Physiological and Morphological Basis of Shade Tolerance in Rain Forest Understory Palms

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ABSTRACT

Shade tolerance results from the interaction of a plant's physiology and morphology. *Geonoma cuneata*, *Asterogyne martiana*, and *G. congesta*, three shade-tolerant palm species, have similar photosynthetic capacities, but differ in leaf morphology, crown size, and total biomass. Analyses of biomass allocation and leaf display show that size-dependent costs of whole-plant light interception strongly determine the minimum light conditions that can support growth and reproduction. *G. cuneata*, which reproduces at small sizes, has the lowest biomass costs of light interception, and can exploit the shadiest microsites within the rain forest understory.

RESUMEN

La condición de ser tolerante de sombra resulta de una interacción de la fisiologia y morfologia de la planta. *Geonoma cuneata*, *Asterogyne martiana*, y *G. congesta* son tres especies de palmas tolerantes de sombra con capacidades fotosintéticas muy parecidas, sino distintas formas de hojas, tamaños de copa, y biomasa total. Análisis de la distribución de biomasa y de la presentación de hojas indica que los gastos de interceptación de luz determinan las cantidades minimas de luz que permiten la regeneración. *G. cuneata*, la cual reproduce cuando es pequeña, tiene los gastos más bajo de interceptación de luz, y puede explotar los sitios más sombroso dentro del sotobosque.

Seventy-five percent of the world's palm species are found in rain forest habitats (Dransfield 1978). Within the forest, palms occupy a wide range of habitats: streambanks, ridges, swamps, clearings, forest regrowth, and mature forest. To add to this ecological complexity, many palm species experience dramatic changes in microenvironments during the course of their lives. Subcanopy species, such as *Welfia georgii*, from Central American lowland rain forests, germinate in the deep shade of the forest understory and gradually grow up through the lower layers of the forest (Vandermeer 1983). As the crowns reach higher levels, microenvironmental conditions change; light intensity, air temperature, and wind speed increase, while relative humidity decreases (Longman and Jenik 1974, Yoda 1974). The diversity and abundance of plant and animal life also change with height in the forest canopy. Ecological studies of rain forest species require a consideration of the range of environmental conditions that species encounter during their entire life history. This is particularly true in studies of plant physiological ecology, the study of the physiological basis of ecological patterns.

In many rain forests, the majority of palm species spend their entire life in the understory. These species are small in stature and are tolerant of shade, two characteristics that have led to their growing popularity as plotted plants. My doctoral research focused on the ecology of several species in the neotropical Arecoid tribe, Geonomeae, which includes the genera *Geonoma* and *Asterogyne* (Dransfield and Uhl 1986). These genera are distributed in wet, shaded habitats, and are thought to have diversified within rain forest understory conditions (Wessels Boer 1968). The objective of my study was to

1.   *Geonoma cuneata* in the arboretum at La Selva.

explore the ways in which physiology and morphology interact to produce an ecological result: shade tolerance. Rather than considering the physiological and morphological features of leaves in isolation from the whole plant, my approach to studying shade tolerance was oriented to the whole-plant level. The three species I investigated were appropriate for this study; they are well adapted to shaded understory conditions, are abundant, and differ in leaf morphology, plant size, and growth form.

Because the term shade tolerance has been used in many different ways, I will explain my definition here. Shade tolerance is the degree of shade that will permit growth, survival, and reproduction (=persistence) of an individual plant. This definition implies that: 1) shade tolerance is a matter of degree, not of simple presence or absence; 2) shade tolerance is measured by comparing growth and reproduction under a *range* of light con-

ditions (species 1 may have higher growth than species 2 in the same condition, yet may be less shade tolerant); 3) shade tolerance is a property of the whole plant, and not of its leaves. Shade tolerance involves both physiological and architectural characteristics. Photosynthetic responses to light determine the efficiency of light utilization at the leaf level. However, leaf display and canopy structure influence the amount of light that is available for photosynthesis. The distribution of biomass and energy to photosynthetic and non-photosynthetic structures also influences patterns of whole-plant productivity.

Study Area and Species

The study was conducted at La Selva Biological Station (10°26′N and 83°59′W), in the Caribbean lowlands of Costa Rica. The station is owned and operated by the

2.   *Asterogyne martiana* in extreme shade, La Selva.

