Ecological Studies of the Cabbage Palm, *Sabal palmetto**

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From its center of distribution in central and southern Florida, *Sabal palmetto* (Walt.) Lodd. ex J. A. & J. H. Schult., exhibits two far-reaching, narrow range extensions along the Atlantic and Gulf coasts. It was this distribution pattern, especially along the Atlantic coast, and the desire to explain it, which led to this study.

The usual tool for such a study is the ecological life history (Pelton, 1951, 1953) which provides information basic to understanding how a species, in all stages of its life history, is adapted to survive in nature.

Realizing the longevity of *S. palmetto*, the major emphasis of the study was concentrated on the stages from flowering to seedling establishment. Thus, the objectives of the study were to determine the strategy of reproduction in *S. palmetto* and with this information attempt to explain the distribution of the species in nature.

I. Floral Biology

Information on pollination mechanisms in the palm family is quite sparse. Although entomophily was recognized, anemophily was considered to be the primary mode of pollination in the palms by early workers (Schmid, 1970). More recently, Schmid (1970) found that *Asterogyne martiana* (H. Wendl.) H. Wendl. ex Hemsl., a small Costa Rican palm, was pollinated by syrphid flies (Diptera), and Essig (1971) found that two other Costa Rican palms, *Bactris guineensis* (L.) H. E. Moore and *B. major* Jacq. were pollinated by beetles.

Sabal palmetto has several features characteristic of anemophilous species: production of enormous numbers of small, visually inconspicuous flowers; exserted anthers; and few ovules per flower (Faegri and van der Pijl, 1966; also see Fig. 1). On the other hand, preliminary observations revealed that *S. palmetto* has several distinctive features of an entomophilous syndrome: production of nectar; production of strong odor; anthesis and attractant production synchronized with potential pollinator activity; production of sticky pollen; and visitation by many species of insects, some in large numbers.

To determine the precise nature of the pollination mechanism in *S. palmetto*, field studies were conducted throughout the natural range of the species during the flowering seasons of 1971 and 1972. Preliminary observations of floral morphology and phenology as well as insect collections were made at Smith Island, N.C., Hunting Island, S.C., Tomoka State Park and Apalachicola, Fla., during May through August, 1971. Detailed observations of the daily floral sequence and insect behavior were made at Ft. George and Longboat Key, Fla., in July and August, 1971 and 1972 (see Fig. 2 for locations). Trees were tagged and observed between 0430 and midnight EST. Periodic visits were made for several days at both sites. An 18-hour vigil

