<td>64.09</td>
<td>64.09</td>
<td>4,408</td>
<td>0.001</td>
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<tr>
<td></td>
<td>Residual</td>
<td>15</td>
<td>0.0189</td>
<td>0.015</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Combined</td>
<td>Regression</td>
<td>1</td>
<td>92.23</td>
<td>92.23</td>
<td>2,333</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>Residual</td>
<td>25</td>
<td>0.993</td>
<td>0.040</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ancova</td>
<td>Species</td>
<td>1</td>
<td>0.0023</td>
<td>0.0023</td>
<td>0.0556</td>
<td>&gt;0.10</td>
</tr>
<tr>
<td></td>
<td>Residual</td>
<td>24</td>
<td>0.9937</td>
<td>0.0414</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
had a higher total light interception capacity (Fig. 6; Table 2). However, absolute biomass costs of light interception were also highest in *A. martiana* (Fig. 6). The allometric relationship between light interception capacity and crown biomass shows that *A. martiana* adults had greater size-specific biomass costs of light interception relative to *G. cuneata*. Biomass costs of light interception include investments in nonphotosynthetic leaf-support structures, such as rachises, petioles, and leaf bases. The higher biomass costs of light interception in adult *A. martiana* can be attributed to higher size-specific biomass costs of leaf-support structures (Chazdon, 1984) as well as lower light interception efficiency (Fig. 5C).

Assuming similar photosynthetic capacities, plants that have relatively lower biomass costs of light interception should be more shade tolerant; that is, growth is possible under greater degrees of shade. Thus, *G. cuneata*, with lower biomass costs of light interception, should be more shade tolerant than *A. martiana*. Measurements of PAR in closed-canopy understory microsites indicate that reproductive individuals of *A. martiana* receive higher daily total photosynthetic photon flux densities compared to *G. cuneata* (Chazdon, 1984). Furthermore, seedlings of the two species have similar photosynthetic rates (Chazdon, 1984). Because the lower biomass costs of light interception in *G. cuneata* are mainly attributed to small crown size (Fig. 6), small size at reproductive maturity is an important feature enabling this species to complete its life cycle in the most shaded understory microsites in the rain forest.

The model of light interception used in this study assumes that light interception is maximized by horizontally oriented, nonoverlapping leaves. This assumption is valid for most closed-canopy understory conditions, where light comes mainly from above. However, in some rain forest microenvironments, such as gap edges, much of the PAR may come from sidelighting. To the extent that the PAR reaching the forest understory does not come from directly overhead, the vertical and angular distribution of leaves within the crown is important for maximizing total light interception (Blackman, 1962; deWit, 1965).

Whole-plant light interception in these understory palms is not a simple function of total leaf area or crown biomass. Increases in leaf number and leaf size during development impose constraints on light interception at the whole-plant level. Crown size in plants of deeply shaded environments may, in fact, be limited by these constraints as well as by the struc-

![Fig. 6. Allometric log/log plot of light interception capacity (cm²) vs. crown biomass (g) in *Geonoma cuneata* (■) and *Asterogyne martiana* (▲). Solid symbols indicate reproductive individuals.](image)

**LITERATURE CITED**


