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Growth Form, Growth Characteristics, and Phenology of *Raphia taedigera* in Costa Rican Palm Swamps

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Raphia taedigera, one of the several palms that form large, nearly monospecific swamp forests, extends through the Caribbean lowlands of Colombia, Panama, Costa Rica, and Nicaragua. Disjunct populations occur in the Golfo Dulce region of Pacific coast Costa Rica and in the delta of the Amazon River. Palms forming vast monodominant stands are largely unstudied. Presented here are data on the phenology and growth of *Raphia taedigera* studied in the swamp forests near Tortuguero in the northeast corner of Costa Rica (Fig. 1).

The physiography of the Caribbean lowlands of Costa Rica consists of a broad alluvial plain known as the Llanuras de Tortuguero. The plain is bordered on the east by the Caribbean Sea, and on the west by a gradual undulating incline that ultimately abutts the steep eastern slopes of the Cordillera Central. As the coast is approached the undulations become less pronounced until there is a flat coastal wetland interrupted only by several isolated volcanic hills that range from 100 to 300 m. The vegetation on the plain consists of several types of palm swamps dominated by either *Raphia taedigera* or *Manicaria saccifera* (Fig. 2).

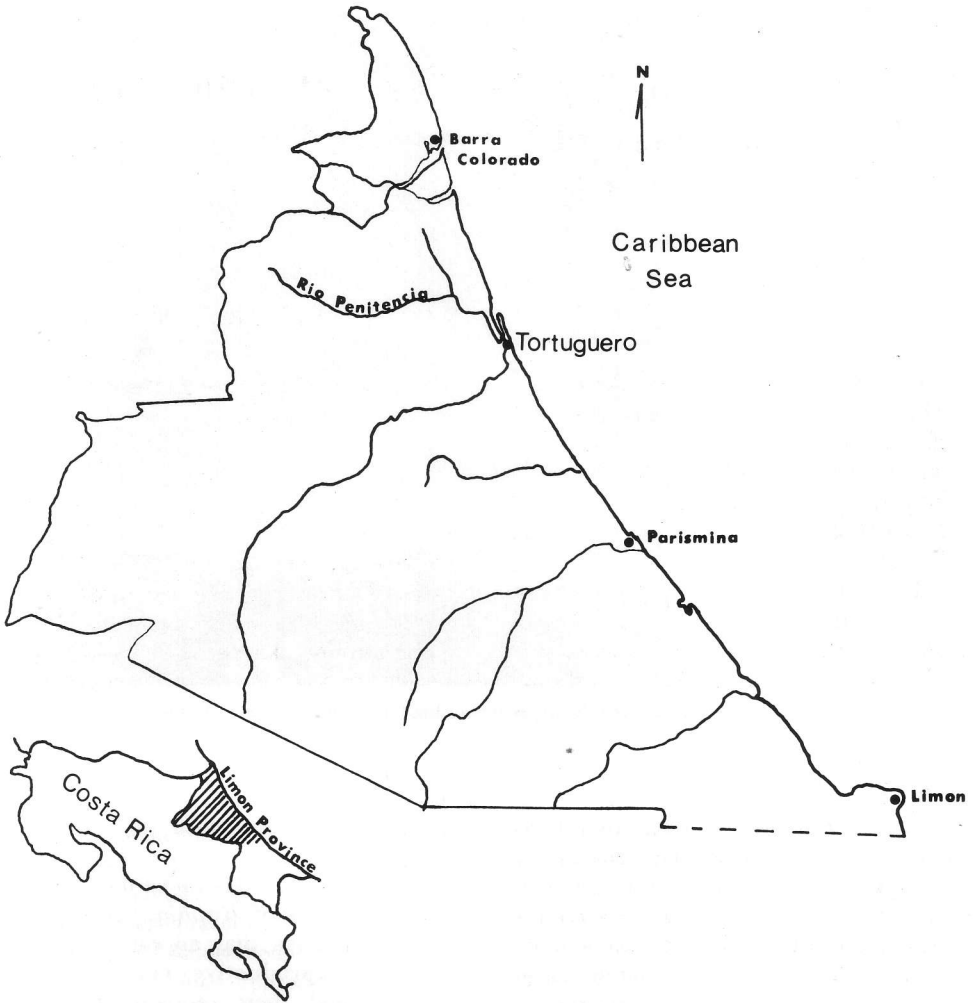
The climate in the Tortuguero area is aseasonal, but heavy rainfall and extensive flooding routinely occur in July-August and November-December. Drier months are less predictable, but January through April and the month of Septem-

