Ecological Studies of the Cabbage Palm, Sabal palmetto. II. Dispersal, Predation, and Escape of Seeds

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In an earlier article (Brown, 1976) the floral biology of *Sabal palmetto* was considered. This article continues the ecological life history of the species by addressing problems associated with dispersal of seeds to safe sites in the environment.

According to Janzen (1970), the ability of a plant species to recruit new members is a function of the number of seeds in the area and the probability of seed and seedling survival. This is in turn determined by the number of seeds produced, the distance from the parent tree, and the efficiency of predators.

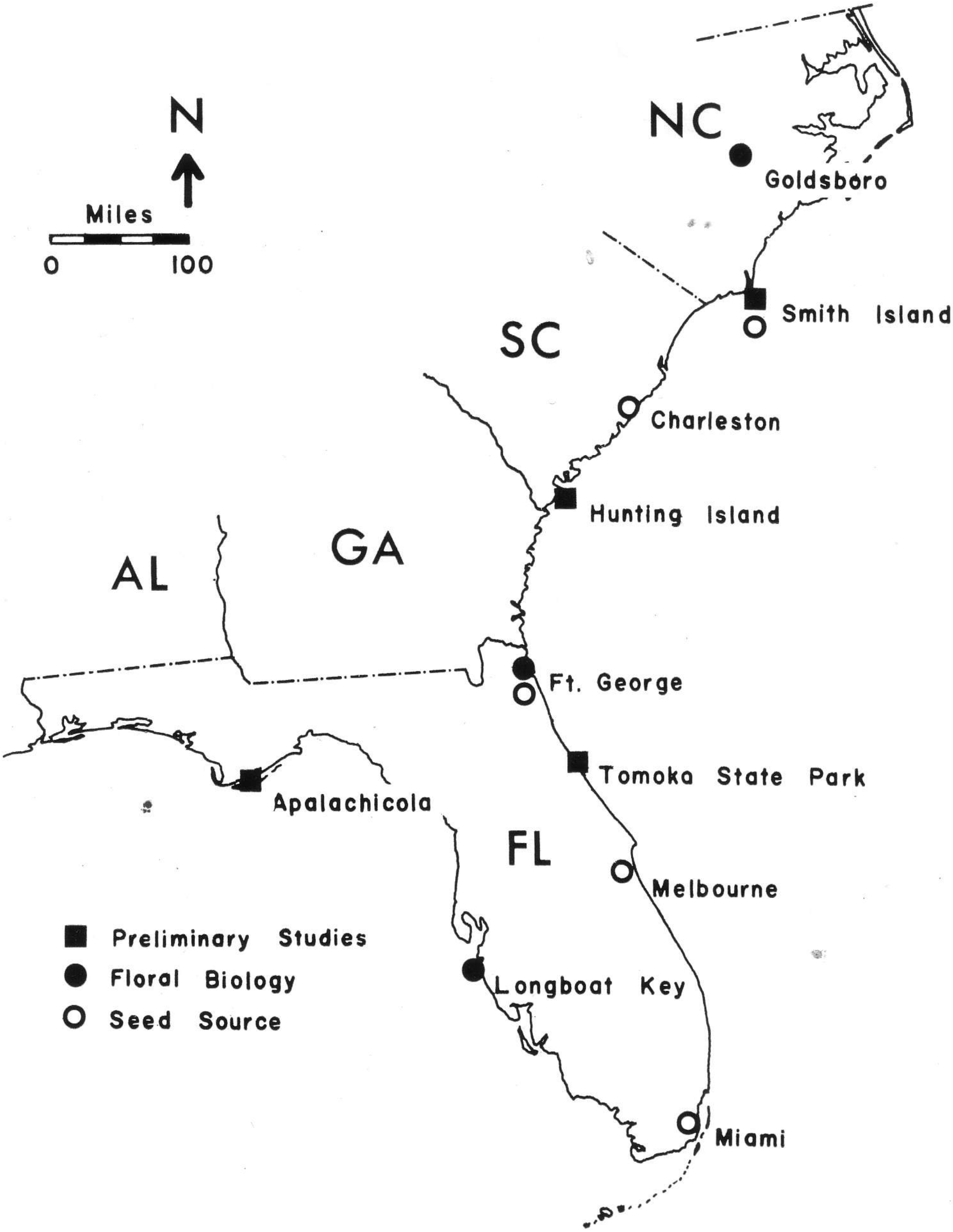
Dispersal of Seed

The mature fruit is the diaspore or unit of dispersal in *Sabal palmetto*. It contains a single seed and is spherical in shape, averaging 10 mm. in diameter. The fruit is indehiscent and persists on the infructescence during the winter. As the fruit dries, the mesocarp shrinks, as does the seed to a lesser degree, leaving an airspace within the mesocarp.

