LIGHT INTERCEPTION EFFICIENCY OF THE UNDERSTORY PALM *CALYPTROGYNE GHIESBREGHTIANA* UNDER DEEP SHADE CONDITIONS

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Abstract. The tropical rain forest understory palm, *Calyptrogyne ghiesbreghtiana* Linden ex H. Wendl. (Arecaceae), exploits forest microhabitats characterized by dense shade conditions. In plants exploiting light-limited environments natural selection has shaped the architecture and pattern of leaf display to increase the efficiency of light interception. The optimal strategy of leaf display is to maintain a minimal overlap while keeping the display angles of the physiologically active leaves close to the horizontal, thus increasing the chances of maintaining a positive carbon balance. To measure the efficiency of leaf display in light interception, and determine how plant architecture and leaf display adjust to deep shade in reproductive individuals of *C. ghiesbreghtiana* under a narrow range of shade conditions, we randomly sampled 20 palms located under primary forest in Braulio Carrillo National Park, Costa Rica. We measured crown structure and efficiency of light interception, calculated as the proportion of the difference between total effective leaf area (horizontal projection of the leaf blade) and overlapped leaf area relative to the total leaf area of the plant. Within the sampled height range (0.6–2.0 m) we found an average of 12 leaves per plant. Leaves were large (0.26 m², S.D. = 0.08), arranged in spiral and distributed homogeneously around the stem. The average efficiency of light interception was high (93.88%, S.D. = 8.6%, range = 67–100%) compared with efficiencies reported in previous studies for other understory palms. The number of overlapped leaves and total overlapped area increased with the total number of leaves, showing that the plant must continuously adjust its architecture of leaf display (produced in a different light environment) to accommodate for increased leaf area. This type of architecture (spirally produced leaves) could be the most effective response under the intense shade conditions of forest understories.

Resumen. La palma de sotobosque del bosque húmedo tropical *Calyptrogyne ghiesbreghtiana* Linden ex H. Wendl. (Arecaceae), ocupa microhábitats caracterizados por condiciones de sombra profunda. En plantas de ambientes limitados en luz, la selección natural ha modificado la arquitectura de la planta y el patrón de despliegue foliar para aumentar la eficiencia en la intercepción lumínica. La estrategia óptima de despliegue de hojas consiste en mantener un traslape mínimo, y a la vez, mantener los ángulos de despliegue de las hojas fisiológicamente activas cercanos a la horizontal para mantener un balance carbónico positivo. Para medir la eficiencia del despliegue foliar en la intercepción de la luz, y determinar cómo la arquitectura de la planta y el despliegue foliar se ajustan a condiciones de sombra profunda en *C. ghiesbreghtiana*, muestreamos al azar 20 individuos reproductivos a lo largo de un rango estrecho de condiciones de sombra en el bosque primario del Parque Nacional Braulio Carrillo, Costa Rica. Medimos la estructura de la copa y la eficiencia en la intercepción de luz, calculada como la proporción de la diferencia entre el área total efectiva (proyección horizontal de la lámina foliar) y el área foliar traslapada con relación al área foliar total de la planta. Dentro del rango de alturas muestreado (0.6–2.0 m) encontramos un promedio de 12 hojas por planta. Las hojas de gran tamaño (0.26 m², D.E. = 0.08) estuvieron organizadas homogéneamente en espiral alrededor del tallo. El promedio de eficiencia en la intercepción de luz fue alto (93.88%, D.E. = 8.6%, rango = 67–100%) en comparación con estudios previos en plantas de sotobosque. El número de hojas traslapadas y el área total traslapada aumentó con el número total de hojas, lo cual demuestra que la planta debe adecuar constantemente su arquitectura de despliegue foliar producida en un ambiente lumínico diferente al actual, para balancear el aumento en área foliar. Este tipo de arquitectura (hojas en espiral) podría ser la alternativa más plástica bajo las condiciones de sombra profunda del sotobosque. *Accepted 15 November 2006.*

Keywords: Calyptrogyne ghiesbreghtiana, *Costa Rica*, *optimal leaf display*, *palm ecology*, *plant architecture*, *understory palms*.