ber usually experience the least rainfall. Annual rainfall varies between 4,000 and 7,000 mm.

Vegetative Characteristics

Woodson and Schery (1944), in their *Flora of Panama*, describe *Raphia taedigera* as a thick-trunked soboliferous palm forming clumps of stems with massive ascending and arching leaves (Fig. 3). The leaves average 12-14 m, but lengths up to 20 m have been recorded (Allen 1965), making them among the largest leaves in the plant kingdom. Hallé (1977) mentioned leaves even longer in *R. regalis*. The trunks in the multi-stemmed clumps are stout (approx. 30 cm in diameter) and erect (8-9 m tall), arising as if from a platform. They are never leaning or curved. The stems are always sheathed by both live and persistent dead petioles, which are not entirely sloughed off until after the stem dies. Vegetative offshoots are numerous around the bases of the stems.

Aerial negatively geotropic roots or pneumatophores cover the swamp soil. They develop from horizontal subterranean roots and protrude 10-40 cm above the soil. They are denser and taller near the base of the clump, and they may branch profusely, forming a dense mat. Cardon (1978) described the morphology and anatomy of these roots in several African species of the genus. Never men-



1. Map of the northeast corner of Costa Rica showing the location of Tortuguero and Rio Penitencia.

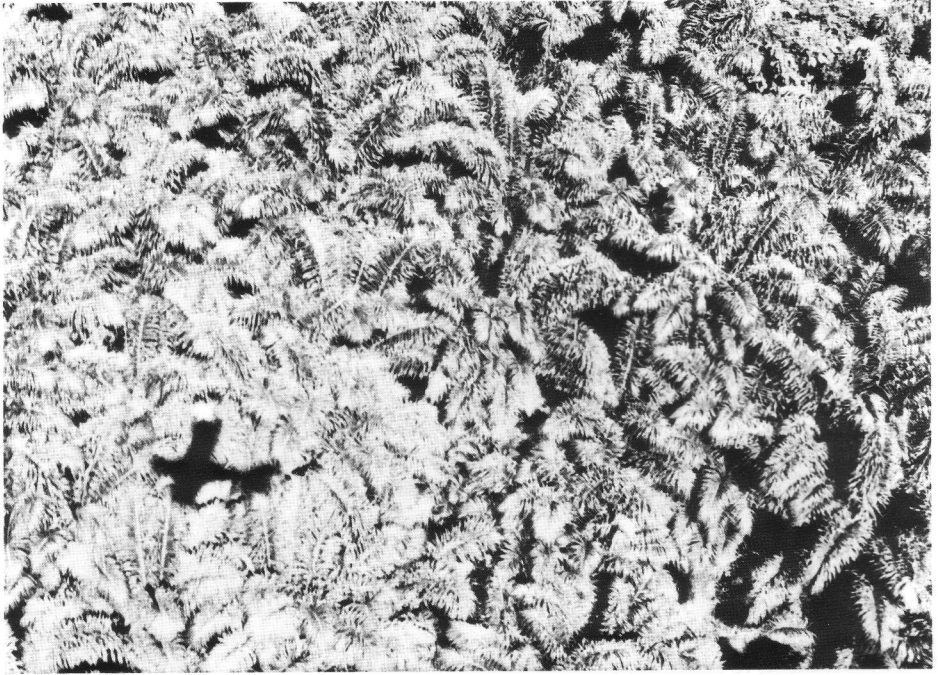
tioned in the literature are the negatively geotropic roots that arise from the stem and grow up the stem under the dead petioles. They may be found originating up to 3 m above the ground.

