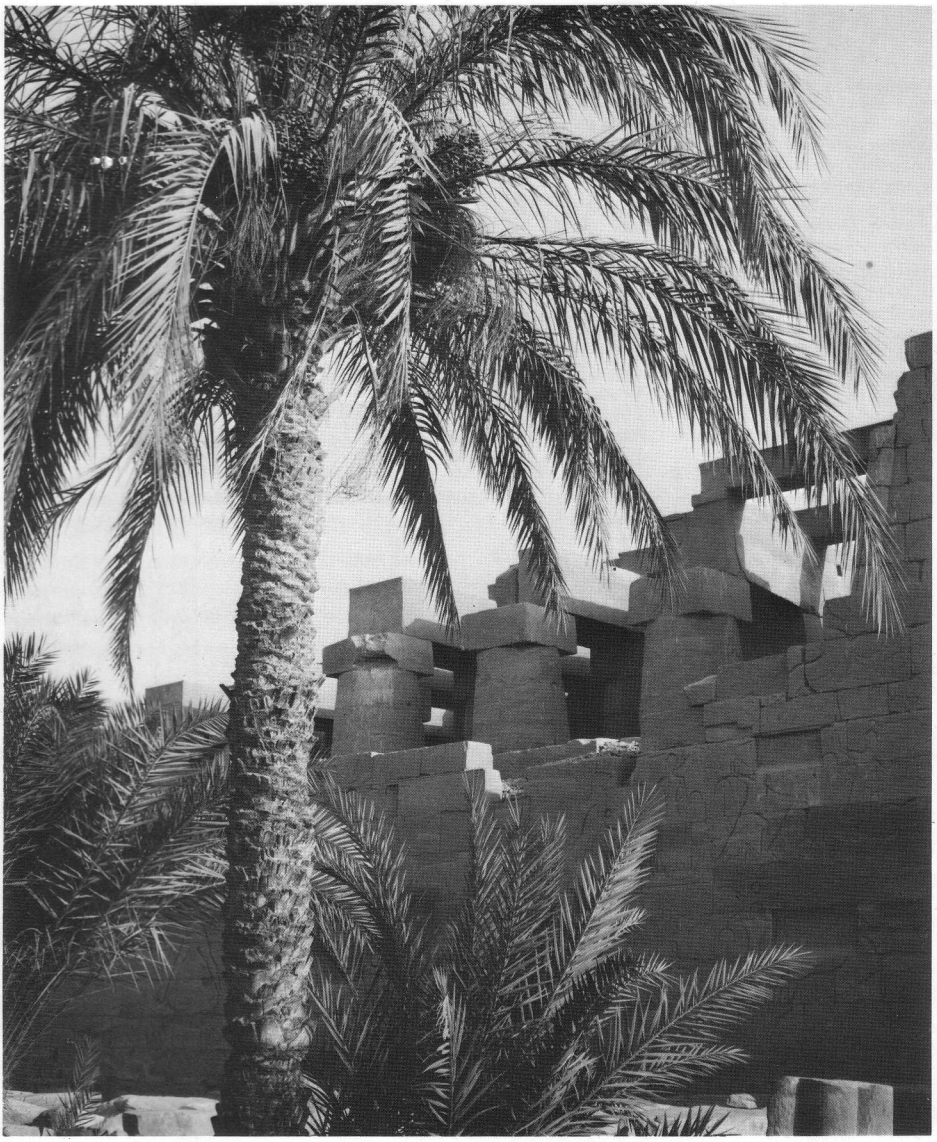


Ecology Issue

PRINCIPES

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Studies in Palm Ecology: An Introduction

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The ecological articles in this issue are based on papers presented during a symposium entitled "The Ecology of Palms," part of the 1985 American Institute of Biological Sciences meeting at the University of Florida. Topics covered range from biomechanics and physiology to population biology and community ecology. It has become obvious that palms are excellent subjects for ecological investigations; the economical, botanical, and ecological importance of palms more than justify all the attention they have received.

Why have palms recently attracted so much attention from ecologists? There are probably as many answers to this question as there are ecologists but most are related to the relatively simple growth forms of plants in this family. Studies of biomechanics, for example, are facilitiated by the usual lack of above-ground branches. An even more fundamental feature of palms is that their age can be estimated by counting the scars of fallen leaves. Although it is becoming increasingly clear that leaf production rates vary considerably, population biologists who study palms are far better off than those who work on dicotyledons in tropical forests where such trees apparently do not produce annual growth rings.

Much of what is included in the following papers is new to science and possibly of fundamental importance to the field of ecology. Palms are glorious organisms but nevertheless are sufficiently peculiar that some caution is advised in extrapolating the results to other taxa. Whether or not the results lead to generalities, investigations of palm ecology can serve as "outgroup" comparisons in studies of other sorts of trees; models of demography or biomechanics developed for palms, for example, can be tested with data from other species.

Emphasis during the symposium was on population biology; consequently, coverage of the field of palm ecology was not thorough. For example, aspects of reproductive biology that are under active investigation (e.g., pollination and seed predation) were given little attention. Herbivory and below-ground ecology were also not emphasized, but this may reflect our profound ignorance of these topics.

Many of the exciting recent developments in palm ecology seem to be on the interfaces between scientific disciplines. In the papers that follow, it becomes obvious that the tools and techniques of engineers, anatomists, mathematicians, and physiologists can be of great use in studies on the ecology of palms. It is comforting that with all the high-powered methods at their disposal, researchers in palm ecology still pay due respect to natural history. They seem inspired by the organisms they study.

Principes, 30(3), 1986, pp. 92–99

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



3. *Geonoma congesta*, La Selva.

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 1986*b*).

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 1986*b*). 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 1986*b*).

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 1985*b*). 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 1985*b*). 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 1985*b*). 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 1985*b*). 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 1986*a*). 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 1986*b*). 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 1986*b*). 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 1986*b*). 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 1986*b*).

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 1986*b*). 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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Comparative Demography of a Clonal Palm (Oenocarpus mapora subsp. mapora) in Panama

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As one facet of palm ecology, demographic studies are useful in providing information about the status and performance of species populations in a community. Palms are attractive subjects for studies of demographic processes (e.g., Bannister 1970, Bullock 1980, Piñero et al. 1984). Because they are widespread, and abundant in tropical forests, palms are important food sources for tropical animal communities. They also have a relatively fixed pattern of morphological development that provides convenient features for population analysis. In 1980, I started a demographic study of a colonial or vegetatively-reproducing palm, *Oenocarpus mapora* subsp. *mapora* (syn. *O. panamanus*), in central Panama, in order to evaluate the contribution of the clonal habit to the palm's overall population dynamics.

The ecological and evolutionary significance of clonal reproduction in plants is a subject of recent theoretical interest, and at least two potential, though not mutually exclusive, benefits have been suggested (Cook 1979, Abrahamson 1980). The first is that clonal spread allows an individual plant to exploit new "resources," whether in the form of more space, a new area of soil and its associated nutrients, or a different light environment. The second is that the vegetative production of identical plant units (shoots or ramets) reduces the probability of ecological extinction of the genetic individual (genet), since the risk of mortality is "spread" among the ramets within a genet or clone. These hypotheses are frequently difficult to evaluate in field populations because the form of clonal proliferation in many plant species makes it nearly impossible to distinguish different genetic individuals in a population. The clustering palm *Oenocarpus mapora* subsp. *mapora* provides two aspects useful for evaluating the importance of some hypothesized benefits of clonal growth. First, the clustering of stems resulting from limited lateral spread allows genetic individuals to be identified easily, and thus it is possible to study both the dynamics of the "population" of vegetative ramets and the contribution of ramet dynamics to the population dynamics of genets or clones. Second, since the growth of any palm stem is dependent upon a single terminal meristem, loss of the meristem results in death of the stem and, for a non-clonal palm, in death of the individual genet. Thus, for palms, the potential benefit of clonal growth in reducing mortality risk to the genet may be particularly pertinent.

Here I present an overview of the *Oenocarpus* study system and objectives. Current population monitoring is designed to examine the consequences of clonal growth for genet demography and for variation in genet demography in different forest types on Barro Colorado Island, Panama, a tropical moist forest where the palm is abundant.

Natural History

Oenocarpus mapora subsp. *mapora* is a member of an arecoid genus whose distribution is centered in South America, although this particular species occurs primarily in Costa Rica and Panama. It is found in all forest types on Barro Colorado Island. Clones consist of clumps of vegetative shoots of various ages that are produced from lateral buds at the base of other shoots. Clumps remain distinct from each other because there is very little rhizome extension of the buds prior to rooting. Basal diameter of adult clones ranges from 0.5–3.0 m, depending on the number of stems in the clone.

Shoot growth follows a typical palm pattern and allows the delineation of developmental phases for use in demographic analysis. There is initially a seedling phase characterized by distinctive leaf morphology with crowded, almost palmate leaflets. After several years the pinnate leaf morphology develops, and the palm enters a long juvenile phase of establishment growth during which the shoot axis increases in diameter with little or no stem elongation between nodes. As nodes accumulate on the shoot, a juvenile grows from a height of about 0.1 m to about 1.0 m (measured to a standard point on the juvenile shoot axis) before rapid stem elongation begins due to increased internode length. This change signals an immature phase in which the palm undergoes rapid growth in height to reproductive size. The adult or reproductive phase begins when the palm reaches a height of about 8 m (the shortest palm which I have observed flowering) and continues as the palm grows to a mature height of 16–20 m. Sexual reproduction is seasonal, with an average of 50% of adult-sized stems flowering each year, producing an average of 1–3 inflorescences per stem each year. About 36% of the inflorescences consist of staminate flowers only, while the remaining 64% have both staminate and pistillate flowers.

Table 1. Functional stages assigned to Oenocarpus *clones.*

Seedling
Non-clonal juvenile
Small (<0.5 m)
Large (0.5–1 m)
Clonal juvenile (largest ramet 0.5–1 m)
Immature (largest ramet 1–8 m)
Adult (largest ramet >8 m)

An inflorescence may produce about 400 mature single-seeded fruits, but fruit production varies as a consequence of losses from abortion and predation. There appears to be no seed dormancy, and seeds germinate 1–2 months after fruit fall.