INTRODUCTION

The architectural arrangement of leaves in a plant canopy affects light interception, heat exchange, and gradients of atmospheric water vapor and CO_2 concentration experienced by individual leaves, which in turn influence overall plant performance (Ezcurra *et al.* 1991, Ackerly & Bazzaz 1995, Pearcy & Valladares 1999, Valladares 1999). Although plant architecture varies greatly due to environmental factors (Horn

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1971), there is an underlying optimal arrangement, selected within the context of the spatial and temporal changes in resource availability where the species has evolved (Hallé 1978, Sterck & Bongers 2001).

Under deep shade conditions, such as the tropical forest understory, leaf display strategy is critical for survival and reproduction. Here, light that reaches the canopy is rapidly absorbed by the tree crowns and only 1–2 % of the photosynthetically active radiation penetrates to the forest floor (Kira & Yoda 1989). Despite the importance of lateral light influencing tree growth under dense shade conditions (Clark & Clark 1992), the majority of the energy-rich, actinic radiation reaches the understory at a vertical angle from the canopy, especially around noon (Chazdon et al. 1996, pers. obs.). It is reasonable to expect that in this environment natural selection has shaped the phyllotaxy and crown structure of understory plants to increase the efficiency of intercepting perpendicular light (Poorter & Werger 1999). The best strategy to increase light interception under light-limited conditions is to invest more in horizontal crown expansion (Poorter & Werger 1999), although the diversity of plant forms in the understory reflects the variety of alternatives of maximizing light capture (e.g., Valladares et al. 2002).

Horn (1971) suggested that shade-adapted species reduce self-shading by constructing a leaf monolayer. This is not necessarily the case in many understory palms, where a spiral leaf display significantly reduces leaf overlap without being oriented in the same horizontal plane. According to mathematical models, spiral leaf arrangement represents one of the most common phyllotaxies that increases light interception while decreasing overlap (Niklas 1988, 1992, Valladares 1999). With little overlap, the effective leaf area (i.e., the vertical leaf projection over a horizontal plane) is higher, increasing the chances of maintaining a positive carbon balance under intense shade.

Considering the energetic limitations of the understory, increasing light interception is critical since several short-term (e.g., speed of photosynthetic induction and stomatal conductance, Chazdon & Pearcy 1986) as well as long-term responses that imply chances in resource allocation (e.g., leaf structure, leaf turnover rates, and biomass allocation for growth and reproduction, Fetcher et al. 1987, Chazdon 1991, Cunningham 1997a) are dependent on sufficient access to light. The combination of these responses directly affects plant fitness, and thus plant reproductive output (Cunningham 1997a). Overall plant architecture and allometry are the outcome of selective pressures acting upon the optimality of displaying leaf area to benefit from current light conditions (static function of architecture), as well as upon the plasticity to correct leaf display in the face of temporal changes in light (dynamic function of architecture, Kohyama 1987, King 1990). Niche differences in habitat selection are thus reflected in the leaf display strategy, segregating species according to light preferences and flexibility of temporal responses to light changes (Kohyama 1987, Canham 1988, King 1990, Poorter & Werner 1999, Poorter et al. 2003). Since leaf display interacts with a suite of morphological and physiological traits that compensate for suboptimal leaf phyllotaxies (Niklas 1988), it is critical to understand how crown architecture in shade-adapted plants integrates the overall adjustment of the individual to different spatial and temporal changes in light conditions.

The aim of this study is to characterize the strategy of leaf display in the tropical forest understory palm *Calyptrogyne ghiesbreghtiana* Linden ex H. Wendl. (Arecaceae). We focused on the following questions:

a) What is the efficiency of leaf display for vertical light interception in reproductive individuals established under a very narrow range of deep shade conditions?

b) What is the extent of leaf overlap?

c) To what degree does the actual leaf display approach the expected optimal, considering that palms would minimize leaf overlap but maximize leaf area index as the palm adds more leaves, under the assumption that most of the light reaches the understory at a vertical angle from the canopy?

Calyptrogyne ghiesbreghtiana is a single-stemmed, long-lived palm whose reproductive output is influenced by plant size, number of leaves, and light environment (Cunningham 1997a). Studies on the growth form, architecture, and biomass distribution of other understory palms (e.g., Chazdon 1985, 1986a, 1991) have shown a relatively high light interception efficiency, but it is not known to what extent these results are general to other palm species that complete their life cycle in the understory.