The leaves are pinnate. The pinnae or leaflets are subopposite, reduplicate (i.e., roof-shaped in cross-section on the rachis), 1–1.5 m long, and 4–5 cm wide. The margins bear widely spaced, minute, sharp spinules that go unnoticed until the leaves

are handled. The petiole is 15–20 cm thick near the base, and its upper surface is deeply concave, forming a trough.

Reproductive Characteristics

Raphia taedigera is monoecious. The inflorescences arise in the axils of the distalmost, often reduced leaves; each stem is hapaxanthic, dying after fruit fall. It is not a true monocarpic species because



2. Monospecific *Raphia taedigera* swamp in the Caribbean lowlands of Costa Rica.

there are usually several other large stems and numerous sprouts. Occasionally a reproductive individual is found without other stems or sprouts. It is not known if this is genetic or the result of competition.

The pendant spadices are immense, at times over 2 m long. The flowers occur in clusters on distichous hand-like rachillae. At fruiting time the persistent stamiferous "fingers" protrude beyond the fruit. The fruit is oblong, 5–7 cm long, 3–4 cm thick, and completely covered with shiny, brown imbricate scales giving it the general appearance of an unopened pine cone, hence the English common name of *pine-cone palm*. Inside the outer shell is a dense, fleshy orange-brown integument that encases an oblong, extremely hard seed, 3–5 cm long. The surface of the dark seed is coarsely grooved; the endosperm is deeply ruminate.

Methods

Phenology. To determine the periodicity of flowering of *Raphia*, two hundred *Raphia* clumps that appeared to have reached reproductive maturity were marked and their reproductive status noted. To facilitate observation, all of the individuals selected occupied a fringe along the Penitencia Lagoon and River near Tortuguero. These trees appeared larger and more vigorous than those inside the swamp, so their reproductive behavior may have been different from that of the more crowded individuals in the swamp.

Once a month for 12 months observations were made on the flowering status of each clump. Eight categories were used to describe the flowering/fruiting status of each stem within each clump. They were: 1) no inflorescence, 2) new unexpanded inflorescence, 3) expanded yellowish-green



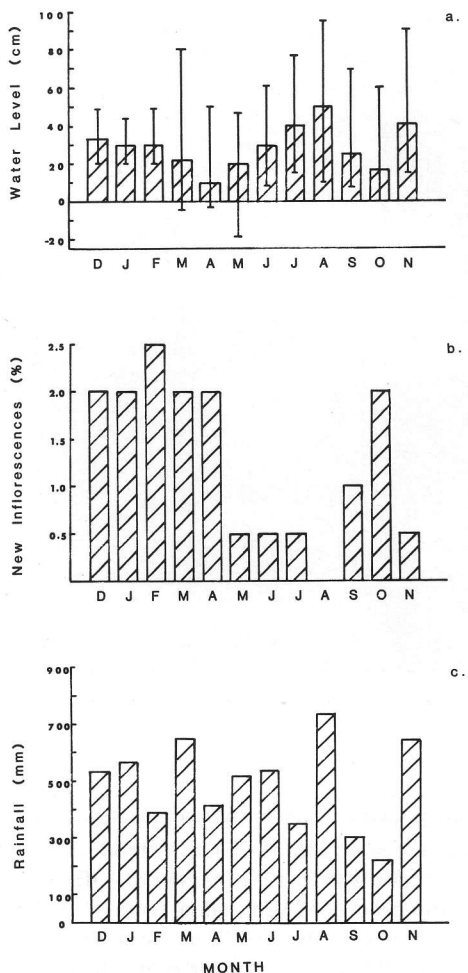
3. *Raphia taedigera* along Rio Penitencia.

inflorescence indicating that the individual flowers had not yet opened, 4) brown inflorescence indicating mature flowers, 5) immature fruit present, 6) mature fruit present, 7) old inflorescence, i.e. all fruit fallen, and 8) dead reproductive stem. Easily accessible individuals were observed more frequently to determine time of pollen release and duration of fruit development and fruit fall.