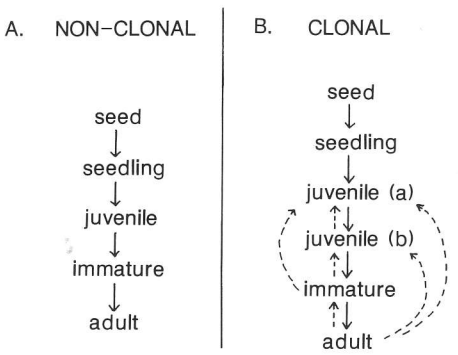
A vegetatively-produced shoot (ramet) starts out as a small "juvenile" with pinnate leaf morphology; the "seedling" morphology stage is bypassed. An individual palm begins producing ramets in the late juvenile phase; over a three year period, less than 1% of juveniles <0.5 m tall produced ramets while 18% of juveniles >0.5 m produced new ramets. Only about 12% of small (1–3 m) immature palms lack one or more ramets and all large immature individuals have them; thus, in a developing *Oenocarpus* genet, the primary shoot tends to become clonal before it enters the immature phase of rapid height growth. Presumably a shoot axis has a limited number of basal buds available for ramet production; however, the ramets in turn begin producing their own ramets as they reach the appropriate size. This leads to the development of the large clump of varying-aged shoots that constitutes an *Oenocarpus* clone.

Demographic Analysis

Instead of evaluating clones according to their size (number of ramets), I classify individual genets or clones by the developmental stage of the largest (oldest) ramet, since this defines the *functional* status of the individual in the population

Table 2. Three-year stage-specific survivorship of Oenocarpus *genets.*

Stage Class	Genet Survival	Survival of Ramets Within Genets
Seedling	.27	—
Non-clonal juvenile		
Small	.76	—
Large	.98	—
Clonal juvenile	1.00	.87
Immature	.98	.78
Adult	.99	.78



1. Developmental transitions in the life histories of a non-clonal (A) and clonal (B) palm. See text for explanation.

(Table 1). Ramets within clones can be classified into the same developmental stages, e.g., an immature clone may have juvenile ramets in addition to the one or more immature stems that define its functional stage.

A significant consequence of clonal growth is evident from the survival rates of genets at specific stages (Table 2). Seedlings suffer high mortality due largely to debris fall and herbivory, while mortality from the same causes declines somewhat for small juveniles. Continued increase in size is associated with decreased mortality, as large non-clonal juveniles have high survival. Clones have extremely high survival, although individual ramets within these clones appear to suffer higher rates of mortality than do the clones themselves, particularly the stemmed ramets within the immature and adult clones. Most mortality in the larger stages is due to treefall damage. These patterns of survival suggest that clonal proliferation reduces the probability of genet extinction.

The classification of clones by developmental stage (Table 1) allows me to focus upon the demographic behavior of genets rather than just on the vegetative ramets. While ramet births and deaths may affect clone size, the functional behavior of the clone as a genetic individual in the population is determined by the oldest ramet(s); consequently, addition of new ramets to a clone does not alter its functional status in the population. However, death of ramets can change a clone's functional status if the oldest ramet(s) dies, since the clone's developmental stage will be redefined by that of the oldest *surviving* ramet. This produces the qualitative difference between non-clonal and clonal life histories illustrated in Figure 1. Individuals in a non-clonal population (1A) grow through a fixed sequence of developmental stages, with mortality removing individuals from the population and thus reducing recruitment to subsequent stages. In a clonal plant (1B), individual development initially may resemble the non-clonal pattern (solid arrows) for the phases that lack vegetative reproduction (seedling and juvenile "a") and for the cases where entire clones die. However, with initiation of clonal reproduction by larger individuals (juvenile "b" and older), attainment of subsequent stages may be assured if clones die infrequently; instead, death of ramets, depending upon which ones die, may simply "push back" the functional status of the genetic individual to an earlier point in the developmental sequence (broken arrows). This obviously creates a more complex demographic pattern than in a

non-clonal species, since there are a number of possible "regressive" pathways that ramet mortality can generate for different clones.

Comparative Demography

Barro Colorado Island has a mixture of forest types (see Foster and Brokaw 1982 for a detailed description). I am monitoring *Oenocarpus* populations in three areas. Old forest (OF) is estimated to have been free of major disturbance for at least 200 years; it has a tall heterogeneous canopy with many old trees and a fairly high degree of canopy turnover from branch and tree falls. Secondary forest represents advanced regrowth from old clearings and is probably at least 100 years old; it has a shorter canopy and higher stem density than the old forest. A third area (disturbed forest, DF) is located near the site of a several-hectare canopy blowdown that occurred in 1973. The forest canopy near this blowdown site is composed of short, young trees and appears to have been repeatedly windthrown. *Oenocarpus* is a subcanopy species in the old forest, is more frequently near the canopy in the shorter secondary forest, and is a dominant canopy-level species in the disturbed forest.

Oenocarpus population density and structure differ considerably between forest types (Table 3). Population density varies widely, with very low density in the old forest and extremely high density in the disturbed forest. Excluding seedlings, which are a highly variable fraction of the population from year to year, the most striking difference among sites is that the old forest population has a high proportion of adult clones and a low seedling/adult ratio in comparison with the other two sites, which suggests that regeneration is poor in mature forest. That the mature forest population is an old, persistent population is also suggested by the presence of more large, many-stemmed adult clones

Table 3. Oenocarpus *population structure in three Barro Colorado Island forest types.*

Genet Stage Class	% of Population in Stage Class		
	Old Forest	Secondary Forest	Disturbed Forest
Non-clonal juvenile	38	66	70
Clonal juvenile	6	8	7
Immature	14	16	9
Adult	42	10	14
Estimated palm density per ha (excluding seedlings)	109	244	1,744
Plot size sampled (ha)	1	.7	.16
Average seedling/adult ratio	2.5	8.5	11.8

there than in the other two sites. Overall, the high population densities and high seedling occurrence in the disturbed forest site suggest that the palm is favored in windthrown areas, perhaps because clones can survive canopy fall despite some ramet death and subsequently show strong growth response to increased light levels.

Long-range Objectives

Detailed monitoring of the growth and survival of both genets and ramets in all three *Oenocarpus* populations will allow me to estimate the demographic status of genet populations in each of the three contrasting forest types, and to evaluate the contribution of ramet dynamics to the status of each. The importance of vegetative reproduction to genet population dynamics is likely to vary under different regeneration conditions. Where ramet mortality is low, clonal growth may provide little additional advantage over a solitary growth habit; however, clonal growth would allow longer genet persistence under conditions of high ramet mortality. Fur-

ther analysis, including projection matrix techniques in which both genet and ramet values are utilized to estimate population status, will explore these questions.

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Principes, 30(3), 1986, pp. 105–107

Plant Architecture and Population Ecology in the Palms Socratea durissima and Scheelea zonensis on Barro Colorado Island, Panama

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In recent years there has been considerable interest in the great diversity of architectural forms in tropical trees. In an effort to investigate the ecological significance of plant forms, studies of plant architecture, photosynthetic responses, and population biology were carried out on the palms *Socratea durissima* and *Scheelea zonensis* (Fig. 1) on Barro Colorado Island from 1981 to 1985.

The growth forms of the palm species *Socratea durissima* and *Scheelea zonensis* were analyzed as a test of the hypothesis that plants show patterns of biomass allocation and canopy architecture that can be used to explain their light requirements, and that differences in architecture between species will lead to predictable consequences at the population level. Results are summarized in Table 1 and are discussed below.

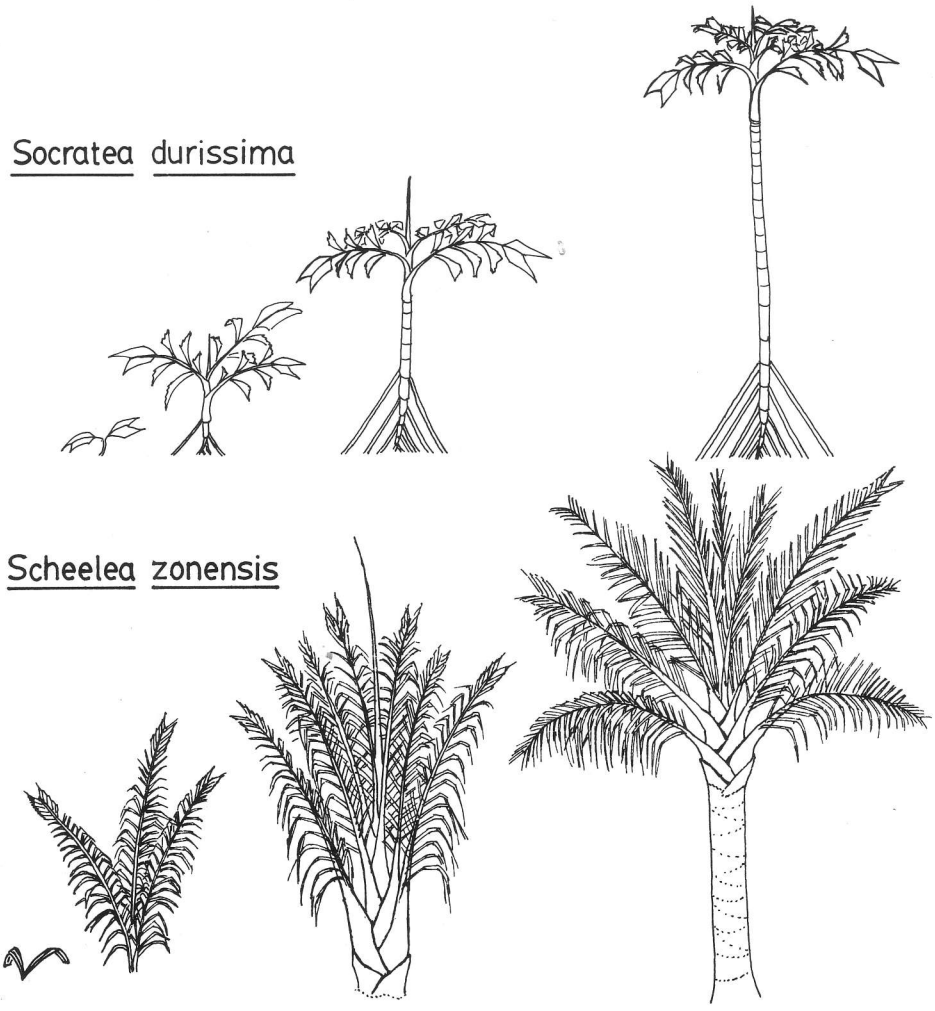
Scheelea allocates more biomass to leaves as a juvenile than *Socratea* does, which may result in a relatively lower respiratory load and allow the light-demanding *Scheelea* to persist in the understory. However, as *Scheelea* grows it accumulates non-photosynthetic biomass and self-shading increases. These factors in combination probably cause the light requirements of whole plants to increase significantly as they mature.

