

The Flowering and Fruiting of *Corypha umbraculifera* in Miami, Florida

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A sign of a maturing botanical garden is often the age of its plantings. One of the most striking symbols of maturity in Fairchild Tropical Garden, though it is barely fifty years old, was the flowering of the talipot palm, *Corypha umbraculifera* L., during May 1984 (cover photo). Few palms exhibit flowering in such a spectacular way as the talipot.

This event drew international publicity. The staff of Fairchild Tropical Garden, as proud parents, were excited about the flowering talipot, the first documented flowering of this species in the continental United States. Another species, *Corypha utan* Lam., had been reported (as *C. elata* Roxb., see Kew Bull. 37(1): 109) and studied in 1972 at the Subtropical Horticultural Research Station (U.S. Department of Agriculture) which is also in Miami (Tomlinson and Soderholm 1975). Locally, the talipot was described as the "Giant palm due to deliver" (South Dade Newsletter, 21 March 1984), or as the "Blooming miracle" (The Miami Herald, 11 June 1984). Across the country, other feature writers were even more anthropomorphic in their appreciation: "fatal reproductive frenzy" (A. Lacey in The Wall Street Journal, 14 May 1984), "palm bearing seeds . . . ends its own life" and "palm stages spectacular death dance" (D. Kollars in Knight-Ridder, Boston Globe, and Arizona Republic, 17 June 1984). As a result of the publicity from these articles, the flowering talipot attracted thousands of people from all over the world. During anthesis, May-June 1984, attendance at

Fairchild Tropical Garden was double that in previous years.

Although commonly found cultivated in S.E. Asia, the talipot is rarely encountered in natural stands. It is an example of one of the wonders of nature because of its ultimate, fantastic size and its unusual life history. Generally talipot palms develop trunks 9-25 m tall and 0.6-0.9 m wide. The fan-shaped leaves, each of which can shelter a dozen people from the rain, have blades ca. 5 m in diameter with spiny petioles ca. 3 m or more long. Each inflorescence branch can extend 3-6 m from the main axis. Millions of tiny flowers orderly arranged on branches compose the inflorescence. Reputedly, a ton of fruit may be produced.

Phenology

In October 1937, seeds of the talipot palm were received from Hope Botanical Garden in Jamaica. A young plant from this accession (P-1909) was included in the permanent collection (plot 80) of Fairchild Tropical Garden in May 1943. For most of its life, the talipot generated palmate leaves ca. 3 m in diameter arranged in a crown at the top of a stately grey trunk that was eventually 13 m tall and ca. 0.6 m wide. After 47 years of vegetative growth, there was an abrupt change from this stage to the reproductive stages (Figs. 1,2; Table 1). The only subtle suggestion of this switch was the diminishing size of the gigantic palmate leaves at the end of 1983. In January 1984, the first

evidence of the flowering spike was a huge pyramidal spear emerging from the leafy crown (Fig. 1a). Rapid development occurred from this initial inflorescence "bud" to complete expansion four and a half months later at anthesis (Figs. 1b-d, 2a-c). Garden visitors came to see a palm that grows only trunk and leaves for 20 to 80 years of its existence. Then, because of some unknown internal biological signal, an inflorescence is initiated. The inflorescence towered 6.15 m above the trunk. Millions of creamy white flowers were borne on the branched panicle.

To document this flowering, one of us (RWS), assisted by Dade County employees, rode a bucket lift to a height of ca. 14 m and cut a first-order branch axis and leaves from the crown for herbarium vouchers (*Sanders & Watson 1664*, FTG) and morphological studies (Fig. 3a). Another of us (NE) took close range photographs of the crown from the bucket lift. At this height one could examine the reduced leaves which wrapped around the main axis (Fig. 2c) as well as have a panoramic view of the palmetum. When the branch was brought to ground level, staff members snapped many photographs and commented on the fragrance of the flowers. Opinions varied widely. One suggested the flowers smelled like the ungulates' stall at the Bronx Zoo. Another suggested the fragrance was spicy-floral.