METHODS

Study area. The study was conducted in August and September 1999 at Quebrada González, Braulio Carrillo National Park (BCNP), Costa Rica (47 583 ha,

400–500 m a.s.l., 10°97′N, 83°05′W) a Tropical Premontane Wet Forest (Tosi 1969) located on the Caribbean side of the Central Mountain Slope. Rainfall at this site averages 4 500 mm/year and temperature ranges between 25°C and 28°C (Herrera 2000). In Braulio Carrillo, elevation ranges from lowland tropical rainforest (30 m) to tropical montane forest (2 906 m), representing one of the last protected elevation gradients still covered by continuous forests in Central America. These conditions support dense evergreen forests, complex in structure and highly diverse in species composition.

Study species. The Neotropical understory palm *Calyptrogyne ghiesbreghtiana* Linden ex H. Wendl. is widely distributed from Chiapas, Mexico, to Panama, from sea level to 1 550 m, being a common component of the understory of lowland, premontane and montane forests across this range of elevation (Henderson *et al.* 1995, Grayum 2003). *C. ghiesbreghtiana* has a rosette leaf arrangement, where leaves emerge from the center of the spiral in a vertical angle and open towards a horizontal angle. As the leaves get older their display angle changes until it reaches an almost vertical angle towards the ground. The leaves are large, undivided or sparsely pinnate, and can be intensively dark red to maroon-colored when young. The leaf apex is bifurcated and the venation pronounced. The reproductive system of this palm has been intensively studied by Cunningham (1995, 1996, 1997a,b, 2000) and Tschapka (2003), since it constitutes the only well-documented case of bat pollination in palms.

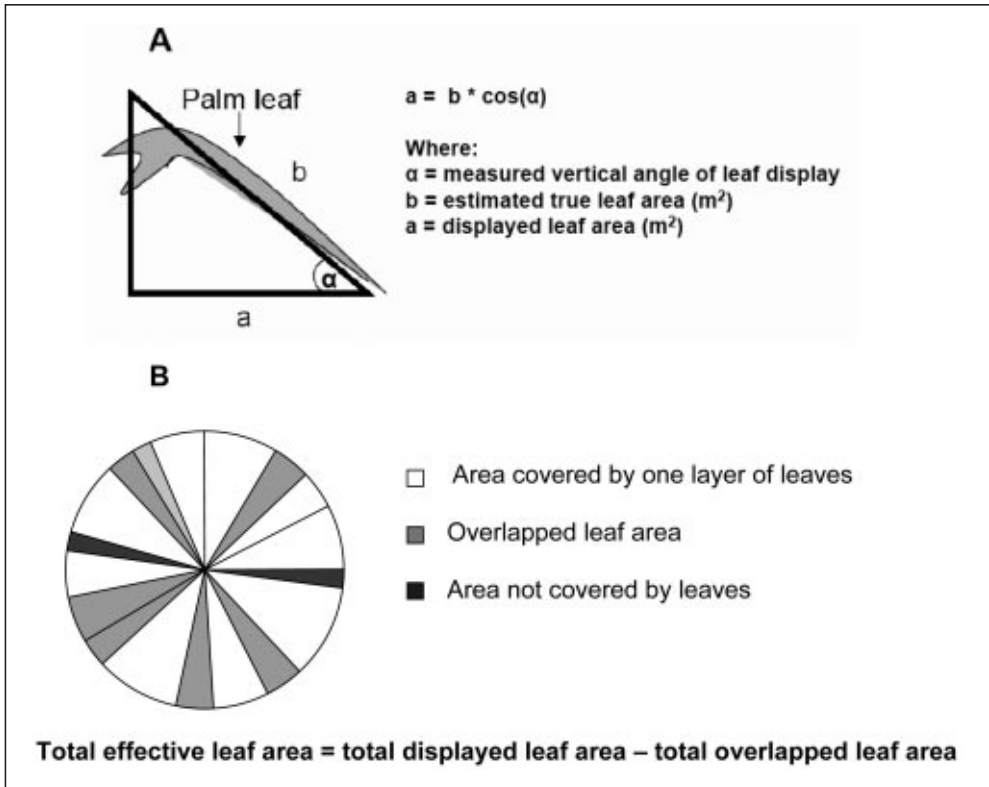FIG. 1. (A) Total displayed leaf area (m²) obtained from the summation of the horizontal projections of the leaf blade. The displayed leaf area was calculated from the cosine function X the estimated true leaf area. (B) Total effective leaf area (m²) is calculated by constructing a diagram of the crown of each individual palm, and then subtracting the overlapped leaf area from the total displayed leaf area.