Socratea, in contrast, has a canopy architecture that produces a horizontally oriented leaf display with relatively little self-shading. This species allocates biomass to stem tissue even as a seedling, which could reduce its shade tolerance, but elevating the leaf display may in the long run be beneficial, especially where vertical gradients of light are steep.

Integrated measurements of light levels indicate that light attenuation with increasing depth in the canopy of an individual plant is greater in *Scheelea* than in *Socratea*.

Photosynthetic responses to variation in the light environment enhance the effects of architectural differences. Photosynthesis is better adapted to low light in *Socratea* than in *Scheelea*. Photosynthetic responses in *Scheelea* show a greater ability to acclimatize to high-light environments.

The above results have established that 1) the two species differ in their architecture, 2) the differences in architecture have a significant effect on the distribution of light within the canopies of individual plants, and 3) differences in light requirements resulting from the differences in architecture are enhanced by the differences in photosynthetic responses to light intensity. In order to establish that plant architecture has significant consequences for the ecology of these species, it is necessary to show that growth-rate responses to light differ between species in the man-



1. Developmental stages of the study species.

ner one would predict from the architectural differences. For this purpose plants in natural populations and seedlings in experimental gardens were used to assess the effect of canopy openness on plant growth rates and leaf demography. *Socratea* is better able to grow under low light than is *Scheelea*, but leaf survivorship is lower in *Socratea*. Growth in *Scheelea* shows a greater response to increased canopy openness than in *Socratea*. Average growth rates for size-classes and the degree of canopy openness above individual plants of each species suggest that *Socratea* may be able to attain maturity under relatively closed forest conditions, while *Scheelea* on average is growing slowly or actually declining, suggesting that it may require a large gap in the canopy in order to grow to maturity. Higher rates of leaf turnover in *Socratea* are in contradiction with expectations for sun vs. shade plants, but

Table 1. Summary of architectural, photosynthetic, and population-level differences between Socratea durissima *and* Scheelea zonensis *on Barro Colorado Island, Panama.*

Character	*Socratea*	*Scheelea*
Seed dormancy	no	yes
Percent total biomass in leaves	low	high
Leaf overlap	low	high
Leaf angles	more horizontal	less horizontal
Light attenuation in individual canopies	low	high
Photosynthetic responses	shade-adapted	less shade-adapted
Photosynthetic acclimation to high light	lower	higher
Vertical growth	begins as seedling	delayed until attainment of full diameter
Leaf survivorship	lower	higher
Ability to grow in shade	higher	lower
Response to large canopy opening	lower	higher
Max. density of reproductive-size individuals in old forest (per ha)	~50	~5
Size of spatial aggregations	small	large

this difference may be related to *Socratea*'s stilt-rooted form in contrast to the more typical palm growth form seen in *Scheelea*.

Demographic analyses suggest that *Socratea* populations may be maintaining themselves under current conditions in the old forest on BCI. However, the extreme dry season of 1983, associated with the El Niño event that began in October 1982, resulted in approximately 12% mortality in the *Socratea* study populations; such levels of mortality are inconsistent with the persistence of *Socratea* populations in this forest. Because the age of the old forest on BCI is probably several times that of the maximum lifespan of an individual *Scheelea*, it appears likely that *Scheelea* is also maintaining itself, but *Scheelea* population dynamics are more difficult to assess due to seed dormancy, slow growth of suppressed individuals, and wide spacing of reproductive adults.

Preliminary analyses of spatial relationships within populations of the two species indicate that *Socratea* shows aggregation at much smaller scales than does *Scheelea*. Information on spatial patterns of the two species are consistent with the interpretation that *Scheelea* requires large gaps in the canopy, while *Socratea* may grow to maturity through closed forest or in small gaps.

This study demonstrates that an understanding of plant growth form contributes to an understanding of the factors that produce population level patterns. An understanding of the ecological significance of plant growth forms is useful in interpreting the possible significance of within- and between-species differences in plant architecture.

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Demographic Studies in Astrocaryum mexicanum and Their Use in Understanding Community Dynamics

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Demographic studies in plants have been shown to be useful in understanding the regulation of population numbers (Silvertown 1982) as well as in designing management techniques for use with wild populations (Soulé and Wilcox 1980). Demographic techniques are also used to ascertain the aspects of the life history that may be under intense selective pressure (Law et al. 1977, Dirzo and Sarukhán 1984). These techniques started being used in studies of tropical trees more than ten years ago (Bannister 1970, Hartshorn 1975, Sarukhán 1978). The basic demographic data usually estimated are: a) the age or stage of the individual, b) the survival probabilities in each age or stage category and, c) the fecundity during the reproductive phase. If the time scale used to estimate these vital statistics is shorter than the time interval considered in each age or stage category, then transition probabilities from one stage or age category to the next should also be calculated. With these data a matrix (usually a Lefkovitch matrix in which the categories do not have the same duration) is constructed and an estimate of the finite rate of population increases (λ) can be obtained. With this basic information, the aspects of the life cycle that most affect the finite rate of increase can also be determined (Caswell 1978, de Kroon et al. 1986). The reliability of the estimates usually depends on the population's sample size and the duration of the study. Unfortunately, detailed demographic studies spanning over many years are rare. Palms have been shown to be a very cooperative life form in demographic analyses because growth often can be directly recorded as the number of leaves produced, especially in the tropics, where palms are frequently abundant and trees generally lack growth rings (Bannister 1970, Sarukhán 1978, Vandermeer et al. 1974, Bullock 1980, Piñero et al. 1984, Oyama 1984).

We have been carrying out field studies on the demography of the tropical understory palm *Astrocaryum mexicanum* Liebm. since 1975. These studies have been useful not only in helping us to understand the population dynamics of this species but also in learning about the ways in which the number of leaves in an individual crown is regulated, as well as in describing the dynamics of canopy gap formation within the forest. Even though the demography of a population may be the main objective of a given study, detailed understanding of a population can in time yield information about the whole community. In this paper we describe how our studies are scaled from the individual to the community levels as well as some of the restrictions to this type of approach.

One of the aspects that we have started

to study is the demography of leaves within individuals. The construction of life tables for leaves has been used to predict the life expectancy of an individual leaf and the relative contributions of individual leaves to future leaf production (Abul-Fatih and Bazzaz 1980), as well to assess the effects of defoliation on leaf demography (Hartnett and Bazzaz 1984). This information coupled with physiological data on photosynthetic rates and nutrient concentrations in leaves can be used to better understand the adaptations of plants to their environment (Chabot and Hicks 1982).

Our study plots are located at the Los Tuxtlas field station (Universidad Nacional Autónoma de México) at Veracruz, México. The site includes a Tropical Rain Forest with trees up to 40–50 m. Rainfall is usually over 4,000 mm per year and average temperatures vary around 24–25° C. Soils are shallow, acidic, rich in nitrogen, and of volcanic origin. The total number of tree species within the 700 ha field station is approximately 210 (Ibarra 1985).

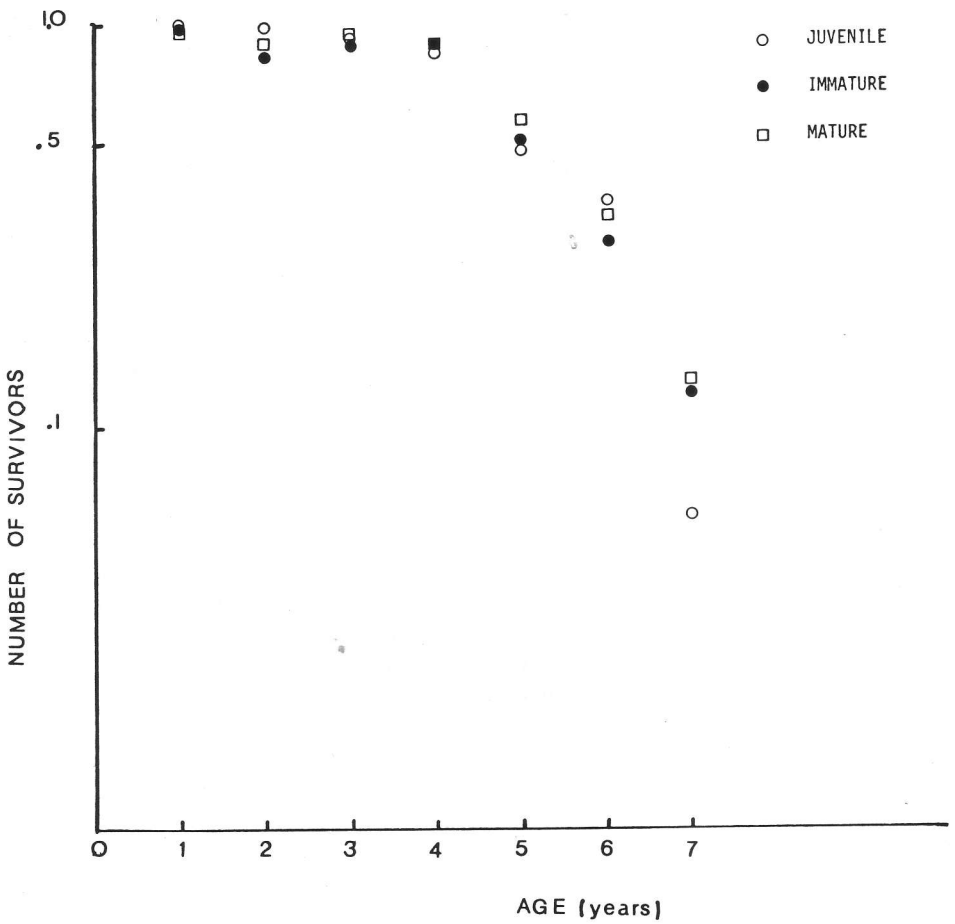
Demographic data have been obtained from 8 permanent plots (600 m^2 each) that include different *A. mexicanum* densities (from 500 mature individuals per ha to 1,200/ha), as well as sites in which large gaps were produced by treefalls in 1970 and 1974 (for details see Piñero et al. 1977, Martínez-Ramos 1980). Ages of palms were estimated using data on leaf production and transition data from one height category to the next over a six year period; survival probabilities and fecundity estimates were obtained from data on individual palms censused each year (Piñero et al. 1984). Data to construct leaf life expectancy tables came from the census of the cohorts of leaves starting in 1975 and ending in 1982. Fecundity of leaves (the photosynthetic contribution of a leaf to the production of new leaves) was assumed to be a function of the concentration of nitrogen in individual leaves.