Dead stems were not initially recorded but were noted if they died during the observation period. Changes from new to yellowish-green to brown inflorescences were quite abrupt and easily ascertained. It was more difficult to determine the changes from brown inflorescence to immature fruit to mature fruit. Most likely the length of the "mature fruit" period was overestimated. A reproductive stem was classed as "mature" when fruit fall was in process. At times this was difficult

to ascertain as fruit fell into the water and disappeared into the mud. Although deterioration and death of leaves on a fruiting stem proceeded while some fruit remained on the tree, the "old" category was designated when no fruit remained on the tree. The "dead" category was used when all leaves were brown. At the beginning of the observation period it was impossible to determine cases where monkeys had destroyed a fruit crop or where fruit set had failed to occur, even though both situations are not uncommon.

Growth and Biomass. *Raphia* growth was measured by selecting 14 stems as they were encountered along a line transect on the lower slope of the natural levee along Rio Penitencia and running parallel to the river. Six clumps were involved. One had four large stems, another had one stem, another three stems, and the rest two stems. The youngest leaf of each



4. a). Mean monthly water level and ranges in the Rio Penitencia swamp during the study period. b). Monthly percentages of *Raphia* genets producing new inflorescences (sample size 200). c). Monthly rainfall during the study period.

stem was marked with paint at its lowest point, the number of leaves was counted and after a year the number of new leaves was determined. All leaf material produced during the year was then harvested, and the petioles and rachis separated from the leaflets. The two categories were then weighed to within ± 200 g using a Salter

suspended weigher. Subsamples were taken, oven dried at 105° C until there was no further weight loss, and weighed to 0.1 g. In the case of marked leaves, only the portion that expanded below the orange paint was harvested. This underestimated the total biomass produced by those leaves because at the time of marking the leaflets above the mark were not fully developed and expanded.

To determine the amount of stem produced per leaf, ten dead stems with prominent leaf scars were measured and the mean amount of stem produced per leaf calculated. An equivalent sized live sample was cut, weighed, and subsampled for dry weight determination.

Four mature inflorescences were harvested, the fruits removed and counted and both the inflorescences and fruit weighed and subsampled. Using forest structure data for the Rio Penitencia swamp (Myers 1981), the number of clumps and stems per hectare was calculated. The expected number of inflorescences per hectare per year, an estimate of the number of reproductive stems per ha, and the number of stems that die per year were obtained from the phenological data. From these, *Raphia* growth, leaf turnover, and biomass were estimated. Pneumatophore biomass and growth were not measured.

Results

Phenology. At the onset of the study 53 percent of the clumps had no stems flowering or fruiting. Initially 2 percent had new inflorescences, 2.5 percent had expanded inflorescences, 11.5 percent had open flowers (many of these may have had small unnoticed fruit), 9.5 percent had immature fruit, and 19.5 percent had mature fruit. Seven percent had old inflorescences and during the course of the year 4.0 percent died. Many others were in advanced stages of senescence. At the end of one year 44.5 percent of the orig-

Table 1. Summary of *Raphia* leaf and stem data

	Mean	Sample Size	Standard Deviation
Leaves			
Length of leaves (m)	11.9	56	1.45
Total No. of leaves per stem	5.4	14	1.15
No. of new leaves per stem	0.9	14	0.47
No. of expanded leaves per stem	4.0	14	1.24
No. of senescent leaves per stem	0.4	14	0.51
No. of leaves per clump	12.5	6	
No. of new leaves produced per stem per year	2.1		0.63
No. of new leaves produced per ha per year	954.3		
Stems			
No. of stems per clump	3.3	50	1.47
No. of clumps per ha	163.3		1.53
No. of stems per ha	537.3		
No. of stems per ha producing new leaves	452.3		
No. of stems per ha with inflorescences	85.0		
Stem turnover per ha per year	25.3		

inal non-reproductive clumps still had not reproduced.