Relative to the total age of the plant, the reproductive stages were brief. Anthesis lasted six weeks, development of the fruit took 12 to 15 months. Fruits began developing in August 1984, continued through the winter of 1985 (Fig. 2d), and began maturing in June 1985. The yield of fruit collected in June through September was only 5.4 kg instead of the anticipated ton.

Inflorescence Structure

The shoot of *Corypha* is hapaxanthic, that is there is a defined period of vege-

tative growth in which the shoot bud produces new leaves and stem, followed by a defined period of reproductive growth in which the inflorescence and flowers are produced. The act of flowering terminates the growth of the stem. In a single-stemmed palm like *Corypha*, flowering and fruiting end the life of the individual plant. During its vegetative phase of 50 or so years from the time of seed germination, only stem and leaves are produced by the growing point or apical meristem. No lateral buds are formed until the reproductive phase begins. At this time a series of modified leaves develop in which the petiole and blade regions become smaller in successive leaves until only the sheath portion is developed (Fig. 2c). These reduced leaves which are termed bracts enclose the main inflorescence axis, itself a direct continuation of the trunk. Lateral buds in the axils of these bracts grow out as the main or first-order branches (Fig. 3a) of the massive terminal inflorescence. Using the terminology proposed by Tomlinson and Soderholm (1975), we can describe the mature reproductive structures of our specimen as follows:

The central vertical axis (ax_0) decreases in diameter towards the tip (Figs. 1,2). Bracts enclose this axis and subtend 27 lateral, horizontal, first-order branches (ax_1) which push out through the split bases of most bracts (Fig. 2c). These first-order branches in turn produce bracts. In a representative first-order branch cut from the lower half of the inflorescence (Fig. 3a) there is a thick, two-keeled bract or prophyll at the base, followed by two empty (=branchless) tubular bracts, and then 25 bracts subtending second-order branches (ax_2). Each second-order branch (Fig. 3b) lacks a prophyll and has very reduced, non-tubular bracts, often represented only by a tissue ridge, below the third-order branches (ax_3). Further branching occurs up to fifth-order branches (ax_5) in the basal region of the first-order branch. Bracts do not subtend third and higher orders of



1. Inflorescence development in *Corypha umbraculifera*. a. Early appearance of inflorescence spear, Feb. 1, 1984 (Photo: S. Kantor). b. Early growth of first-order branches, Feb. 23, 1984. c. Elongation of first-order branches, March 1, 1984. d. Appearance of second- and higher-order branches, March 25, 1984.



2. Inflorescence development, continued. a. Development of rachillae, April 11, 1984. b. Anthesis, photographed from lift at level of the inflorescence, May 9, 1984 (composite of 2 frames). c. Close view of proximal portion of main axis (ax_0) after the sampled first-order axis (ax_1) was cut off, May 9, 1984. Note reduction series of bracts, white arrows point to reduced blades. d. Developing fruit, Feb. 1985.

branching. The distal second-order branch (number 25 in our sample) is an extension of the first-order axis beyond the last tubular bract and had a total of four branching orders. We interpret this region as having a main axis (=ax₂) and ending with a maximum fifth-order axis (=ax₅). Although the main axis appears to be a linear extension of the first-order axis, the tubular bract is interpreted as subtending a theoretically axillary branch system which only appears to be terminal. Further study of early stages of development is necessary to clarify this speculative interpretation.

A similar question of interpreting branch position arose in dealing with the distal-most first-order branch of the whole inflorescence. Is the distal-most branch a direct continuation of the central trunk, or is it a lateral branch which only appears to be terminal? In all cases the terminal branch units bearing the flowers are called rachillae and can be third- to fifth-order branches depending upon their positions within the whole inflorescence.

Flower and Fruit Structure

Flowers occur in clusters which are interpreted as cincinni or highly reduced, adnate sympodial branching systems (Fig. 4). The flower clusters are arranged more or less in a spiral on the rachillae (Fig. 4a). Each flower (Fig. 4b) in a cluster is subtended by a tiny bracteole, and the whole cluster is subtended by a tiny bract which is often barely recognizable in the mature rachilla (Fig. 4c). The number of flowers varies from seven or eight in large clusters near the base of a rachilla to about three near the tip of a rachilla. Single flowers are found at the very tips of many rachillae.