When a tree or a large branch falls and bends over an *A. mexicanum*, the palm usually survives and starts growing upwards again. By knowing the rate at which palms produce new leaves under such conditions we can estimate the time that has elapsed since the treefall during which the palm was bent over. These data were obtained from censusing all *A. mexicanum* individuals in a 5 ha permanent plot. Besides the usual data (height, the number of leaves on the crown, and localization), measurements were also obtained on the length of the trunk between angles in the stem that were produced in response to the fall of a tree or a large branch.

One way to understand the dynamics of gap formation and closure is to use *A. mexicanum* to age gaps up to eighty years old. This information is translated into a frequency distribution of gap formation, a kind of age structure for gaps of the past. To our knowledge, this is the first demographic study of palms or any other plant that has been utilized in understanding the regeneration mosaic of a tropical forest and also in aging the different parts that form it.

Leaf Demography

Understanding the dynamics of populations has sometimes been followed by an analysis of its possible causes. One way to approach this problem at the individual level in plant populations has been to describe the dynamics of plant parts (e.g., Sydes 1984). While leaf survival is relatively easy to estimate, leaf fecundity estimates are difficult to obtain because we would need to know the proportion of a leaf's photosynthates that is allocated to the production of new leaves. In studies of this kind, it is generally assumed that for leaves of different ages, the same proportion of photosynthates is allocated to the production of new leaves. Leaf fecundity is then assumed to be proportional to photosynthetic activity (e.g., Hartnett and



1. Survivorship curves for leaves of juvenile, immature, and mature individuals of *Astrocaryum mexicanum* in Veracruz, México. Each point is the proportion of living leaves in 1982 of those originally marked in the 600 m² plots (with no gap disturbance) between 1975 and 1981.

Bazzaz 1984), which is in turn assumed to be proportional to the relative concentration of nitrogen in a leaf (Gulmon and Chu 1981). We estimated leaf fecundity as the proportion of the contribution of leaves of different ages towards the leaves produced in a year, using the relative content of nitrogen as an indicator of photosynthetic rates. Leaf survival estimates were obtained by marking annual cohorts of leaves (a cohort is defined as those leaves produced in a year) between 1975 and 1981 and counting those still alive in 1982. In other words we estimated survival for independent cohorts of leaves.

Survival data for leaves from other plants generally fit a convex curve with high survivorship during early age (Bazzaz and Harper 1977, Abul-Fatih and Bazzaz 1980, Hartnett and Bazzas 1984, Sydes 1984). *A. mexicanum* is no exception to this (Fig. 1). For the first three years survivorship probability is close to one for leaves of individuals between 12 and 150 years old. After an individual is approximately 12 years old, the same proportion

Table 1. Life expectancy table for leaves of mature individuals of Astrocaryum mexicanum *at the 600 m² permanent plots (with no recent gap formation) in Veracruz, México.*

Age Category (years)	Probability of Survival (leaf × leaf^{-1} × year^{-1})	Fecundity (leaf × leaf^{-1} × year^{-1})	Mean Leaf Life Expectancy (years)	Age Structure (leaves)
0	1.00	0.24	5.16	3.10
1	0.94	0.21	4.46	2.79
2	0.89	0.13	3.67	1.82
3	0.92	0.16	2.57	2.35
4	0.87	0.16	1.69	2.23
5	0.57	0.14	1.32	1.42
6	0.33	0.15	0.91	0.87
7	0.13	0.15	0.54	0.35

of remnant leaves die each year. These estimates are based on data from all six 600 m² plots in which there are large treefalls. Leaf mortality patterns may change when a gap is produced in the forest.

Life expectancy for leaves varies from 6 months for 7 year old leaves, to 5 years for newborn leaves (Table 1). Fecundity estimates show that leaves during their first two years (usually there are about six leaves younger than two years in a crown with 15 leaves) contribute approximately half of the photosynthate used by the newly produced leaves while the rest of the leaves in the crown (9) contribute the other half. There is then a hierarchy of leaves, with the younger ones more productive. We are now working to obtain similar data for palms growing in treefall gaps because we think that a comparative approach using a demographic technique to understand crown dynamics in palms will help us determine which are the factors that limit growth, survivorship, and reproduction in *A. mexicanum*.

Population Dynamics

Six years of survivorship and transition data and 8 years of fecundity estimates (Piñero et al. 1984) are available for *A. mexicanum*. The general pattern shows that individuals can live up to 150 years at which time the palms are approximately 6.5 m in height if they have not been knocked over. The population has a Deevey type III survivorship curve with the highest mortalities in the first stage of the life cycle and little mortality during the reproductive stages which start when individuals are 25–30 years old (1.0–1.5 m in height). Leaf production is highest and constant once the individuals start flowering (Table 2). We have found very little temporal variation during the six years for which we have observed leaf production. This contrasts with the high annual variability found for reproductive characteristics (Piñero and Sarukhán 1982). Fecundity increases with age until it reaches a plateau when individuals are approximately 50 years old.

Elucidating the causes of variation in growth and reproduction appears to be a very interesting avenue for future research. This variation has also been observed in other plant species and thus it is a phenomenon that has to be considered in demographic analyses of all plant populations (Silvertown 1982). Due to the variation, conclusions from demographic studies are not definitive unless many years of data are available on a large number of individuals. It will be extremely difficult

Table 2. Average annual leaf production per year for Astrocaryum mexicanum *individuals between 1975 and 1981 in Veracruz, México. Means are followed by one standard deviation.*

	Number of Leaves Produced per Year
Juveniles	1.64 ± 0.48
Immatures	2.08 ± 0.77
Matures	2.42 ± 0.55

to obtain reasonable estimates for demographic parameters for some species that live in frequently disturbed environments. When mortality is so high that very few of several hundred individuals are left after two or three years, it is also difficult to have good estimates of variation in growth, survival, and reproduction. Ways around this problem consist of marking many plants but not doing any observations on them until they reach an age with a smaller mortality.

We have described the variation in demographic parameters for *A. mexicanum* and proposed some possible causes for it, such as the heterogeneity of the light environments within the forest (Piñero and Sarukhán 1982). Without demographic data from different forest plots we would not have been able to identify the causes for such high variation. Whether aspects such as light and forest dynamics affect other palms in the tropics in the same way is not known, but it is clear that both have been recognized as key factors in the establishment and growth of other tree species (e.g., Vázquez-Yanes and Orozco-Segovia 1984, Brokaw 1985*a*, Martínez-Ramos 1985, Hubell and Foster in press).

The growth rate of a population can be expressed as the dominant latent root of the demographic matrix, a parameter known as the finite rate of increase (lambda). Values larger than one mean that the population is growing, while values between zero and one show that the population is decreasing in numbers. Although we have estimated the finite rate of increase for the plots with no gaps (Piñero et al. 1984) we have not been able to incorporate a variance term in the estimates of lambda. The analysis of variability in the demographic parameters appears to be particularly relevant in species like *A. mexicanum* in which finite rates of increase are very close to one (Table 3). To determine the way in which demographic variation affects the estimates of the finite rate of increase, we obtained an estimate of the variance in lambda.

Table 3. Finite rate of increase and its statistics for the 600 m^2 permanent plots (with no recent gap disturbance) of Astrocaryum mexicanum *in Veracruz, México. Estimates followed by the same letter are not significantly different at the 5% level (t-test).*

Plot	Finite Rate of Increase (λ)	Variance (λ)	Different from $\lambda = 1.00$
A	1.0040 ab	0.00178	no
AA	1.0114 ab	0.00346	no
B	1.0194 ab	0.00232	no
BB	0.9932 a	0.00397	no
C	1.0399 b	0.00326	yes
CC	1.0228 ab	0.00205	no
All plots	1.0046	0.00121	no

To estimate the variance of lambda we simulated for each plot 50 transition matrices similar to those published by Piñero et al. (1984). Each value of these matrices was obtained from a randomly generated function. If it was a fecundity value, a normal distribution function with the mean and variance obtained from field observations was used. If it was a transition or a survival estimate, then a binomial distribution was assumed with the parameters being the observed probabilities and

the sample sizes used. Another assumption was that the values of the demographic matrices are independent, an assumption that would not be necessary if we knew how the parameters influence one another. We need to know more about the causes of "good" and "bad" demographic years. The variances associated with the estimation of the finite rates of increase are small and range from 0.00121 (all plots) to 0.00397 (plot BB). Only the finite rate of increase for plot C (1.0399) is different (using a t-test) from a non-growth expectation and among plots, only plot BB (0.99320) is significantly different from plot C.

One final point that needs to be considered is that estimates of age also have an associated variance because they assume that leaf production is constant. We have estimates of the variation in leaf productions (Table 2), and a technique similar to the one described for the finite rate of increase could be used to estimate the variance associated with age estimation.