Fruit is removed from trees by external forces, such as wind during the winter and spring storms, and to an unknown degree by animals. Fish crows are reported to include the fruit in their diet (Sprunt and Chamberlain, 1970) and I have observed song birds (cardinals and blue jays) taking fruits. These species may be involved in dispersal within the local populations. However, direct dispersal to more northerly latitudes by migrating birds, as proposed by Small (1923), is discounted for two reasons. In the fall when fruits are ripe, succulent, and assumed most attractive to birds, migratory movements are to the south. In the spring when birds are moving north, palmetto fruits are dry, seeds bone-hard, and most have been dispersed from the trees.

Fruits falling to the ground are manipulated by mammals, including rodents. Squirrels were observed carrying off fruits, and on several occasions in the field I found either groups of seeds or young seedlings in dense clusters of as many as 30 or more within an area of 1.0 square meter. In some cases these were out of sight of the nearest bearing tree. I suspect that this was the result of activities of cache-hoarding mammals such as squirrels and mice. However, as with the observed birds, these animals are nonmigratory, have small home ranges, and thus offer no opportunity for direct dispersal to distant sites.

Although few palms owe their dispersal to sea currents (Ridley, 1930), such dispersal seems a distinct possibility in



1. Location of field study sites and seed sources.

S. palmetto. The plant is quite commonly found on banks of bodies of both fresh and brackish water. Therefore fruits do fall into water and are subject to being wafted away by waves, currents, or tides. While local dispersal might occur in fresh water, salt water holds the potential for direct long-range dispersal.

Table 1. Tolerance of seeds to salt water. Values given as germination percentage after indicated number of weeks in 3.5% NaCl solution. Numbers in parentheses are percentages of normal seedlings developed from seeds which germinated.

Week	Miami	Melbourne	Ft. George	Charleston	Smith Is.
1	100 (100)	100 (100)	90 (100)	100 (100)	100 (100)
2	100 (100)	100 (100)	100 (100)	80 (100)	100 (100)
3	100 (100)	100 (100)	100 (100)	100 (100)	100 (90)
4	90 (89)	80 (75)	100 (100)	70 (100)	100 (70)
5	90 (67)	90 (89)	100 (100)	90 (78)	90 (33)
6	100 (60)	80 (50)	100 (70)	90 (67)	80 (88)
7	80 (38)	70 (71)	50 (100)	80 (75)	80 (50)
8	80 (38)	100 (60)	80 (75)	70 (71)	60 (50)

A study to determine tolerance of seed to salt water and buoyancy of mature fruit was conducted based on the methods of Stevens (1958).

To test tolerance to salt water, 100 seeds from each of the five seed source locations (Fig. 1) were placed in 1.0 liter beakers with 500 ml. of 3.5% NaCl solution. The solution was changed twice a week to maintain proper density and salinity. Beakers were stirred once a day. Viability of seeds was determined by removing ten seeds weekly for eight weeks, rinsing one minute in distilled water, then placing on moist filter paper in a petri dish and incubating at 30° C for 28 days.

Buoyancy was tested by placing 25 mature, dry fruits from each location in 1.0 liter beakers with 500 ml. of 3.5% NaCl solution. These were maintained as in the salt-tolerance test. Observations were made daily. All fruits and seeds were screened for infestation by seed predators before tests were begun. In those few cases where larvae were not initially detected, test results (percentages) reflect true values, excluding those seeds or fruits found infested.