Organization for Tropical Studies. The forest at La Selva is classified as Tropical Premontane Wet Forest on the west and Tropical Wet Forest on the east (Tosi 1969). Elevations range from 35 to 150 m. Mean annual rainfall is approximately 4 m and mean daily temperature is 25° C. The palm flora of La Selva is described by Chazdon (1985*a*).

Of the three species I studied, *Geonoma cuneata* Wendl. ex Spruce is the smallest in size. Reproductive individuals average about 1 m in height and have an average of 9 leaves (Fig. 1). Mean rachis length is 50 cm (Chazdon 1984). At La Selva, this species occurs in two forms; one form has bifid leaves, the other form has 2–3 irregularly placed splits per leaf. In my study, I considered only the bifid-leaved individuals. *Asterogyne martiana* Wendl. ex Burret is intermediate in size, reaching 1.5–2.0 m in height (Fig. 2).

Adults have an average of 17 leaves with a mean rachis length of 63 cm. Leaves are always bifid and are narrower than leaves of *G. cuneata* (Chazdon 1984). Both of these species are solitary.

Geonoma congesta Wendl. ex Spruce has multiple stems, and reaches 3–5 m in height (Fig. 3). Clones may possess as many as 20 or more stems. Each crown holds about 11 leaves, with a mean rachis length of 62 cm. Seedlings of *G. congesta* have bifid leaves, but leaves of juvenile and reproductive individuals are irregularly split. Leaves below 30 cm in length are always bifid, but above this size, the number of splits increases with rachis length. Most reproductive plants have from 3–6 splits per leaf (Chazdon 1984).

The three species in my study are among the most abundant understory plants at La Selva. Densities of reproductive plants range from 256–517 stems per

hectare (Chazdon 1984). In almost all shaded areas of La Selva, these species are found together. Although they are absent from large clearings and gaps, they are common in closed-canopy, gap-edge, and small-gap habitats. They range in distribution from Nicaragua to Panama, and occur only in moist forests (Wessels Boer 1968). *A. martiana* and *G. congesta* are widely used for thatch, but are otherwise not economically important.

Light Environment and Photosynthesis

Levels of photosynthetically active radiation (PAR) in the understory at La Selva are among the lowest recorded for any terrestrial habitat (Chazdon and Fetcher 1984, Chazdon 1986*b*). Despite the low light conditions that characterize understory habitats, the light environment is highly heterogeneous. Canopy gaps of a range of shapes and sizes produce irregular and unstable patterns of light availability within the understory. To characterize the photosynthetic light environments of the three species, detailed measurements of photosynthetically active radition (PAR) were made over a 3-yr period in 4 200 m² plots using PAR sensors (Chazdon 1986*b*). All individuals of the three species were marked for studies of microenvironment and growth.

Because these three palm species occur in the same understory habitats, there is a great deal of overlap in photosynthetic light conditions. Light conditions vary greatly both spatially and temporally. On sunny days, brief sunflecks can provide over 50% of the total daily quantum flux (measured as the moles of photons per unit area per unit time) (Chazdon and Fetcher 1984, Chazdon 1986*b*). Within canopy gaps created by tree falls, total daily quantum flux may be 10–20 times greater than in adjacent closed-canopy sites, whereas along the gap edge they are 3–8 times greater (Chazdon and Fetcher

3. *Geonoma congesta*, La Selva.

1984, Chazdon 1986*b*). Within closed-canopy understory, total daily quantum flux does not exceed 1 mol m⁻², even when there are sunflecks.

Although the three species grow together in closed-canopy sites, measurements of PAR above the crown of individual plants indicated that the light conditions experienced by reproductive stems tend to increase with crown height. A difference in mean height of less than 1 m results in increased light availability for reproductive individuals of *A. martiana* relative to *G. cuneata*. In *A. martiana* and *G. cuneata*, median total daily quantum flux for leaves less than 1.5 m tall was 0.39 mol m⁻² but for leaves above 1.5 m, the median increased to 0.51 mol m⁻² (Chazdon 1986*b*). Although this difference may appear very slight, increases of PAR in this range are linearly related to net photosynthesis, so that a doubling of total daily PAR could lead to a doubling of total daily net photosynthesis. Leaves of *G. congesta*, at heights of 3–4 m, received the highest daily quantum flux (median of 0.59 mol m⁻²), although there

was a great deal of variation. Within clones of *G. congesta*, total daily quantum flux increased markedly with leaf height, suggesting a substantial degree of shading within clones (Chazdon 1986b).