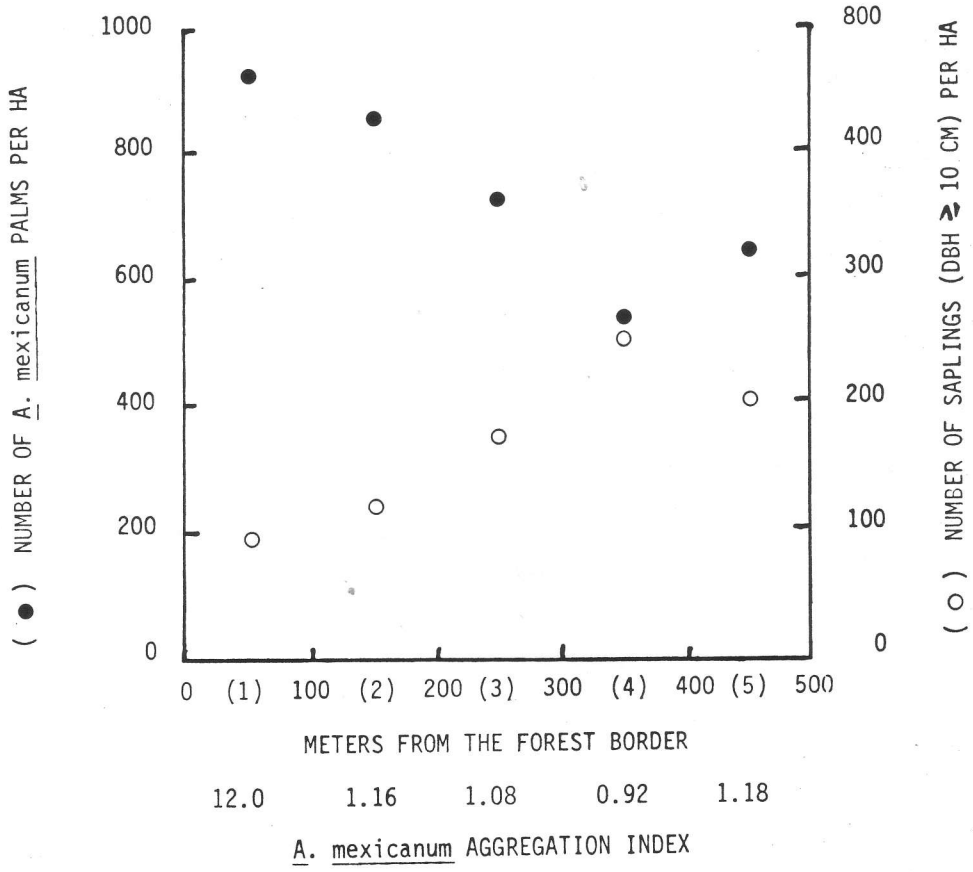
Gap Dynamics

Gap-phase regeneration has been shown to be very important in forest dynamics in the tropics (Brokaw 1985*b*, Martínez-Ramos 1985). The rain forest at Los Tuxtlas is no exception to that rule (Sarukhán et al. 1985). The main responses that *A. mexicanum* individuals have to gaps are: a) an increase in leaf production, b) an increase in fecundity through increasing both the probability of flowering and the number of fruits produced, and c) an increased probability of transition from prereproductive to reproductive stages which produces a demographic "wave" that modifies a normally J-shaped age structure. These "gap cohorts" in *A. mexicanum* appear to limit the recruitment of other species. There is an inverse relationship between the density of adult *A. mexicanum* individuals and the number of tree species in the 600 m² plots. Other data which support this idea have been obtained from monitoring a 5 ha permanent plot that runs across a slope gradient from the edge to the inner part of the forest. We censused all trees more than 1 m tall. For four years (1982–1985) we also recorded and measured each gap formed according to the criteria given by Brokaw (1982). Finally, using 2000 25 m² plots we calculated the approximate time when the last gap was formed in each quadrat (see also Sarukhán et al. 1985). We have found that the turnover rates of this forest are significantly higher towards the edges. The central part of the forest with the smallest slope, had the lowest gap disturbance rate (Table 4). Other workers have suggested that gap opening favors the regeneration of most tree species (Hartshorn 1980, Denslow 1980, Brokaw 1985*a*, Martínez-Ramos 1985). One would expect a higher regeneration (e.g., more abundant saplings) at the sites with a larger proportion of area with gaps and

Table 4. Parameters of gap dynamics in a 5 ha linear transect in the Los Tuxtlas rain forest, (hectare 1 is near the forest edge and hectare 5 is in the inner part of the forest). Turnover rate is defined as the average time elapsed between the formation of two gaps at the same site. Estimations are based on four years of gap monitoring. Minimum gap size considered was 5 m².

Ha	Turnover Rate (years)	Mean Number of Treefall Recurrency per 25 m² Square	Aggregation Index (Variance/Mean)
1	38	0.74	1.70**
2	50	0.64	1.53**
3	258	0.31	1.53**
4	52	0.32	1.65**
5	53	0.41	1.56**

** Significantly different (t-test) from an aggregation index of 1.00 at a 0.01% level.



2. Number of *Astrocaryum mexicanum* individuals (●– – –●) and number of tree saplings (O– – –O) in a 5 ha permanent plot in Veracruz, México.

regenerating forest but we found the opposite. The plots near the edge have a lower number of saplings than was observed in the more centrally located plots with lower turnover rates (Fig. 2). One hypothesis we propose to explain this difference is that an increase in *A. mexicanum* density lowers the sapling density of other tree species. The highest density of the palm occurs precisely in the part of the 5 ha plot with greatest disturbance while the lowest density occurs in areas with lower disturbance. We also predicted that a higher disturbance will produce a greater aggregation of these palms. The aggregation at the edge of the forest is the greatest ($s^2/\bar{x} = 12.0$) while in areas with lower disturbance palms are randomly distributed ($s^2/\bar{x} = 1.0$; Table 4). A high palm aggregation appears to produce a closed subcanopy which limits regeneration of light demanding species. Surely, *A. mexicanum* does not affect all tree species in the same manner. And we are now analyzing relationships with 60 different tree species. Will it be possible to predict the

forest structure by changing the degree of disturbance and/or the density of *A. mexicanum*? There is evidence that suggests that, for temperate forests, structure can be predicted using the relative abundance of tree guilds (Runkle 1985). By experimentally manipulating densities of *A. mexicanum* this question may be answered. Possibly new ideas about the mechanisms that operate in tropical rain forests at the community level will emerge from such experiments.

Conclusions and Perspectives

The ecology of palms has been one of the most active areas in tropical plant ecology. Palms have proven to be a very amenable group for both demographic and ecophysiological studies. We have shown that detailed long-term demographic studies can broaden our understanding of both population and community dynamics. We also showed that there are limitations in these studies mainly related to the high variability at the individual level in growth, survival, and reproduction. One way of dealing with this problem is to develop the relevant statistics for age and population growth estimates. Another method of research would be to understand the relative importance of different factors on the variation described. We think that ecophysiological studies are needed to complement the approach presented here. At the population level, on the other hand, analysis of the genetic structure of the population appears to be the most rewarding approach. The analysis of pollination biology that we started some years ago may help us make predictions about the way in which the genetic variation is maintained in these populations. Finally, an experimental analysis at the community level on the effect that *A. mexicanum* has on the establishment of other tree species appears to be very promising. We have started working in these three directions to further understand the biology of *A. mexicanum*.

Acknowledgments

We thank the organizers of the Symposium "Ecology of Palms" at Gainesville, Florida on August 13, 1985 for inviting us to present this work. Drs. Natalie W. Uhl and Francis E. Putz have arranged for its publication in *Principes*. Field assistance by A. López Flores and J. Nuñez-Farfán is gratefully acknowledged. An earlier version of the manuscript was kindly reviewed by Dr. Francis E. Putz.

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Mechanical Architecture of Arborescent Rain Forest Palms

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ABSTRACT

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

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

Stem Function and Resource Allocation

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

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

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

Developmental Morphology of Palms

New stem and leaf tissue of palms originates from an apical meristem located within the leaf crown. The apical meristem initiates each new leaf within the sheathing leaf base of the next older leaf. A large number of leaf primordia are enclosed within the crown. Each leaf expands in turn at the top of the crown. A single stem internode is associated with each leaf. In general, cell division and differentiation continue in the crown region. Leaves shift in position from the top to the bottom of the crown as new leaves are produced. Thus, tissue is youngest toward the top of the stem and oldest toward the base. Where the leaves abscise cleanly, leaf scars constitute a record of past leaf production (Corner 1966). Palms lack a vascular cambium in the stem, so the original set of vascular bundles is used for supply and support throughout the life of a palm (Tomlinson 1961, 1964, Tomlinson and Zimmermann 1967). Palm stems consist of a central cylinder of woody tissue and a narrow cortical region. Vascular bundles are distributed throughout the central cylinder, but usually concentrated toward the periphery. Each bundle has a fibrous mechanical sheath, but bundles toward the stem periphery have the most extensive sheaths. Consequently, strength and stiffness are concentrated toward the outer portion of the stem.

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

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

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

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

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

Mechanical Structure of Palms

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

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

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

Study Site

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

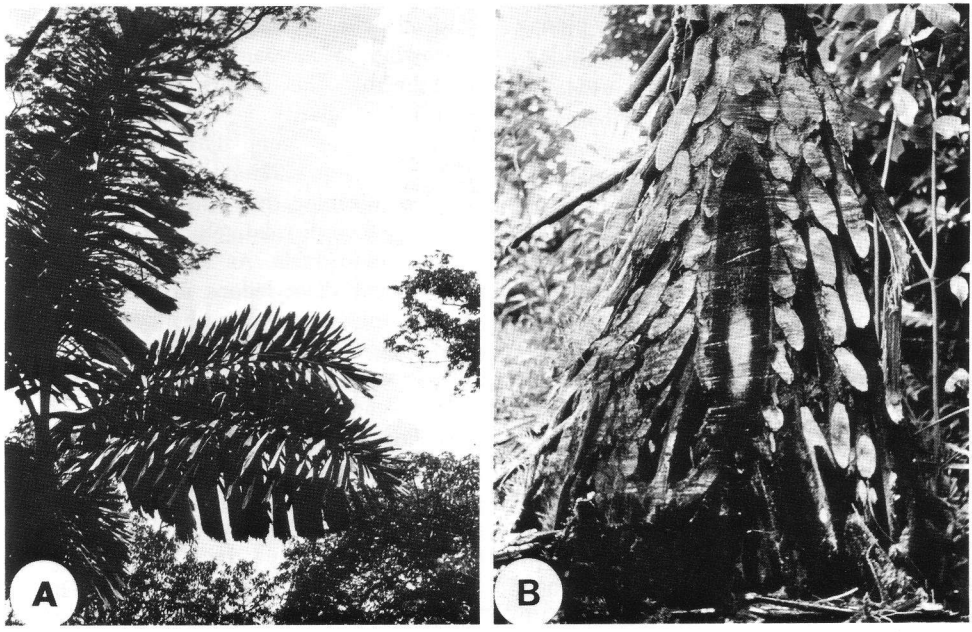
Study Species

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

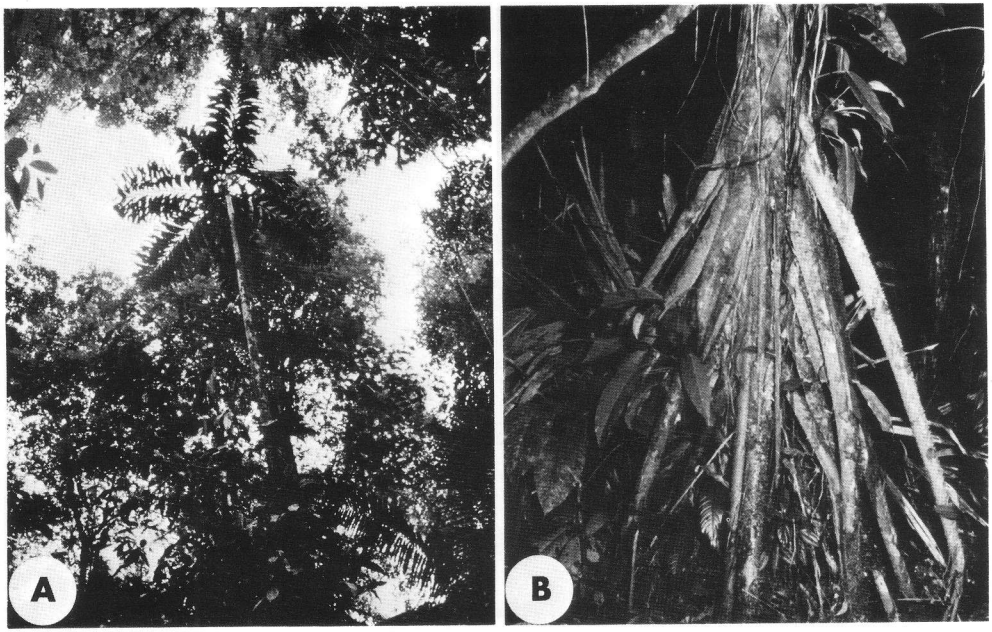
Welfia georgii (Fig. 1), a monoecious geonomoid palm, is distributed from Colombia to Costa Rica (Standley 1937). *Welfia* has a long period of establishment growth in which it remains as a large-leaved rosette with no above-ground stem while a bulbous underground stem is produced (Schatz et al. 1985).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



1. *Welfia georgii*, A) the general habit, and B) the bulbous undergound stem.