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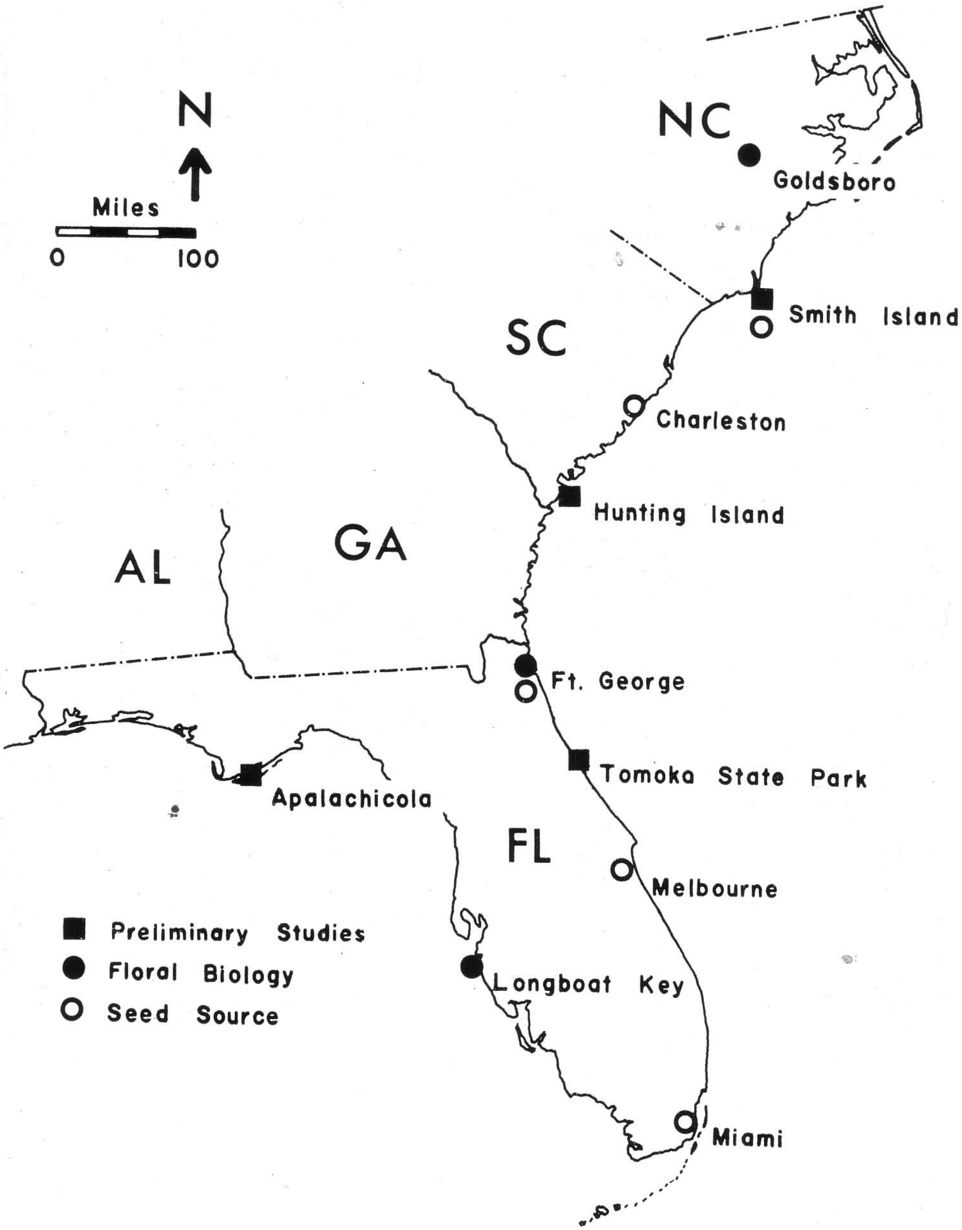
* This is the first in a series of articles taken from earlier work by the author (Brown, 1973).

1. The inflorescence of *Sabal palmetto.* A, trees in full bloom; B, a single inflorescence; C, close-up of flowers; D, the flowers and their most common insect visitor, *Apis mellifera.*

on July 28, 1971, at Longboat Key, provided much information. Presence or absence of nectar and pollen on flowers was determined visually. Insect behavior was observed visually and recorded in detail. Insects were mounted for later examination and identification. Slides were made in the field of both anther-pollen and insect-pollen loads for later microscopic examination.

Floral Morphology

Detailed floral morphology is described by Bailey (1944). Individual flowers are 4–5 mm. long, sessile and bisexual. Septal nectaries which occur near the base of the ovary are assumed to be responsible for producing the pungent odor and nectar associated with open flowers. Pollen grains are sphe-



2. Location of field study sites and seed sources.

roidal to ellipsoid and average 36.6 microns long and 30.8 microns wide. Pollen viability, assumed of fully formed grains mounted in methyl-green glycerine jelly, is 98.4%. Pollen is obligately carried by insects, for glycerine jelly slides left exposed near flowers for 24 hours collected no wind-borne pollen.

Seasonal Phenology

Reproductive events exhibit seasonal periodicity. The exact mechanism of floral initiation is unknown but latitudinal differences in both time of first flowering and duration of flowering period exist. Southern populations around Miami may begin flowering as early as April and normally continue until at least August. Initial flowering activity proceeds up the coast reaching Ft. George (approximately mid-range) about July 1, and finally Smith Island in the second to third week of July. The period of flowering is condensed with increasing latitude such that at Smith Island it lasts only four to six weeks.

Even though growth of the inflorescense is basal, flower opening occurs randomly on individual panicles over a one- to two-week period after elongation of the panicle is complete.

Daily Events

The following description of daily phenology is a composite of observations from the two intensive study sites. All times are Eastern Standard equivalents for July 28 or Julian Day 209 and average time for each event.