The monthly appearance of new inflorescences, rainfall, and waterlevels are shown in Figure 4. New inflorescences developed during every month except August, and even in August they were observed on individuals not included in the study. The monthly average of clumps producing reproductive stems was 1.3 percent, and the maximum was only 2.5 percent. In total, 31 clumps or 15.5 percent of the individuals had a stem produce a new inflorescence during the year. Twenty-two clumps (11%) had three stems in different stages of flowering/fruitletting. At no time was a clump observed that had two or more inflorescences in the same stage of development.

Growth and Biomass. Table 1 summarizes *Raphia* leaf and stem data. Table 2 gives estimates of above-ground standing crop and organic matter production of *Raphia*. In calculating the values several assumptions were made that may not be valid. I assumed that a new leaf is produced as an old one is sloughed off. In general, this is the case with palms (Tom-

linson 1963), and the number of leaves on each stem at the end of the study was approximately equal to the number at the beginning. Additional leaf loss occurs through the death of reproductive stems. I assumed that this is balanced by the leaves of sprouts that move into the "mature" category.

The amount of stem produced per leaf (large stems only) was calculated to be 2.53 kg dry weight. It was easy to estimate stem production because palms possess little or no stem diameter growth after a leaf has matured, stem diameter in

Table 2. Estimates of above-ground biomass and organic matter production of *Raphia*

	Biomass (kg ha ⁻¹)	Production (kg ha ⁻¹ yr ⁻¹)
Leaves	11,789	5,516
Stems	29,904	2,414
Inflorescences	1,840	548
Fruit	749	749
Sprouts	—	2,036
Totals	44,283	11,263

Raphia is fairly uniform, and prominent leaf scars on dead stems mark the amount of stem produced per leaf. These are only true after the internodes have started to greatly elongate, i.e., after establishment growth. Biomass accumulation per stem was calculated to be 5.3 kg per yr. Since only non-reproductive stems accrue stem biomass, total stem production was 2,414 kg per ha per yr. Sprout production was estimated by considering it equal to the loss of reproductive stems and their leaves. Overestimation of some biomass components was quite likely. For example, stem biomass was calculated assuming all large stems were the same diameter and height. Because sprouts are continually moving up to the "mature stem" category, all stems are not the same size.

There were approximately 85 inflorescences in some stage of development per ha. The mean dry weight of a mature inflorescence was 21.7 kg. Assuming that an expanded inflorescence weighs the same regardless of its stage of development, they account for 1,840 kg per ha. Since 15.5 percent of the clumps (or 25.3 stems per ha) produce new inflorescences during the year, inflorescence production was 548 kg per ha per yr.

The mean dry weight of a single seed with fruit was 0.046 kg. The mean number of seeds per inflorescence was 643, but was highly variable (Standard Deviation = 333). Because the appearance of new inflorescences was fairly uniform throughout the year, I assumed that the same number of stems that have mature fruits equals those that were producing new inflorescences. Based on this assumption the fruit-seed production was 749 kg per ha per yr.

Discussion

Phenology. The one year duration of the study gave a clear indication of inflorescence development from the "new" to the "open flower" stage. These stages were

quite abrupt and easily determined. Other stages were more difficult to distinguish. Closer observation on selected individuals suggested the following time periods for each stage: 1) appearance of new inflorescence to expanded inflorescence: one month, 2) expanded inflorescence to open flowers: less than one month, 3) mature flowers to immature fruit: less than one month, 4) immature fruit to initial fruit fall: greater than one year, 5) initial fruit fall to last: minimum of six months. The entire process may exceed two years.

The small, but consistent number of individuals that produced new inflorescences each month suggest that reproductive events of *Raphia* are nonperiodic and occur independently of seasonal cues. In the aseasonal environment of Tortuguero there are few predictable periods that a species like *Raphia* can use to facilitate pollination, seed dispersal, or seed germination. Favorable periods for any of these processes are very short and can occur at any time during the year. Heavy rainfall and flooding can occur during every month. Even the relatively predictable dry periods in March, April, and September rarely expose the soil in the habitats where *Raphia* is found. Unpredictable rainfall can interfere with pollination. Lack of flooding may expose seed to predation. The only option is to have some individuals in each stage of reproduction throughout the year. The long period of fruit fall for an individual increases the probability that at least some seeds will escape post-dispersal predation or find suitable conditions for germination.