Each flower is perfect (bisexual) and elevated on a thickened, rugose pedicel (Fig. 4b). Terminating the pedicel are three small, lobelike sepals, three cream-colored petals, six stamens, and three carpels, which are fused to form a three-lobed ovary. Usually only one carpel develops into a single fruit per flower. The flowers are abscised below the pedicel if none of the ovules are fertilized or if fruit development ceases; the pedicel scars remain (Fig. 4c).

We have no information on the self compatibility of flowers or the need for cross pollination for fruit set. The tree at Fairchild Tropical Garden clearly had reduced fruit set as compared with reports of other trees of this species (Douglas and Bimontoro 1956) and with *C. utan* (= *C. elata*, Tomlinson and Soderholm 1975). The mature fruit (Fig. 3c) was ca. 4.5 × 4.5 cm at maturity and contained a single seed (Fig. 3d) with more or less homogeneous endosperm and a straight embryo (Fig. 3e).

The entire inflorescence produced approximately 24 million flowers. We estimated the number produced by the tree by extrapolating measurements made on the first-order branch sample. The details of calculations are given in the Appendix.

Conclusions

The inflorescence of *Corypha umbraculifera* is the largest known among palms, as well as all other flowering plants. This immensity, in part, is a consequence of having the apex of the entire plant converted into an inflorescence structure. However, in making direct comparisons, the concept of inflorescence becomes a problem. The whole inflorescence in other palms is equivalent (possibly homologous)

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3. *Corypha umbraculifera*. a. First-order branch, collected May 9, 1984. b. Second-order branch, note that the most proximal third-order branching occurs within the bracts subtending the second-order branch. c. Fruits (left, whole; right, exocarp and mesocarp removed), collected summer, 1985. d. Seed cut longitudinally; arrow points to embryo cavity (embryo removed). Note thin testa-like endocarp. e. Embryo removed from seed, slightly injured on right by forceps during dissection.

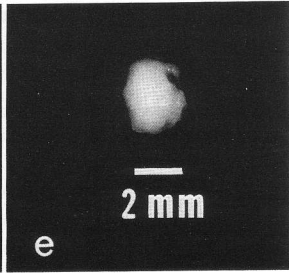
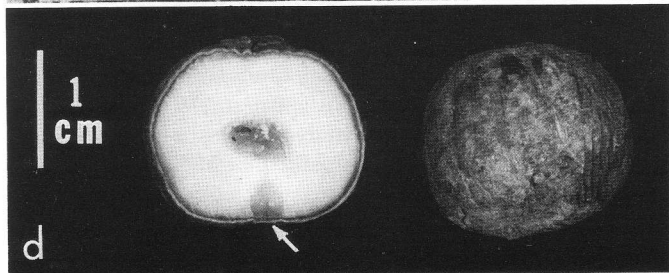
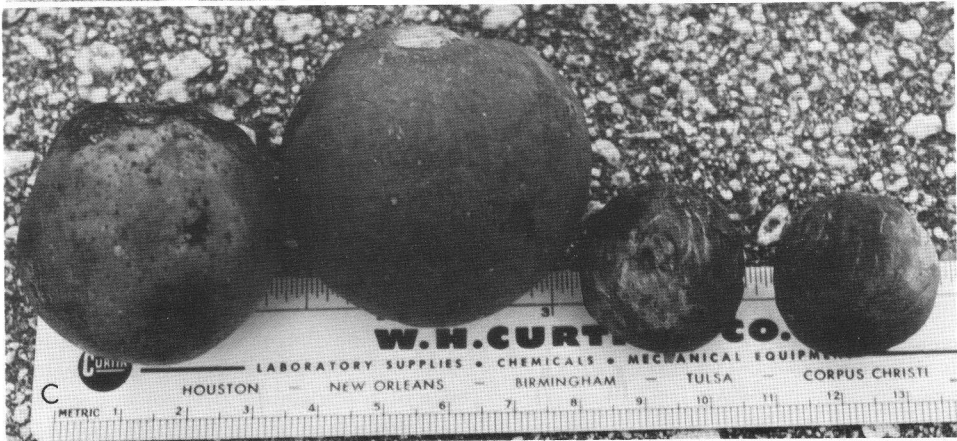


Table 1. Chronology of flowering and fruiting in *Corypha*.