The daily flowering cycle begins in darkness (0430) with production of a strong fragrant odor. Flower buds begin expanding such that by 0500 the first flowers are at anthesis. The stigmas, which at this time are white, glistening, and slightly sticky, are assumed to be receptive. Nectar is pooled at the base of the ovary and visible to the naked eye. Between 0530 and 0540, when a flashlight is no longer needed for observation, the first bees and flies begin exploiting the flowers for nectar and the majority of expanding flowers are open.

Anthers are visibly swollen by 0630, and by 0730 the first anther dehiscence occurs. These first-dehiscing anthers are, significantly, in the sun. Shortly after dehiscence the first pollen loads on bees start accumulating. By 0810 all anthers exposed to the sun are dehisced. Those on shaded flowers complete dehiscence by 0910.

The delayed dehiscence of anthers results in a functional dichogamy of at least two and one-half hours in the first flowers of the day. The few flowers opening later in the morning have only a brief anther delay or practically none at all. Protogyny was reported in *Sabal minor* (Jacq.) Pers. by Müller (1863). In the case of *S. palmetto*, it appears that the degree of protogyny is determined by anther moisture balance which controls anther dehiscence. Anthers on whole flowers from shaded locations began dehiscing within five minutes when secondary branchlets were excised. Dehiscence was even more rapid when branchlets were excised and placed in full sun.

By 0910 some stigmas lose their sheen and turn brownish. These are assumed to be pollinated. All new flowers for the day are open by 1100, but nectar and odor production continue through the day. By 1630 most anthers are stripped clean of pollen. At sunset a change in insect visitors from Hymenoptera/Diptera to nocturnal Lepidoptera/Coleoptera occurs. At 2300 odor is no longer detectable and the nonessential flower parts are withered and brown.

Before the beginning of the next flowering cycle all flowers from the previous day are spent. Individual flowers thus have a life span of less than 18 hours, probably 12 hours at most, if those opening at 1100 are the same ones ceasing to emit odor at 2300. The spent flowers dehisce tardily, but they cause no further response from insects.

The events just described apply to dry weather. Rainfall interrupts the normal

Table 1. Daily floral phenology. Based on observations at Longboat Key and Ft. George, Fla., during July and August, 1971 and 1972. Times are average for events and adjusted to Eastern Standard equivalents for July 28.

Time	Events
0430	Production of odor begins
0500	First flowers at anthesis; stigmas receptive
0530	First bees arrive
0730	First anther dehiscence
0910	Anthers in shade finish dehiscence
1100	All new flowers are open
1630	Anthers stripped clean of pollen
2300	Odor no longer detectable; flowers withered and brown

sequence whenever it occurs, for it will delay anther dehiscence in the forenoon, and it will terminate insect visitations at any time. The termination by rain is a function of the shape and size of the flowers which is such that water droplets encapsulate the reproductive organs. One rain which occurred at 1500 resulted in a cessation of visitation by insects for the remainder of the day. Flowers were still covered with water at sunset, over four hours after the rain had stopped. A summary of daily floral phenology is presented in Table 1.

Insect Visitation and Behavior

With a few sporadic exceptions, herbivory was not an important activity of attracted insects. The only directly observed herbivory was on unopened buds by an unidentified orthopteran (Tethigonidae) and several unidentified lepidopteran larvae. During the preliminary observations at several locations, a stripping of early inflorescences in bud stage suggests possible herbivory of a seasonal but devastating nature.

A complete list of visiting insect species may be found in Brown (1973). Although of interest for other reasons, many of these species did not behave in a manner likely to affect pollination. Some passively collected pollen on their bodies in small amounts, but these species never occurred in numbers sufficient to be considered important pollinators. This group also included spiders of entomophagus families.

A summary of the more active insect visitors by orders, including pollen loads and behavioral observations follows. Descriptions are for adults unless specified.

Coleoptera—Five families and seven species were represented. Pollen was found in sparse amounts on all. All were feeding either on nectar or pollen. Only two species were found at all locations in numbers sufficient to be pollinators. *Caryobruchus gleditsiae* (L.) (Bruchidae) is nocturnal and never contacted freshly opened flowers. The other, *Notolomus basalis* Le Conte (Curculionidae), is small and in seeking nectar rarely ever contacts the stigmas.