No detailed studies of pollination were undertaken, but observations on a few individuals showed that when the inflorescences change from yellow to brown, pollen is released. I do not know if female flowers on the same inflorescence are mature when pollen is released. Indications are that both wind and insect pollination occur. *Raphia* produces a large number of small, inconspicuous, unscented

(at least to humans) flowers characteristic of anemophilous species. Bumping a mature inflorescence releases a powdery pollen. Its habit of growing in nearly pure stands may facilitate anemophily, but the small number of receptive flowering stalks in a given area at any one time, coupled with the frequent rainfall, may limit outcrossing by anemophily. *Raphia* does occur in more seasonal environments on the Pacific coast of Costa Rica and in the Amazon River delta in Brazil where anemophily may play a far more important role. Within the palm family anemophily was originally considered to be the primary mode of pollination (Tomlinson 1979). More recently the importance of entomophily has been recognized (Schmid 1970; Uhl and Moore 1977).

Entomophily appears to occur in *Raphia*. At maturity a number of insects are found on the inflorescences. I observed two species of euglossine bees visiting the flowers during this time. Insect activity as a whole seems to vary little during the year.

Inflorescences that did not develop fruit were fairly common. It may be that the stems were merely acting as males. Janzen (1978) pointed out that the lack of fruit set does not mean a reproductive event has not taken place, but only that the flowers on that individual may have acted as males. Another explanation for the observed lack of fruit on some inflorescences was predation of the immature fruits by two species of monkeys (*Cebus capucinus*, *Ateles geoffroyi*). They were observed to strip immature fruits off the inflorescences. They would bite off the end of the fruit, suck out the gelatinous immature endosperm then discard the fruit. Evidence of their activity could always be found at the base of the clumps.

The long period from fruit set to fruit maturity exposes the seed to these and other predispersal losses. Apparently the advantages of producing large heavy seeds that mature at different times on the same

inflorescence outweigh any disadvantages associated with extended fruit exposure on the tree, or for some reason the cost of rapid fruit maturation cannot be borne by the plant.

Growth and Biomass. The most notable feature of *Raphia* growth is the large amount of energy that goes into reproduction. Each year 2,036 kg per ha in reproductive stems and their leaves die. A total of 1,297 kg per ha per yr goes into inflorescences and fruit. The loss of a reproductive stem opens a small gap that must be filled by a sprout if the clump is to continue to occupy the site. The long period of senescence of one stem may allow sufficient time for a sprout to move into the canopy position of the dying stem.

The above-ground biomass of 44,283 hg per ha (that does not include *Raphia* sprouts, understory vegetation, and infrequent hardwoods) is considerably less than that reported by other researchers for forests in the humid tropical lowlands. A mean of 25 biomass values reported by Brown and Lugo (1980) was 290,000 kg per ha. In Colombia, Golley *et al.* (1976) measured three types of marsh vegetation in a life zone equivalent to that of Tortuguero and reported values of 41,500 kg per ha in a *Paspalum repens* marsh, 34,400 kg per ha in a *Montrichardia arborescens* stand, and 38,500 kg per ha in a *Heliconia latispatha* marsh. It appears that monospecific *Raphia* swamps do not support nearly as much biomass as more diverse tropical forests and are more comparable to some of the herbaceous marshes.

New growth totaled 11,133 kg per ha per yr. This was offset by a loss of 8,843 kg per ha per yr through leaf senescence, death of reproductive stems, leaves, inflorescences, and through fruit dispersal. The difference, if the forest is in steady state, may be balanced by the occasional death of non-reproductive stems, sprout leaf turnover, and death of sprouts. The range of 9 to 11 mt per ha per yr is similar to

that reported for most forests in the humid tropics (Brown 1980). If these values are valid it appears that *Raphia* swamps are as productive as other, more diverse forests in the tropics.

Acknowledgments

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