Measurement of crown structure. Following Las Palmas trail we randomly chose 20 reproductive individuals of *C. ghiesbreghtiana* with recently formed inflorescences, that ranged in height 0.6 and 2.0 m and were separated by at least 50 m. We selected individuals located only under intense shade conditions (86–98% canopy cover) in primary forest. In every individual we measured the following parameters: a) plant height from the base to the tip of the stem, b) number of leaves, c) leaf position (considering as the last leaf the one closest to the base of the stem, which always corresponded to the oldest leaf, and as the first leaf (i.e., leaf # 0) the newest leaf, which corresponded to the leaf closest to the apex of the stem), d) leaf length from the base of the leaf blade to the leaf bifurcation at the apex, e) maximum leaf width (which corresponded with the upper apex across the leaf bifurcation), f) leaf horizontal orientation relative to the geographic North, and g) the vertical leaf orientation or angle of leaf display. Vertical angles ranged from +90 (indicating a vertical leaf with the apex pointing upwards) to –90 (indicating a vertical leaf with the apex pointing to the ground). A vertical angle of 0 represented a leaf with a horizontal orientation. Leaf angles were measured with a SILVA clinometer type 15 (Binghamton, NY, USA). We did not consider leaves with more than 75% of the leaf blade damaged, although the frequency of such leaves was very low.

Measurement of leaf area. To estimate true leaf area in the field we first collected 16 leaves of various sizes from randomly chosen individuals, different from the ones used for the rest of the measurements. The leaf area from those leaves was measured with a LI-COR LI-3100 leaf area meter (LI-COR, Lincoln, NE, USA). We then used a linear regression between leaf width and length to estimate leaf area (r^2 = 0.95, $F_{2,14}$ = 141.65, P < 0.0001). We substituted the variables in this equation to estimate leaf area in the field, based on leaf width and length measurements.

Percentage of leaf overlap and efficiency of light interception. Based on field measurements of leaf area, vertical leaf angle, and leaf position, we constructed a diagram of every individual plant as seen from above with the leaves following the orientation of the horizontal angles. The total displayed leaf area was calculated as the summation of the areas of all the horizontal projections of the leaf blades as determined by the predominant vertical angle of leaf display (Fig. 1a). We then identified the leaves that overlapped, and added up the area of the leaf sections that overlapped, which constituted the total overlapped leaf area. The total effective leaf area was calculated as the summation of the displayed leaf areas that did not overlap (Fig. 1b). We then calculated the efficiency of light interception per individual plant according to:

Efficiency of light interception = (total effective leaf area) / (total leaf area)

Following this formula, the highest efficiency would be achieved when the effective leaf area equals the summation of the total leaf area (that is, when the vertical angle of leaf display is zero and there is no overlap). The above calculation is equivalent to the leaf area index (LAI).

Magnitude of canopy cover. The proportion of the canopy above every individual plant was measured with a spherical densiometer model C (Forestry Suppliers, Lincoln NE, USA) by obtaining the average of four measurements while pointing the instrument to the geographic North, South, East, and West at approximately 0.5 m away from the stem and 1.5 m above the ground.

RESULTS

Within the height range of the measured individuals (0.6–2.0 m), *C. ghiesbreghtiana* presented an average of 12 leaves per plant (S.D. = 2.19, N = 20, range = 8–18). The leaves were fairly large with an average area of 0.26 m² (S.D. = 0.08 m² N = 234). Leaf position around the stem was homogeneously spiral. We did not detect differences in leaf distribution relative to geographic orientation (North = 3.4 and S.D. = 0.33, East = 2.46 and S.D. = 0.33, South = 3.27 and S.D. = 0.35, and West = 3.13 and S.D. = 0.330, as reflected in a similar distribution of leaves per directional quadrant (χ^2 = 1.92, P = 0.17).