Diptera—Six families and six species were represented. Pollen was found in sparse amounts on all. Visiting was sporadic and limited to nectar-gathering, usually from a hovering position.

Hemiptera—Three families and three species were collected at only two locations. Pollen was not found on any. One was the predatory assassin bug, *Zelus bilobus* Say (Reduviidae).

Homoptera—One species, a tree hopper (Membracidae), was collected on unopened flowers at Longboat Key. Sparse amounts of pollen were found but numbers and behavior preclude this species as a pollinator.

Lepidoptera—Two families and two species were found at Longboat Key.

Small amounts of pollen were present but nocturnal habits eliminate these species as pollinators.

Orthoptera—Two families and three species were found at Longboat Key. Two crickets (Gryllidae) had no pollen and were nocturnal. The grasshopper (Tethigonidae) has been mentioned earlier as an herbivore on unopened buds. None are pollinators.

Thysanoptera—One species was found at all locations. This is a perplexing group due to their extremely small size. *Frankliniella tritici* (Fitch), Thripidae, was at times found in large numbers in and among open flowers. J. W. Hardin (personal communication) considers that thrips may pollinate unopened flowers of chokeberry, *Aronia* spp. However, in *S. palmetto* I found thrips only on open flowers, never in closed flower buds. Most of their activity was below the exserted stamens although they occasionally came in contact with pollen on the anthers. I am assuming, with reservations, that thrips play an unimportant role in pollination.

Hymenoptera—Thirteen families and 45 species were collected. The bodies of every species had pollen present, ranging from scattered individual grains, to visible clumps, to the heavy corbicular and abdominal loads of bees.

Seven families of wasps were represented by adults which were feeding on nectar. Sparse amounts of pollen were found on all 16 species. Most families were represented at all locations. Three families included entomophagus members, especially bee predators. Visits by wasps were always solitary and represent little total time on flowers.

Three species of ants (Formicidae) were collected. At least one species was found at all locations. Pollen was sparsely present. Activities were varied, including feverish activity around unopened buds associated in one case with the tree hopper, *Idioderma virescens* Van Duzea (Membracidae). Ants were less common on open flowers where they appeared to be feeding on nectar.

The suborder of true bees (Apocrita) was represented by five families and 24 species. Of all species observed and collected this group was the most ubiquitous. All species collected were active pollen gatherers and all were equally capable of behavior which could result in pollination. The presence of large numbers of bees, especially honey bees, discouraged activity of wasps. This pattern is the reverse of that reported by Shoudt and Mitchell (1967) in which wasps fended off other insects, including honey bees, on coconut palm.

Two families, Megachilidae (leaf-cutting bees) and Xylocopidae (carpenter bees) are solitary bees. The nine species in these two families, while efficient pollen gatherers, lacked the numbers and time on flowers to be considered important. Of the three other families, the Apidae and Bombidae are social, the Halictidae solitary to primitively social.

Apis mellifera L. (Apidae), the honey bee, was found at all locations except Smith Island. Its pollen- and nectar-gathering activities were obvious. Individuals were at flowers from early morning until sunset and often in large numbers, certainly in greater numbers than any other species of insect.

Bombus species (Bombidae), bumble bees, were observed at all locations except Longboat Key. They were equally efficient at pollen-gathering as *Apis*, and had even larger pollen loads, but like the leaf-cutting and carpenter bees their numbers were few.

The mining bees (Halictidae) were represented by five genera and 11 species. These small bees were ubiquitous and possess all the characteristics of effective pollinators. Their small size was compensated for by large numbers and persistence at the flowers.

Microscopic studies of all bees revealed that in addition to corbicular and abdominal loads, abundant pollen was also present on the mouth parts, legs and ventral surface of the body. Most frequently, pollen occured in clumps rather than in individual grains. Observations on first bee visitors of the morning revealed that all species were carrying some pollen over on their bodies from previous days. All bees except the *Bombus* species were carrying loads of pure *S. palmetto* pollen. Contamination in *Bombus* loads was slight. This fidelity of pollen loads is not surprising since the communication system of social bees normally leads to the exploitation of pollen and nectar sources (Percival, 1965). It was also noted that during peak flowering activity of *S. palmetto* few other native plants were in full flower. It appears that *S. palmetto*, in its phenology and sheer numbers of flowers, provides the various bee species with a major source of food.