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

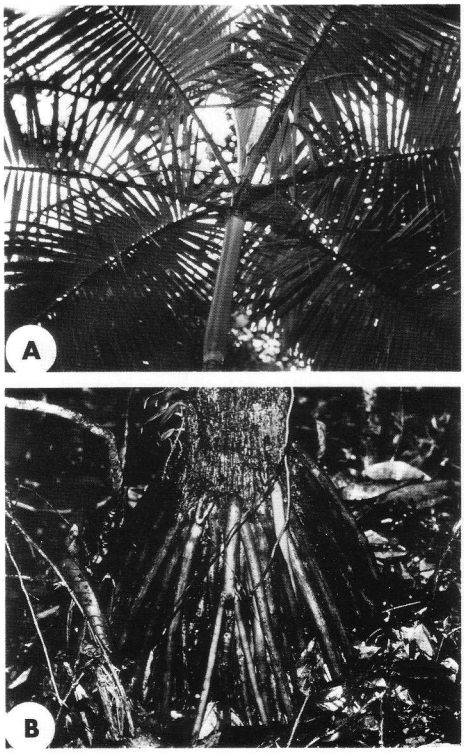


3. *Socratea durissima*, A) the crown, and B) the stilt roots.

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

Allometry of Palm Height and Stem Diameter

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



4. *Euterpe macrospadix*, A) the crown, and B) the above-ground roots.



5. *Prestoea decurrens.*

Mechanical Structure of the Palm Stem

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

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

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

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



6. *Cryosophila albida.*

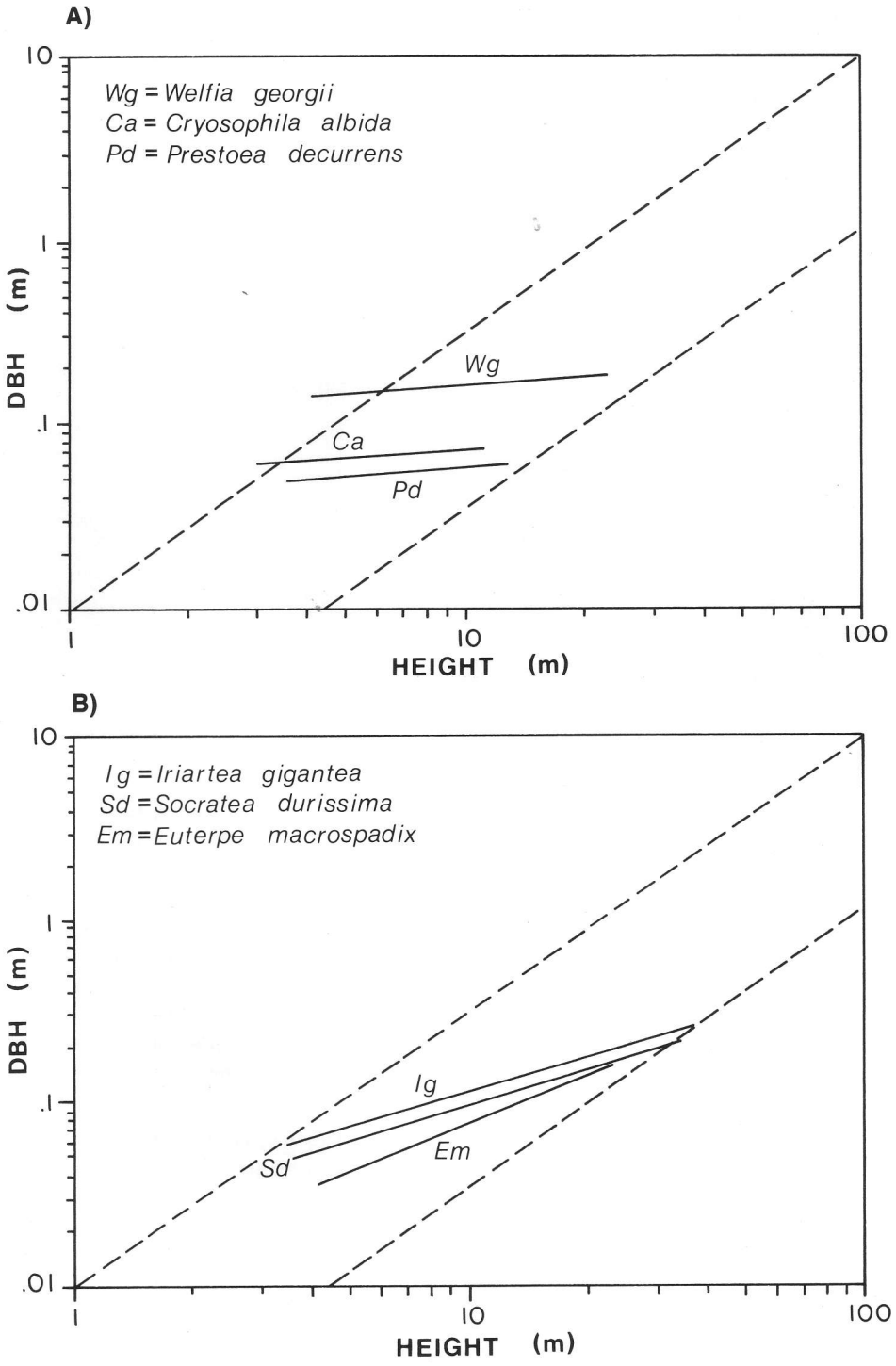
their maximum height, there was a tendency to maintain a constant margin of safety against mechanical failure by means of changes in stiffness and strength, with initial low values increasing to exceptionally high values. The capacity to increase stem rigidity and strength is the major means by which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

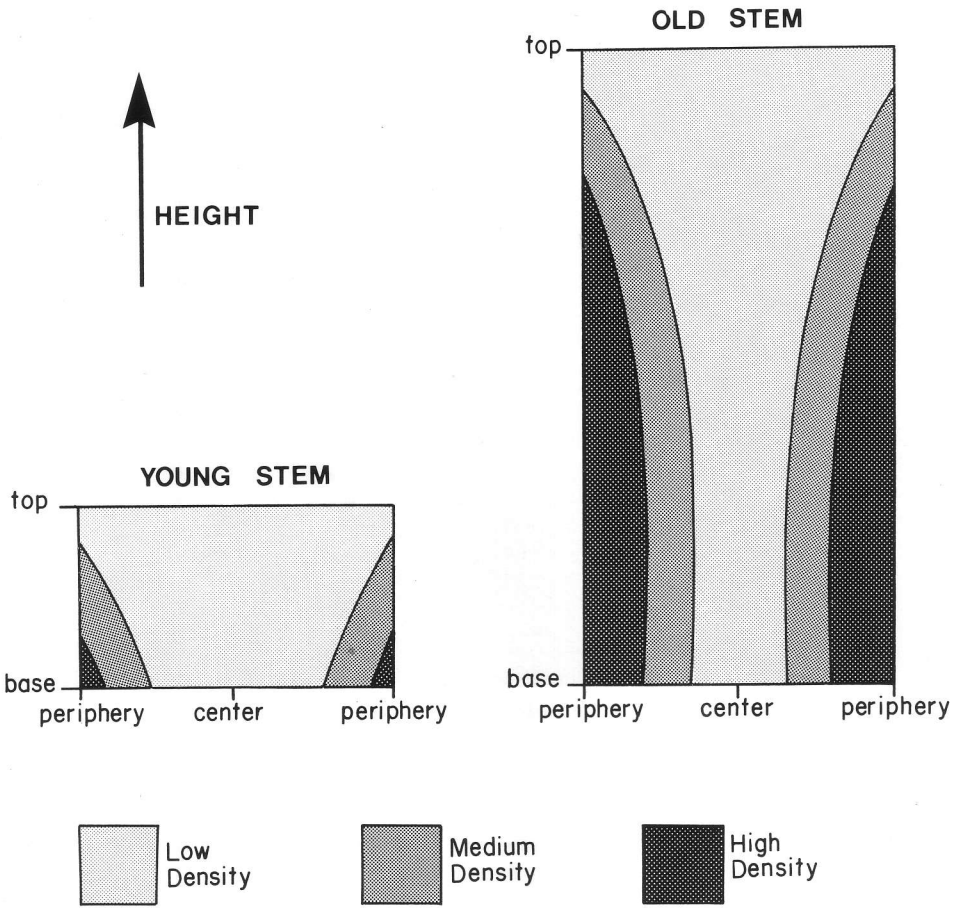
Developmental Anatomy of the Palm Stem

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

→

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


A)
Wg = Welfia georgii
Ca = Cryosophila albida
Pd = Prestoea decurrens
Wg
Ca
Pd
DBH (m)
10
1
.1
.01
1
10
100
HEIGHT (m)
B)
Ig = Iriartea gigantea
Sd = Socratea durissima
Em = Euterpe macrospadix
Ig
Sd
Em
DBH (m)
10
1
.1
.01
1
10
100
HEIGHT (m)



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

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

Weight Distribution and Mechanical Architecture

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

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

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

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

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

Growth Rates and Mechanical Architecture

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

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

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

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

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

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

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

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

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

Conclusion and Perspective

Palms have evolved an effective means for attaining tree stature that is quite distinct from the means evolved among dicotyledonous trees and conifers. Dicotyledonous trees and conifers increase stem diameter by cell division in a lateral cambium, and are thereby able to compensate for increased structural demands during height growth by replacing conducting tissues and adding strengthening tissues. Palms lack a lateral cambium, but rather by primary thickening growth they produce sufficient stem cells to serve permanent functions of supply and support. Hydraulic architecture of palms, the basis of water transport, has received recent attention (Zimmermann 1983, Sperry 1985); however, mechanical architecture has been neglected.