Despite the large variation in vertical angles (which fluctuated between +90° and –90°), most leaves had positive angles (mean = +22.7°, S.D. = 36.66). Younger leaves had very steep and positive angles, whereas the majority of leaves with negative angles were generally old and senescent. Leaf position around the stem explained a significant proportion of the variation in the magnitude of vertical angle of leaf display (r^2 = 0.47, $F_{17,215}$ = 11.25, P < 0.005; Fig 2a). Following the pattern of leaf production in *C. ghiesbreghtiana*, new leaves emerge vertically and acquire more horizontal angles as the blade expands and leaf weight increases. Older leaves are closer to the stem base and over time acquire more negative angles. Due to this process, leaf position did not explain a significant pro-
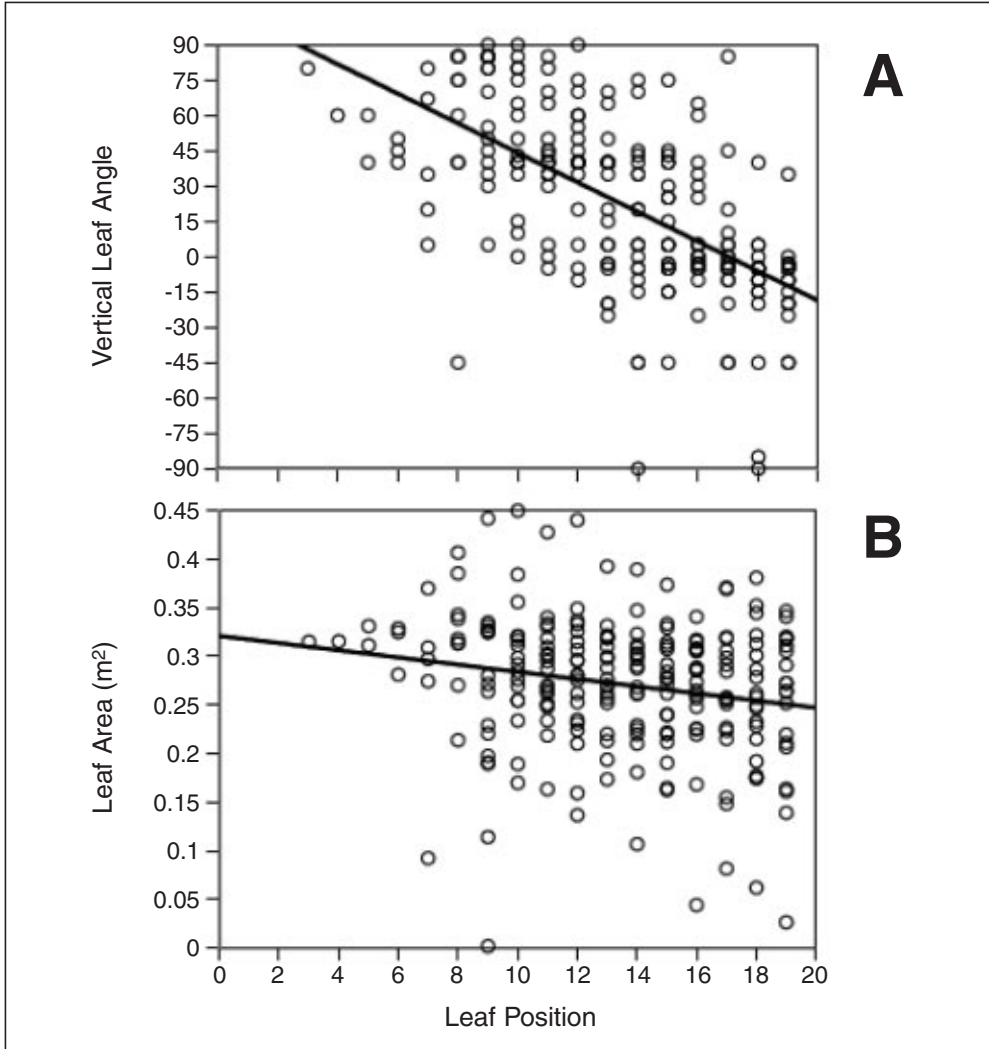
FIG. 2. (A) Variation in the vertical angle of leaf display versus leaf position in *C. ghiesbreghtiana*. (B) Variation in leaf area versus leaf position in *C. ghiesbreghtiana*, Braulio Carrillo National Park, Costa Rica.

portion of the variation in total leaf area ($r^2 = 0.06$, $F_{16,215} = 0.99$, $P = 0.46$; Fig 2b), which demonstrates that leaves, independent of their position, reach similar sizes at the end of expansion, contributing in similar proportion to the total plant leaf area, but not to the total displayed leaf area at a given time. The vertical angle of leaf display affected the magnitude of leaf overlap, and thus the proportion of effective leaf area. The relationship between vertical leaf angle of leaf display and effective leaf area is best described by a second-degree linear regression ($r^2 = 0.65$, $F_{2,231} = 218.63$, $P < 0.0001$; Fig 3). This model accounted for positive and negative values of the display angle. As expected, higher effective area was observed when leaves were displayed at an angle close to the horizontal. The scatter shown around the horizontal display angle (i.e., zero) corresponds to variation in either true leaf area or overlapped area.