Anemophily is discounted in *S. palmetto* due to negative glycerine jelly slide tests and presence of an entomophilous syndrome. This species is rather obviously mellitophilous (bee-pollinated), although other insects, especially wasps, may be of importance locally and at particular times. The bee most effective in pollen transfer is *Apis mellifera.*

The honey bee has not always been the pollinator for *S. palmetto* since it is an introduced species (Borror and DeLong, 1971). The absence of this bee from the Smith Island collection allows speculation as to the native pollinator before the arrival of *A. mellifera.* Of the other bees, several halictids offer the best combination of behavior and frequency to be evoked as the primary native pollen vector for *S. palmetto.* These are *Augochlora pura pura* (Say), *Agapostemon splendens* (Lep.) and *Dialictus* spp. All are present throughout the range of *S. palmetto*, with the green *Augochlora pura pura* replaced by the blue *A. pura masieri* Cockerell in southern Florida.

Sexual System

To clarify the sexual system and determine the pattern of intraspecific fertilization, artificial pollination experiments were conducted. Preparation of flowers was accomplished in the late afternoon followed by appropriate manipulations the next morning. Bagging of flowers was with styrofoam cups, with windows cut out, covered with nylon stocking. Development of fruit was considered evidence of fertilization. Experiments were conducted on several trees at Ft. George and a single tree at Goldsboro (Brown, 1973). The results of these experiments are summarized below.

No evidence of incompatibility mechanisms which would preclude autogamy or allogamy (geitonogamy or xenogamy) were found and all, at least theoretically, can occur with the aid of insect vectors. No evidence of apomixis was found. The results suggest that protogyny is effective, especially on early flowers. It appears that not only is there an initial temporal separation of maturation of female and male parts in early flowers but also that the stigma may in fact be nonreceptive by the time pollen in the same flower is presented. The pollination of early flowers must be accomplished by pollen brought from: 1) exposed flowers on the same tree or different trees; or 2) flowers open on the previous day.

Protogyny facilitates the adaptively favorable event of allogamy, especially xenogamy. Any pollen contacting a protogynous stigma will be allogamous and in all probability effect fertilization

(Faegri and van der Pijl, 1966). Allogamy may be further facilitated in this species by the carry over of pollen from one day to the next on vector insects.

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FOOTNOTES ON PALMS

Have you ever inhaled the fragrance from the bloom of our native cabbage palm? Now who would ever believe that this dowdy old gal would use such sexy perfume? However, with her high laced-up boots she may be more modern than we suspect. In my opinion, this palm is fine in the wild but somewhat unsatisfactory as a landscape palm because of her lack of fastidiousness. Perhaps I am biased because the birds, who love the fruit of the cabbage palm, drop the seeds in my flower beds and I am always having to pull the seedlings out.

Now do not think that I do not like palms, in fact, I consider palms one of the joys of living in Florida. I will never forget my first visit to Florida when I first viewed the magnificent planting of royal palms along McGregor Blvd. in Fort Myers; I could hardly believe that they were living plants!

Palms are of special interest to many people because of religious interest; the people of Jerusalem, when they heard that Christ was on his way to the city, "went forth to meet Him carrying Palm branches." The Bible also states: "the righteous shall flourish like the Palm."

In India, the coconut palm is called "the Tree of Heaven." In Tahiti, the local government has an ordinance that states: "No building in Tahiti shall be higher than two-thirds of a coconut tree."

When Captain William Bligh was cast adrift in a small boat by the mutineers of the Bounty, the fruit of the coconut tree helped save him and his companions from starvation. In his journal he mentions coconuts several times (he spelled it cocoa-nuts). On Wednesday, April 29, the day after the mutiny, his small boat was off the northwestern part of the island of Tofoa, the northernmost of the misnamed Friendly Islands. His journal relates: "We weighed anchor and rowed along shore to see if anything could be got; and at last discovered some cocoa-nut trees; but they were on top of high precipices, and the surf made landing dangerous; both one and the other, we however got the better of it. Some of the people, with much difficulty, climbed the cliffs, and got about twenty cocoa-nuts, and the others slung them on ropes, by

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