Date	Observations
Late Dec 83	Reduced new leaves first noted
24 Jan 84	Inflorescence bud first noted
10 Feb 84	Inflor. 4.05 m tall; longest first-order branch with 4 visible bracts (Fig. 1a)
17 Feb 84	Inflor. 4.95 m tall
24 Feb 84	Inflor. 5.31 m tall; longest first-order branch approx. 2 m (Fig. 1b)
2 Mar 84	Inflor. 5.61 m tall (Fig. 1c)
9 Mar 84	Inflor. 5.76 m tall
16 Mar 84	Inflor. 6.06 m tall; second- and higher-order branches emerge and rapidly elongate over 1-2 days
20 Mar 84	Inflor. at maximum height, 6.15 m; rachillae immature; all 6-8 foliage leaves greenish-brown and bent down (Fig. 1d)
Mid-April 84	Rachillae reach mature size; floral buds begin expansion (Fig. 2a)
4 May 84	Flowers first noted falling on ground
9 May 84	Flowering observed within the crown; representative first-order branch collected (Fig. 2b,c)
August 84	Anthesis completed, young fruits beginning to develop (cover photo)
Nov 84-May 85	Immature (abortive) green fruit falling on ground (Fig. 2d)
Jun-Sept 85	Fruit mature and dropping to ground
August 86	Tree standing with dead leaves and inflorescence intact

Final dimensions:

Trunk height from ground to base of inflorescence = 13.05 m.

Trunk diameter (without leaf bases) at breast height = 61 cm.

Inflorescence length from base to top = 6.15 m.

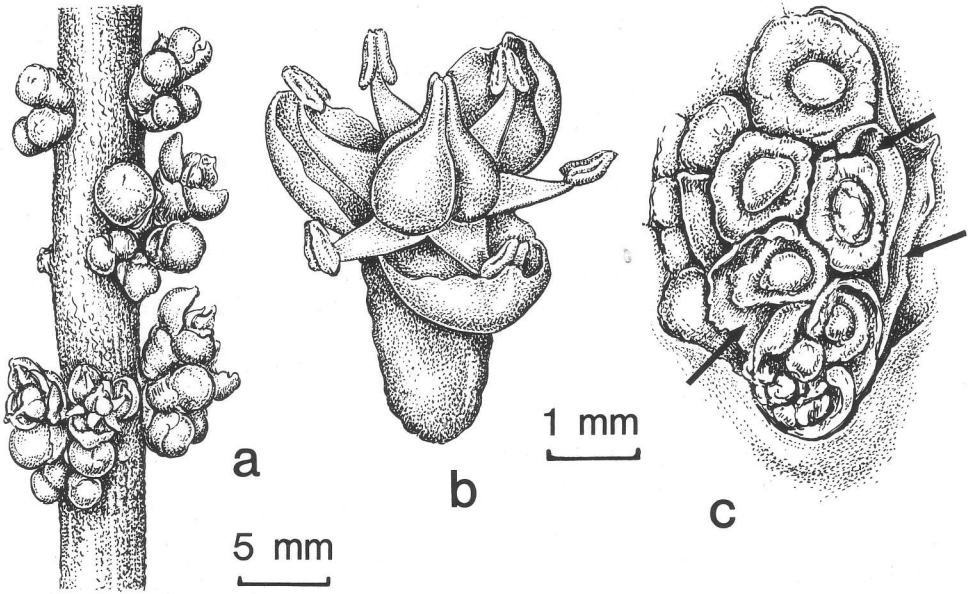
Inflorescence width (longest first-order branch) = ca. 3.5 m.

to a single first-order branch (ax_1) of *Corypha*. Thus, many pleonanthic palms, e.g., *Sabal*, *Borassus*, eventually produce as many (or more) ax_1 's as does *Corypha*, and these are often as long as those in *Corypha*. However, the ax_1 's of these other genera are not as massive as and probably bear fewer flowers than those of *Corypha*.