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

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

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

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

[a] Key to symbols: n = sample size, b = slope, a = Y intercept, r^2 = coefficient of determination.
[b] Statistical test with null hypothesis of b = 0 is a two-tailed Student's t test.
[c] Height growth rate is calculated using the regression equation calculated for 5 and 10 m tall individuals.
[d] *S. durissima* in old growth forest.
[e] *S. durissima* in abandoned cacao forest.

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

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

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

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

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

Acknowledgments

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Panama Collecting Trip

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

IMPORTANT NOTICE

Change in Address of Seed Bank

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

Principes, 30(3), 1986, pp. 132–135

Snakes in Paradise[1]

VIVI LAURENT-TÄCKHOLM
Faculty of Science, Cairo University

I would like permission to sing praises to the date-palm, to write a fine verse about it, and to laud it in every way. The beautiful sighing date palm with its sky-high trunks, waving branches, and red-gold fruit clusters which glimmer and shine like flaming logs.

Date palms edge the shores of the Nile and ring themselves around the oases. They shoot up between the clay huts and give villages their shade. If one travels up to the Mediterranean coastal area, they grow there in the midst of sand dunes.

They start their lives as a groundshoot. Around every palm a cluster of small palms builds up, and these are those which are used for increasing the numbers (of palms). To set out pips takes too long a time, and one cannot tell which gender will result. Perhaps they will be all male, for one cannot tell till the fruit comes. With a basal sucker, one can be certain that both gender and cultivar are known. In Egypt, there are at least 40 varieties, if not more.

Autumn is the date palm's season. That is when the fruit cluster becomes red, and they show in all colors from yellow gold to scarlet-red and chestnut-brown. Each kind has its color, its shape, its size, and the handlers for the most part know how to differentiate between them, merely by the appearance of the wood itself.

Palms also have economic value, capital worth, and are therefore listed and counted. In former times people paid taxes on them, but nowadays that has been abolished.

But, nothing is abolished without consequences! Much work is involved, not only with special handling of the suckers, but also with harvesting the crop.

In the spring when the palms bloom, one must climb up the male trees, and remove the male inflorescences. They must then be cut into small pieces, and then someone climbs the female trees and fastens a tuft in every palm crown. Then the wind does the rest. One male tree usually serves to fertilize 30 to 40 female trees or more.

The stately date palm is much admired by people even when it requires being disseminated. It is the women who take the suckers to the far-off desert springs. The women are the ones who care for them and water them before the roots have taken hold. Without this work by the women, the palm tree would be extinct.

One might well guess that without the date palm, people would not have survived, at least not in the North African desert areas. The date palm is the Bedouin's bread, especially the bone-hard, dry date palm fruit, which is not very sweet to the taste. The Bedouin builds his huts in places wooded with date palms, and makes his household furniture of its leaves and fibers.

Along the Mediterranean coast (Egypt), palms are planted in deep hollows, in order to have a little shade at their start to withstand the strong salt sea winds.

[1] Translated by Eva Filbin from "Pharoah's Flowers (Faraos Blomster)," a book in Swedish by Vivi Laurent-Täckholm who was long associated with the Herbarium at Cairo University and who is author (with Drar) of the "Flora of Egypt." Submitted by Walter H. Hodge.

If one comes to the coast in the autumn, when the fruit clusters are ready to harvest, one can perhaps meet up with someone who fires shots at one palm tree after another. The shots resound among the sand dunes and echo over the whole terrain. What is happening? ask those who don't know.

There is a snake in paradise, a snake being shot at. There is a snake up there in the high crown of the tree. When the dates are ripe, birds come to feast on them, and in the birds' wake, snakes slither in to get their taste. How they manage to enter the stems is a mystery. But now and then, when a shot has sounded, a dead snake falls down from the palm. Then, one's doubts are confirmed, and one knows the shot has been well aimed.

But shots ring out only in the autumn, and only at harvest time. Otherwise, it is peaceful up high in the date palm crowns, and only the wind sighs.

Inseparable Companions

Where does the mighty date palm come from? It is known only as a cultivated plant. But it is grown in the entire desert area from the Atlantic coast of Africa in the west to India's boundaries in the east. It has been found from Asia Minor to and including the southern coasts of Europe, but in those places it seldom bears fruit.

There are three wild date palm species which have competed for the distinction of being considered ancestors of the common date palm. These are the Canary Island date palm, *Phoenix canariensis*, Central Africa's date palm, *P. reclinata*, and one of India's many date palms, *P. sylvestris*. However, the Canary Island palm has different fruit, and the African palm different blossoms, which leaves only the Indian palm as the one to consider as ancestral. The latter differs from the common date palm in that it does not have suckers or offshoots and that it requires more moisture.

If one examines the date palm's area of cultivation, one makes a discovery. It is exactly the same as the so-called Mediterranean population, which includes (in itself) both the Hamitic and the Semitic strains (cultures). The distribution (of the palms) coincides extraordinarily well with these human populations, even in the southernmost areas of the distribution, where the palms are abundant in the territories of the Ethiopian peoples.

One must remember that the Mediterranean peoples originated out of the Indian-Dravidian race ages ago in the Tigris-Euphrates area. At that time the Mediterranean shores were occupied by the Grimaldi strain, people of the Paleolithic period, and deserts did not then exist in North Africa as they do now. Instead, the climate was rich in rain and the herds of cattle of the Grimaldi people fed on luxuriant grasslands.

But the climate changed. Rain became rare, and the grasslands became deserts. Out of many deserts grew the desolate and unwelcoming Sahara. About that time the new Mediterranean people migrated from the east and settled around the shores of the Mediterranean Sea, and it was this people who fostered and cultivated the date palm.

Some have suggested that the date palm evolved within overlapping ranges of the territorial limit for date palm, and the phoenix palm, such as we see in Iran and southern Baluchistan, and that from there it developed as the cultivated species. Others think that the date palm could just as well have developed within its existing limits. Possibly the moisture-needy *P. sylvestris* had a wider range in earlier times. Possibly it followed the now prevailing winds all the way to the Atlantic Ocean, where the Canary Island palm nowadays lives as an isolated species. But when desert conditions took over, it died out and could only then survive in rain-rich India. The only one which could tolerate the new desert climate was the transformed species,



1. Date palms (*Phoenix dactylifera*) in bas relief on walls of terrace temple of Queen Hatshepsut (1515–1484 B.C.), at Deir-El-Bahri, opposite Thebes, Egypt. Photo by Walter H. Hodge.

the common date palm, with its desert-tolerant characteristics.

Men have speculated and wondered, until a report was made recently which shed new light on the origin of the date palm. There were two famous female Egyptologists who were excavating in the Kharga Oasis. They found a layer from

the earliest stone age, a period estimated to have ended at about 14,000 B.C.

They discovered impressed in that river bed the leaves and seeds of a palm. The seeds were as small as coffee beans, but they had a groove which revealed that it was a palm related to the date palm, *Phoenix*.

It was publicized as the seed of the *Phoenix sylvestris*. But later, in 1952, the authors changed their opinion and thought it possibly was the Central African palm.

Which is right? We don't yet know. But if India's famous wild *P. sylvestris* was found in Africa, then Africa could be the cradle of the date palm as well as Iran-Baluchistan.

But whatever the truth, the fact remains that the Mediterranean race of men was the bearer and the disperser of the date palm culture. The two are one and will likely always be that way.

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Effects of Several Plant Growth Substances on Height, Flowering, and Lateral Shoot Development of Chamaedorea seifrizii

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Chamaedorea seifrizii Burret. is one of the most important palm species used in America as an indoor plant. This species grows fairly rapidly and suckers, producing fuller containers during production and withstands the low light intensities of interiors.

Pots containing numerous canes are preferred by buyers, so growers often plant 15 or more seedlings in a 25 cm diameter container. Seed, as well as the labor to transplant numerous seedlings, is a major expense in the production of this palm. It would be desirable to enhance chemically the natural suckering ability of these palms, thereby reducing the number of seedlings required to produce a full, attractive container.

At approximately 100 cm in height, *C. seifrizii* plants mature and begin to flower. These palms usually retain their lower leaves until they begin to flower and the developing inflorescences in the leaf axils force the abscission of all but the youngest 5 or 6 leaves. Rapid growth, though desirable in commercial palm production, can result in excessively long internodes that further detract from the appearance of the palm. Chemical inhibition of flowering and internode elongation in *C. seifrizii* would be a valuable tool for commercial producers of this palm.

Little work has been done on the effects of various classes of plant growth substances on palm growth parameters. The effects of gibberellic acid (GA) applications on fruit characteristics of date palm (*Phoenix dactylifera* L.) have been reviewed by Mohammed (1985), but no other morphogenetic effects due to GA application were reported for this species. Fisher (1980) applied GA, as well as sev-

eral growth retardants, on 6 species of palms to induce juvenility and found GA to be effective in some species, including *C. seifrizii*. None of the materials he used had any obvious effect on lateral shoot development in any palm species, however. In the present study, several different classes of plant growth substances (gibberellins, cytokinins, auxins, and an ethylene releasing compound) were applied to *C. seifrizii* to determine their effects on lateral shoot development, plant height, and flowering in this species. Since high light intensities are known to promote lateral shoot development in other monocots such as *Dracaena marginata* Lam. (Donselman and Broschat 1982), this variable was also investigated for *C. seifrizii*.