Canopy cover was consistently high since sampled individuals were located in primary forest under dense cover (average = 95.29%, S.D. = 3.87, N = 20). Probably due to the small range of canopy cover values (86–98%), effective leaf area per plant did not show a significant relationship with canopy cover (r^2 = 0.02, $F_{1,17}$ = 0.36, P = 0.55, N = 19). In addition, canopy cover did not affect efficiency in the display of leaf area (r^2 = 0.11, $F_{1,17}$ = 2.13, P = 0.16) or the percentage of leaf overlap (r^2 = 0.07, $F_{1,17}$ = 1.31, P = 0.26).

The average efficiency in light interception was 93.88% (S.D. = 8.6%, range = 67–100%). Consistently with the 3/8 phyllotaxy, where crowns with more than 8 leaves must have some self-shading, the number of overlapped leaves (r^2 = 0.74, $F_{1,18}$ = 51.52, P < 0.0001) and total overlapped area (r^2 = 0.31, $F_{1,18}$ = 8.42, P < 0.009, Fig. 4) increased with the total number of leaves. Even though more leaves overlapped as plants increased in size and produced more leaves, overlapped leaf area increased only by a small amount. It is clear that more individuals need to be measured to determine the generality of this trend, since with less than 14 leaves the pattern of overlapped leaf area with increasing number of leaves is not significant (Fig. 4). The percentage of overlapped leaf area per individual was in general very low (average = 7.41%, S.D. = 9.72, N = 20).

DISCUSSION

Calyptrogyne ghiesbreghtiana exploits forest microhabitats characterized by dense shade. As would be expected for understory plants exploiting light-limited environments, the optimal strategy of leaf display is to maintain a minimal overlap while keeping the display angles of the physiologically active leaves close to the horizontal. Our results are congruent with these expectations. *Calyptrogyne ghiesbreghtiana* produces leaves continuously throughout the year, following a spiral arrangement similar to other understory palms such as *Asterogyne martiana* (Chazdon 1985, Cun-
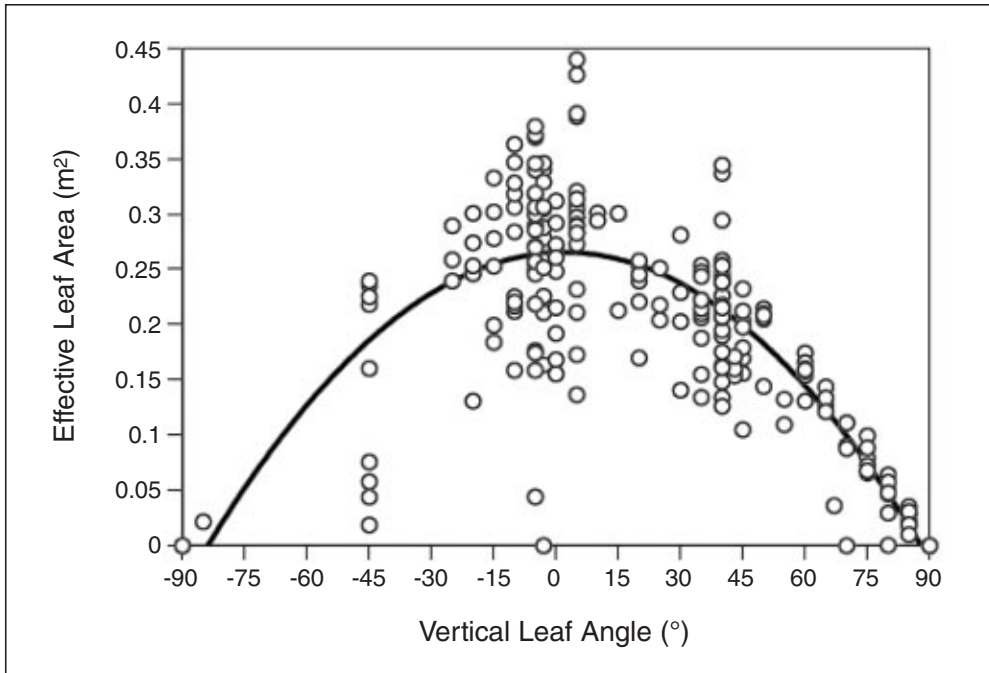

FIG. 3. Variation in effective leaf area as a function of vertical angle of leaf display in *C. ghiesbreghtiana* following a second-order polynomial regression, Braulio Carrillo National Park, Costa Rica. Negative values of vertical leaf angles refer to leaves displayed below the horizontal line.