Our estimate of the total number of functional flowers is about 24 million. The accuracy of this figure depends in part on the representativeness of the first-order branch collected and on our interpretation of the shape of the whole inflorescence. This figure is probably near the upper limit of possible flowers. Tomlinson and Soderholm (1975) estimated 10 million (3-15 million) flowers for *C. utan* (which they called *C. elata*). Their specimen had almost twice as many first-order branches as our specimen of *C. umbraculifera*; the first-order branches were about the same length in both. However, in *C. utan*, they found only 13 second-order branches per first-order branch, 33 rachillae per second-order branch, and 375 flowers per rachilla compared, respectively, to 25, 86, and 440 in *C. umbraculifera*. Thus, our estimate appears to be proportionately similar to theirs for *C. utan*.

Fruits collected from our specimen of *C. umbraculifera* were markedly larger (4.0-4.8 cm diameter) than those collected by Tomlinson and Soderholm from *C. utan* (1.5 cm). In producing larger fruits, our tree may have compensated for a very low fruit set, and thus, the difference in size of fruits may not reflect any genetic difference (specific or individual) between the two trees. The disappointingly small crop from our tree prevents a direct comparison to their study of reproductive biomass in *C. utan*.

In that study, Tomlinson and Soderholm (1975) estimated that 15% of the biomass produced by the *C. utan* specimen went into reproductive effort. This is high for a woody plant and is comparable to the reproductive effort of annual weeds. They



4. *Corypha umbraculifera*. a. Part of rachilla with open flowers and flower buds in each cluster. b. Single flower at anthesis. c. Flower cluster after individual flowers have fallen or were removed; six clear flower (i.e., pedicel) scars and possibly one or two more are visible, arrows point to bracteoles. (Drawn by P. Fawcett)

concluded that "... despite its massive size, *Corypha* has to function essentially as an annual weed in order to survive." The reproductive biology of *Corypha* and other single-stemmed, monocarpic trees (those which die after fruiting once) are discussed in more detail by Hallé, Oldeman, and Tomlinson (1978). Such trees, similar to annual weeds, have a periodically high reproductive rate but are not as short-lived as weeds. They are so called "*r*-strategists" and usually live in unstable habitats. In fact, the natural habitat of *Corypha* appears to be disturbed forests (J. Dransfield, pers. comm.). The opposite extreme in reproductive behavior is found in plants with long-lived, slowly reproducing individuals in a stable population. These so called "*K*-strategists" continue to reproduce for a long time and often in stable habitats. Royal palms (*Roystonea* spp.) are pleoanthic and good examples in which each tree continues to grow while it flowers and fruits throughout its adult life span.

Certain tropical woody plants are distinctly periodic in seed production. Some are monocarpic like *Corypha*. Others are polycarpic and set fruit many times during their lives but only once every several years. Janzen (1978) reviewed this mode of reproduction and recognized two major categories.

1. Unsynchronized periodic fruiting: exemplified by *Cassia grandis* (polycarpic) and *Tachigalia versicolor* (monocarpic; Foster 1977), both legumes.

2. Synchronized periodic (or mast) fruiting: exemplified by polycarpic species, e.g., *Ateleia herbert-smithii* (Leguminosae), *Andira inermis* (Leguminosae), and most species of Dipterocarpaceae in the Malaysian rainforests, and by monocarpic species, such as some bamboos and *Strobilanthes* spp. (Acanthaceae).

Janzen (1978) believed that the biological or adaptive significance is the escape from seed predators by producing such enormous numbers of seed that only a portion can be eaten. In his terminology,

this behavior is predator satiation. The synchronized or mast fruiting allows this escape, not only by excessive individual and regional crops, but also by not supporting the seed predators for several successive years between fruiting events.

The time of fruiting for most polycarpic mast fruiting species apparently is set by external weather cues; whereas, Janzen (1976, 1978) suggested that the monocarpic bamboos and *Stobilanthes* have their timing set by an internal physiological calendar.