Materials and Methods

One year old *C. seifrizii* seedlings were planted one per 15 cm diameter container and grown under 63% shadecloth. Plants grown in a Canadian peat, perlite, sand, cypress shavings medium (8:5:2:5, by volume) amended with 880 g m^{-3} Micromax® (Sierra Chemical Co., Milpitas, CA) and 8.3 Kg m^{-3} dolomite. Containers were fertilized with 18 g Osmocote® 18-6-12 (Sierra Chemical Co.) at 4 month intervals and approximately 2 cm of water was applied daily by overhead irrigation. Ten replicate plants were assigned to each of the following treatments which were applied as foliar sprays at monthly intervals for 1 year: control (water only) benzyl adenine (BA) at 200 mg/l and 500 mg/l, Ethephon at 200 mg/l and 500 mg/l, GA at 50 mg/l and 200 mg/l, and naphthalene acetic acid (NAA) at 1.0 g/l and 2.5 g/l. An additional 10 plants received no foliar sprays, but were grown in full sun and otherwise received identical treatment to shade-grown control plants. After one year, all plants were measured for height, number of lateral shoots, and number of flowers.

Table 1. Effects of various plant growth substances on suckering, height, and flowering of shade-grown C. seifrizii.

Treatment	No. Lateral Shoots	No. Flowers	Height (cm)
Control (water only)	5.3 ab[z]	2.2 ab	161.5 a
BA (200 mg/l)	5.9 ab	2.4 a	153.4 a
BA (500 mg/l)	6.6 a	2.6 a	163.4 a
Ethephon (200 mg/l)	5.6 ab	2.1 ab	127.7 b
Ethephon (500 mg/l)	6.2 a	1.1 bc	93.0 c
GA (50 mg/l)	5.8 ab	2.0 ab	156.8 a
GA (200 mg/l)	6.0 a	2.3 a	154.1 a
NAA (1.0 g/l)	6.6 a	2.0 ab	149.1 a
NAA (2.5 g/l)	4.9 ab	1.5 ab	158.9 a
Full sun	3.8 b	0.3 c	66.8 d

[z] Mean separation within columns by Waller-Duncan K-ratio method, 5% level. Means followed by the same letter are not significantly different.

Results and Discussion

Height of palms grown in full sun was about half that of shade grown plants (Table 1). Palm height was inversely related to the concentration of Ethephon applied, with palms treated with Ethephon at 500 mg/l less than 60% as tall as control plants. No other chemical treatments significantly enhanced or reduced stem elongation in *C. seifrizii*. Fisher (1980) found that Ethephon significantly reduced petiole elongation and leaf blade length in African oil palm (*Elaeis guineensis* Jacq.) but other growth retardants such as chlormequat and daminozide had no such effects. Leaf size was also reduced in *C. seifrizii* by Ethephon in that study.

Mean number of lateral shoots in *C. seifrizii* ranged from 6.6 for plants sprayed with NAA at 1 g/l and BA at 500 mg/l to 3.8 for plants grown in full sun (Table 1). Differences among chemical treatments with respect to number of lateral shoots were not statistically significant, however. Lateral shoot development in *Dieffenbachia* and *Spathiphyllum* has been enhanced by spraying with BA

(Henny and Fooshee 1985, Wilson and Nell 1983), but this was not true for *C. seifrizii*. Although lateral shoot development in *Dracaena marginata* is known to be promoted by growing the plants under high light intensities (Donselman and Broschat 1982), *C. seifrizii* grown in full sun produced fewer lateral shoots than shade grown plants.

Palms grown in full sun had significantly fewer flowers than shade grown palms (Table 1), but also grew more slowly and therefore may not have reached the physiological stage of maturity required for flowering. Ethephon sprayed at 500 mg/l appeared to have some inhibitory effects on the flowering of *C. seifrizii*, but there was no reduction in flowering by any other chemical treatment. GA is known to promote flowering in Aroids (Henny 1981), but there was no significant enhancement of flowering in *C. seifrizii* by this compound.

In conclusion, Ethephon sprays applied monthly at concentrations of 500 mg/l had the most significant and beneficial effects on *C. seifrizii*. This treatment retarded elongation and reduced the incidence of flowering, but had little effect on lateral shoot development. It is doubtful, however, that these rather small effects on palm growth characteristics by Ethephon would justify the commercial use of this material in *C. seifrizii*. Growing these palms in full sun also appeared to inhibit flowering and decreased growth rate, but overall plant quality in sun grown *C. seifrizii* was considered unacceptable for foliage plants.

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Veitchia merrillii and its Karst Island Home

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Towering 300 m above the waters of Bacuit Bay in northern Palawan, in the Philippines, the spectacular assagai karst limestone cliffs of Langen and neighboring islands are a newly recorded locality for *Veitchia merrillii* (Becc.) H. E. Moore.

This elegant palm, now widespread in cultivation, was first collected by Elmer in February 1911 about 400 km south, near Brooke's Point. In contrast to the Bacuit Bay locality, the palm grew in woodlands on sandy soil. Two years later, it was discovered by Merrill growing abundantly on the karst limestone of Apulit Island, some 100 km southeast of Bacuit Bay.

The Bacuit Bay discovery was made by the Palawan Botanical Expedition during a vegetation survey of Palawan in 1984. *Veitchia merrillii* was found to be most abundant on the karst outcrop summits, ridges, and in the sparse forest on steep slopes of fragmented karst blocks of Langen (also known as Malapakan) Island. In these exposed areas it seldom reached over ten meters high, but in protected locations heights of at least 25 m were attained. Only a few specimens were seen within dense forest. A few specimens were also seen growing on exposed rock within a few meters of the sea.

The climate of north Palawan is fairly dry with a rainfall of about 1,500 mm. March to May is very dry. This, combined with the karst limestone habitat, makes a tough environment. Relatively few species were associated with *Veitchia merrillii*. The commonest of these were *Pleiomele cf. multiflora* (Warb.) Merr., *Euphorbia trigona* Haw., *Spondias acida* Bl., *Ochrosia glomerata* (Bl.) F. v. Muell., a squat and arborescent species of *Sterculia*, a massive, red-flowered species of *Bauhinia*, and a scrambling species of *Jasminum*.

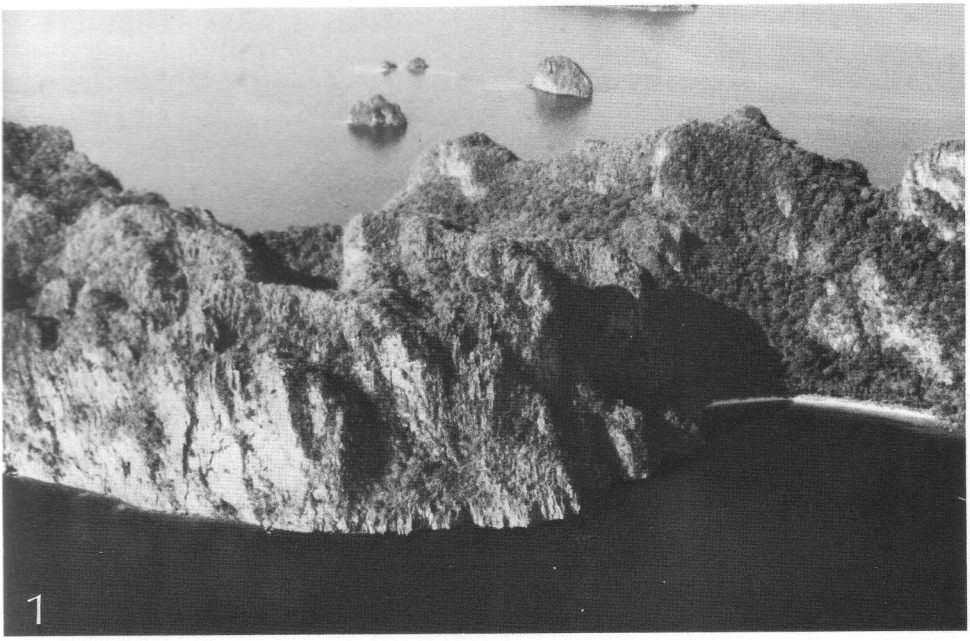
At the time of collection, April 1984, many palms were observed with well developed, but green, fruit.

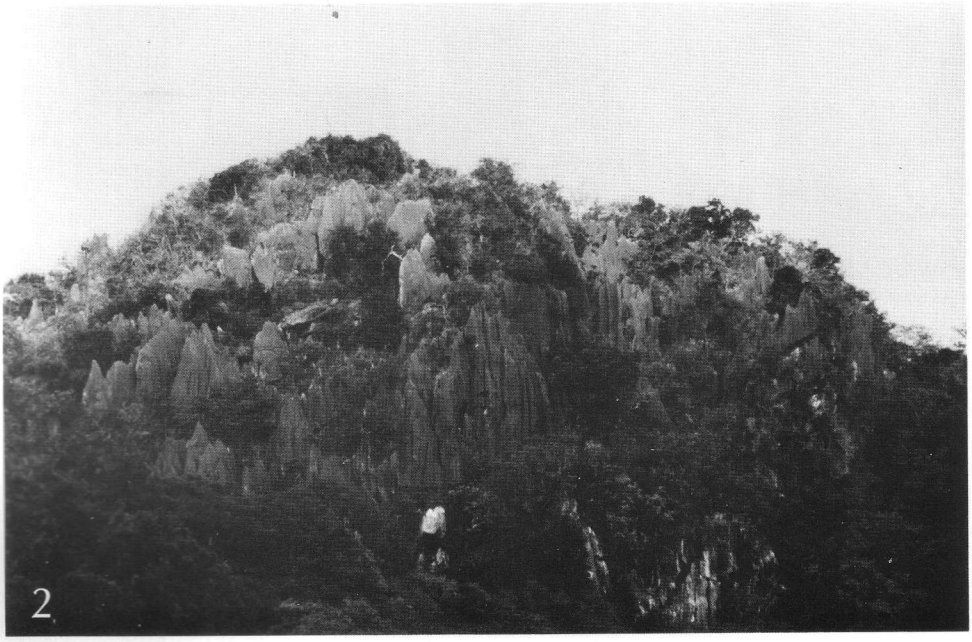
Another interesting discovery was of two colonies of a species of *Livistona* somewhat resembling *L. rotundifolia* (Lam.) Mart. One was on the narrow ledges of a precipitous cliff-face of an isolated karst block. The second was seen from the air to be growing between densely packed limestone pinnacles on the summit of a major karst block. In deference to life and limb, neither population was collected!

At present the habitat of both palms is probably secure from destruction, due not least to the treacherousness of the terrain.

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1. Langen Island, one of the karst island homes of *Veitchia merrillii* in northwest Palawan. 2. A pinnacle field, one of the habitats within which *Veitchia merrillii* grows.





3. *Veitchia merrillii* in fruit. 4. A colony of *Livistona sp.* on Langen Island.