FIG. 4. Relationship between number of leaves and (A) number of overlapped leaves, and (B) overlapped leaf area in *C. ghiesbreghtiana*, Braulio Carrillo National Park, Costa Rica.

ningham 1997a). This type of leaf architecture gives the plant sufficient flexibility to reduce leaf overlap as much as possible despite the increase in self-shading with increasing leaf numbers. The correspondence with an optimal strategy of leaf display was also reflected in having a similar number of leaves in all quadrants into which the crown was divided, demonstrating an even distribution of foliage around the stem.

Most mature leaves (i.e., neither young nor old, senescent leaves) had a vertical angle of leaf display close to the horizontal. As expected, leaves with vertical angles of display close to the horizontal presented a higher effective area. The growth form of *C. ghiesbreghtiana* permits the same leaves to experience different positions and orientations throughout their life span, since young leaves are produced almost vertically and decline with age until touching the ground and abscise from the plant. The high variation of vertical angles within a particular plant increases interception of light approaching the crown from different angles. In addition, it has been proposed that this orthotropic orientation of younger leaves increases water drainage, reducing epiphyllous colonization, which may affect light interception and cause leaf tissue damage (Coley *et al.* 1993). We observed that older leaves, which had been positioned in horizontal angles, usually possessed greater epiphyllous colonization.

Since plants were chosen to be in dense shade, canopy cover showed little variation between plants, and no relationship with effective leaf area, total leaf area, or percentage of leaf overlap. Our measurements of canopy cover were instantaneous, and thus limited in terms of explaining the plasticity of coping with changing light conditions. Understanding the impact of canopy structure on leaf display requires a longer-term perspective, since light distribution determines the intensity of reproduction in *C. ghiesbreghtiana* (Cunningham 1997a).

Chazdon (1985) performed a similar study at La Selva Biological Station, Costa Rica, and recorded efficiencies of 80 % and 71 % in reproductive individuals of the morphologically similar palms *Geonoma cuneata* and *Asterogyne martiana* respectively, which are much lower than the values observed in this study. *Geonoma cuneata* and *A. martiana* can reach greater sizes than *C. ghiesbreghtiana*. The average plant size and total leaf area was much higher in these species (0.9 ± 0.11 and 1.7 ± 0.08 m^2 in *G. cuneata* and *A. martiana* respectively) relative to *C. ghiesbreghtiana* (0.26 m^2 ± 0.08 m^2), and influenced the increased leaf overlap. Although *G. cuneata* had less leaves than *C. ghiesbreghtiana* (9.10 ± 0.3 vs. 12 ± 2.19 leaves per plant), in the latter species leaves are smaller. In contrast to adults, seedlings of *G. cuneata* and *A. martiana* had higher light interception efficiencies (87–88 %).

These results show that smaller palms display their leaf area more efficiently than larger palms, possibly a combination of having a less complex canopy, less leaf area, and smaller height. In addition, there is a strong selective pressure on understory plants to increase the efficiency of leaf display due to their reduced capacity to adjust to temporal and spatial changes in the distribution of resources (Wright 2002).

The extent of leaf overlap (as % of total leaf area) was low in *C. ghiesbreghtiana*, considering that palms with 8 or more leaves must have some overlap due to the growth form of this species. Although increasing leaf number increased leaf overlap, in our case its magnitude was not enough to decrease the effective leaf area. It is thus clear that *C. ghiesbreghtiana* has a leaf number close to the optimum expected for the maximization of light capture. Other morphological characteristics could affect the leaf display strategy of this species, such as the pattern of temporal leaf phenology, the energetic costs of light acclimation, and the costs associated with maintaining the structural traits necessary to sustain new and existing leaves (Chazdon 1986, Ackerly 1999). Future lines of inquiry should be focused on the plasticity of adjustment to spatial and temporal changes in light intensity in this species by modifying plant architecture and physiology across a larger range of plant sizes (*cf.*, Pearcy & Yang 1996).

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