Photosynthetic light responses of shade-grown seedlings of the three species were similar; light compensation points (where net photosynthesis is zero) ranged from 3–5 μmol m^{-2} s^{-1}, and light saturation occurred at 300–400 μmol m^{-2} s^{-1}. Light saturated assimilation rates were 3–4 μmol CO_2 m^{-2} s^{-1} (Chazdon 1986b). These rates are typical of slow-growing tropical evergreen species (Mooney et al. 1984). When grown under higher light conditions (similar to the center of a 200 m^2 gap), unfertilized seedlings of all three species showed reduced photosynthetic rates and exhibited signs of photo inhibition and nutrient stress (Chazdon 1986b).

Canopy Structure and Light Interception

Given the low light conditions that these palms experience, growth requires that plants display a maximal amount of leaf area with a minimal amount of foliage overlap within the crown. In a closed-canopy site, measurements indicate that most of the light comes from directly above the plant. Therefore, a horizontal orientation would maximize the amount of light intercepted by individual leaves and crowns. A plant that holds all of its foliage horizontally with no leaf tissue overlapping would therefore be highly efficient at light interception in a closed-canopy environment. However, the display of leaf tissue requires biomass investments in non-photosynthetic structural material, such as leaf bases, petioles, and rachises. Because these structures impose a metabolic cost on the plant, the degree of shade that an individual can tolerate is determined by the amount of light intercepted per unit of crown biomass (photosynthetic responses being similar).

Results of a comparative study of light interception of *G. cuneata* and *A. martiana* showed that the proportion of total leaf area that actually contributes to light interception was higher for reproductive individuals of *G. cuneata* (Chazdon 1985b). This difference can be largely explained by the fact that crowns of *A. martiana* have roughly twice the number of leaves. In both species, leaf positions change from nearly vertical at expansion to horizontal and ultimately pendant in old age. If leaves are numbered from youngest to oldest, over 80% of leaves older than leaf 9 are oriented below horizontal (Chazdon 1985b). In *A. martiana*, these leaves comprise over 40% of the leaf population compared to only 1% in *G. cuneata*. In crowns of both species, less than 20% of the leaf area was directly shaded from above (Chazdon 1985b). The even distribution of leaves around the axis serves to minimize within-crown shading.

The biomass costs of light interception in the two species were compared by determining the allometric relationship between light interception capacity (the amount of total leaf area that contributes to light interception) and total crown dry weight. This relationship allows a comparison of the rate of increase in light interception capacity with increases in crown size. The analysis showed that, in both species, the light interception capacity increased only 83% as fast as crown biomass (Chazdon 1985b). This means that the proportion of crown biomass that actually contributes to light interception *decreases* as crowns increase in size; smaller crowns have lower relative costs of light interception. Thus, the smaller crowns of reproductive *G. cuneata* are more efficient at light interception compared to the larger crowns of *A. martiana*.

Biomass Allocation, Leaf Size, and Safety

Why is it that the costs of light interception are so much greater in larger crowns? One reason is the decrease in light interception efficiency due to greater numbers of drooping leaves, as discussed earlier. More important, however, are changes in the distribution of biomass within the crown as crown size increases. In palms, increases in both leaf size and number lead to increases in crown size. The increasing biomass costs of light interception associated with increases in crown size is largely a consequence of increased leaf size.

In the bifid-leaved species *G. cuneata* and *A. martiana*, the percentage of leaf biomass that is allocated to blade tissue (the photosynthetic tissue) decreases with leaf size. Leaves of seedlings of *G. cuneata* and *A. martiana* have 69 and 68% of the total biomass in blade tissue, respectively, compared to 60 and 53% in leaves of reproductive plants (Chazdon 1986a). In contrast, allocation to petiole and leaf base tissue increases from 22% in *A. martiana* seedling leaves to 35% in leaves of reproductive plants (Chazdon 1986b). Very little change is seen in allocation to rachis tissue.