Data are not available to classify unambiguously *Corypha* as a plant with monocarpic unsynchronized fruiting (e.g., *Tachigalia*) or as one with monocarpic mast fruiting (as some bamboos). Whitmore (1977) cites the flowering of a 40-year-old tree of *C. utan* (= *C. elata*) at the Singapore Botanic Gardens in 1935 after a drought. Douglas and Bimantoro (1956) noted an abnormal dry period of four months before their three mature specimens of *Corypha* (*C. utan*, age 39 years; *C. umbraculifera*, ages 30–35 years and 65 years) all came into flower over a thirteen-month period. They related this to the observation of Griffith (1850) that in Bengal the *Corypha* species bloom in March and April which is about six months after the beginning of the long dry season (mid-September to mid-June). However, the first physiological change to flowering must have occurred many months before any external change could be seen. Reitz (1974: fig. 1) published a striking photograph of a row of ten trees of *C. umbraculifera* grown in the Peradeniya Botanical Garden (Sri Lanka) that bloomed simultaneously in 1969.

Thus, we suggest that *Corypha* spp. are synchronized or mast fruiting. However, unlike some bamboos, the cue for the one-time flowering may be external. Whether the adaptive advantage to the species of *Corypha* is strictly the avoidance of seed predators is unknown. We believe that

other possible advantages include: 1) reducing the distance traveled between flowering trees by pollinators, 2) providing a light gap for the seedlings to become established after the parent tree dies, and 3) maintaining carbohydrate reserves during the long period of uninterrupted vegetative growth.

Unfortunately, much of our discussion of the reproductive biology of *Corypha* is speculative because our observations were made on a cultivated specimen. Studies of the species in their natural environments are needed to sort out the possible causes and biological advantages of this unusual perennial behavior.

Acknowledgments

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Appendix

Details of estimating the number of branches and flowers in the inflorescence of *Corypha*. Data taken from one representative first-order branch collected on 9 May 1984 (Fig. 3a).

Number first-order branches = 27
 First-order branch (about ninth from base)
 Total length of first-order branch = 345 cm
 Number of second-order branches (including terminal portion) on this first-order branch = 25
 Maximum length of second-order branch = 64 cm
 Rachillae per second-order branch
 Proximal second-order branches (1-15) = 110
 Middle second-order branches (16-20) = 70
 Distal second-order branches (21-25) = 37
 Length of each rachilla: \bar{x} = 165 mm, s = 191, range = 47-253 mm
 Rachilla sum for one entire first-order branch = 2,185

Flower number

Per cluster (range = 2-8)
 Distal $\frac{1}{4}$ of rachilla: \bar{x} = 3.8
 Proximal $\frac{3}{4}$ of rachilla: \bar{x} = 5.6
 Per rachilla: \bar{x} = 441, s = 126, range = 80-755
 Per first-order branch = $(441)(2,185) = 963,585$
 Total for inflorescence before shape factor = $(27)(963,585) = \text{approx. } 26 \times 10^6$

Shape factor as follows: ca. 75% of first-order branches as long as representative branch; ca. 20% of first-order branches were estimated as 77% of the representative branch; and 5% of first-order branches were estimated as 31% of the representative branch.

$$\begin{aligned}
 (.75)(26 \times 10^6) &= 19.5 \times 10^6 \\
 (.20)(.77)(26 \times 10^6) &= 4.0 \times 10^6 \\
 (.05)(.31)(26 \times 10^6) &= 0.4 \times 10^6
 \end{aligned}$$

Estimated total number of flowers in the inflorescence after using the shape factor = 23.9×10^6 .

Palm Research

I am working on an account of the cultivated chamaedoreas to be published by the International Palm Society. I would appreciate members sending me information about chamaedoreas in their collections. Information needed includes but is not limited to name of the plant, source of the plant and name, locality if collected in the wild, parents if a hybrid, general description, germination times, cultural information, photo of leaf and inflorescence/fruit, or any other information that may be useful or of interest to other Palm Society members. Send to DONALD R. HODEL, Environmental Horticulturist, University of California, 2615 S. Grand Ave., Suite 400, Los Angeles, CA 90007, USA.