Leaves of *G. congesta* show a fundamentally different pattern; large split leaves have 65% of their biomass in blade tissue compared to 59% in seedling leaves. Allocation to petiole and leaf base tissue decreases from 34% in seedlings to 22% in reproductive plants, while rachis allocation increases from 7% to 13% (Chazdon 1986b). The change in leaf morphology in *G. congesta* from bifid to split leaves is accompanied by a decrease in petiole length (relative to rachis length), whereas in the other two species, relative petiole length increases with leaf size. Without these increases in petiole length,

the amount of within-crown shading would likely be considerably greater in *G. cuneata* and *A. martiana*.

The allometric relationship between leaf area and the dry biomass of leaf-support tissues shows that, when leaves are small, leaves of *G. cuneata* and *A. martiana* have greater leaf area per unit of support tissue (Chazdon 1986b). However, when leaves are large, the split leaves of *G. cuneata* have a greater leaf area per unit of support tissue. Thus, changes in leaf morphology with leaf size are correlated with changes in biomass allocation to blade and support tissues. At the whole-plant level, however, reproductive stems of *G. congesta* have the lowest total leaf area per plant biomass, whereas *G. cuneata* has the highest (Chazdon 1986b).

As discussed earlier, shade tolerance is increased by maximizing the amount of light intercepted for a minimal cost. However, minimizing investments in leaf-support structures, such as petioles and rachises, may jeopardize the mechanical stability of the leaf support system. Allocation to leaf-support structures must therefore strike a balance between economy and safety.

What are the mechanical consequences of these patterns of biomass allocation? Even though the biomass allocation to support tissue increases with leaf size, this increase is not sufficient to maintain a constant degree of stress on the petiole. Petiolar stresses increase dramatically with leaf size in all three species (Chazdon 1986b). Consequently, the factor of safety decreased from over 100 in small seedling leaves to 3–4 in the largest leaves of each species. A factor of safety of 3 means that the petiole will break if a static load 3 times the load of the leaf tissue is applied at the leaf's center of mass. Despite differences in maximum leaf size among the species, the factors of safety of the largest leaves were similar. These data suggest

that there may be mechanical constraints on leaf size within these species. Furthermore, these data show that the relative cost of constructing a leaf with a constant degree of safety increases greatly with leaf size; smaller leaves are always more structurally efficient (greater strength per unit cost).

The Ecological Significance of Leaf Size and Plant Size

Given that a leaf has positive carbon gain under heavily shaded conditions, relative shade tolerance is a matter of displaying the greatest amount of leaf area (on a whole-plant basis) for the minimal amount of cost, with an "acceptable" degree of safety from breakage. Precisely what this "acceptable" degree of safety might be is difficult to assess, but it must be linked to the frequency distribution of the magnitudes of forces resulting from physical factors in the environment, such as branch falls, wind storms, and leaping lizards.

For bifid-leaved species, small leaves are therefore more shade tolerant than big leaves, largely by virtue of their lesser size. Regardless of leaf morphology, small plants with low biomass investments in stem tissue and low leaf-support costs at the crown level have reduced metabolic costs and can grow in relatively more shaded conditions. The ability of a plant to reproduce while still at a small size creates the evolutionary potential for shade adaptation, given the appropriate selective regime. Shade adaptation may be best viewed as a scaling problem, with plant size at reproductive maturity determining the degree of shade that can be exploited by a given species.

The patterns I have discussed here suggest that differences in plant size at reproductive maturity in large part determine the relative shade tolerance among the three understory palm species discussed here. Light data and personal observation

indicate that *G. cuneata* can reproduce under relatively shadier conditions than *A. martiana*, and *A. martiana* can reproduce under relatively shadier conditions than *G. congesta*, although there is a great deal of overlap in light conditions experienced by the three species (Chazdon 1984). Based on these results, I have hypothesized that phylogenetic changes in plant size may have played an important role in the adaptive radiation of *Geonoma* species within understory environments. Investigations of correlations between plant size, shade tolerance, and leaf morphology in a range of *Geonoma* species provide a focus for my future research.

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