Viability of seed in salt water is retained by some seeds for periods up to eight weeks. After three weeks no reduction in viability was noted and developing seedlings were normal in appearance in all test groups. After six weeks germination remained high at 90% (average for all locations); however, only 67% of these germinated seeds developed into normal seedlings. At the end of eight weeks average germination was still high at 78% but only 59% of the germinating seeds produced normal seedlings. Of those seeds which sprouted but failed to grow normally, about half were abortive in appearance and half succumbed to fungal attack. There was no pattern of differential response among the five populations with all showing decreased viability and survival of seedlings with increasing exposure time (Table 1).

Mature fruits from all locations were initially buoyant and a relatively high percentage remained so for one week. However, a marked tendency toward longer buoyancy occurred in the two northernmost populations wherein 50% or more remained buoyant for two weeks. The ability to remain afloat for longer periods is due to undetermined differences in the fruits, for seeds from all locations sink immediately in salt water.

Table 2. Fruit buoyancy in salt water. Buoyancy is given as percentage of fruits still floating after times indicated. Test 1 compares all populations, Test 2 the extremes of the natural range.

Time	Miami	Melbourne	Ft. George	Charleston	Smith Is.
		Test 1 (25 seeds)			
1 Day	100.0	92.0	100.0	100.0	100.0
1 Week	48.0	56.0	44.6	83.3	77.3
2 Weeks	24.0	20.0	29.1	50.0	59.0
3 Weeks	12.0	4.0	0.0	4.2	9.1
		Test 2 (100 seeds)			
1 Day	72.0				100.0
1 Week	35.0				84.9
2 Weeks	9.0				62.8
3 Weeks	3.0				45.5

A second buoyancy test using 100 fruits each from Miami and Smith Island produced results which seem to verify the tendency for longer buoyancy in the northern portions of the range (Table 2).

The ability to withstand salt water and remain viable, along with a limited buoyancy mechanism, provides *Sabal palmetto* with the potential for direct dispersal to distant sites via salt water. The rate and direction of dispersal in such a system would depend on the direction and velocity of estuarine and littoral currents along a shore line. Theoretically the fruit could be carried just over 1,000 miles in two weeks by a three-mile-per-hour current. Alongshore currents on southern Atlantic coast beaches develop a persistent northerly flow with prevailing southerly winds during late spring and summer when *S. palmetto* fruits are dry and buoyant. Currents on the continental shelf south of Cape Hatteras are also predominantly northerly, flowing at rates of up to several miles per hour during late winter to summer (Bumpas, 1955). Offshore currents along the Gulf coast are not as clearly developed or persistent as along the Atlantic. However, alongshore currents tend to be northerly along the peninsula but westerly along the panhandle coast during the spring and summer. Neither are as strong or as persistent as their Atlantic counterpart.

If one accepts southern and central Florida as the center of distribution for *Sabal palmetto* (evidence for which will be considered in a later article), then the above salt water dispersal system becomes a feasible explanation for the distributional extremities along both Atlantic and Gulf coasts. Buoyant fruits from southern populations could have begun an outward migration of the species in a series of steps along the coasts northward and westward to the current termini at Smith Island, N.C. and St. Andrews Bay, Fla. Selection for trees with buoyant fruits would have occurred naturally in such a system, with the expected result of a high percentage of buoyant fruits in remote populations. This seems to be what has occurred at Smith Island.

Table 3. Rates of seed infestation by Caryobruchus gleditsiae. *Based on the 1971 seed crop as percent infested from samples of 500 seeds.*

Sample	Miami	Melbourne	Ft. George	Charleston	Smith Is.
1	2.8	8.8	4.0	10.7	39.0
2	4.4	12.4	3.8	11.5	37.4
3	4.5	12.7	4.0	15.0	37.7
4	4.1	—	6.7	—	45.2
Average	4.0%	11.3%	4.6%	12.4%	39.8%

Predation of Seed

Whereas the herbivorous lepidopterans and other unidentified insects which attack immature fruit are local and quite periodic, certain beetles are ubiquitous with *S. palmetto* (Brown, 1976). Beetles were first discovered in seed collections obtained for germination studies, and later in the field. One, *Cocotrypes* sp. (Scolytidae), was found in small numbers on dispersed fruits in southern populations from Ft. George southward. Identification to species is still pending but it is similar to the species which Janzen (1972) has reported attacking dispersed fruits of the sierra palm, "*Euterpe globosa*" [*Prestoea montana* (Graham) Nicholson], in Puerto Rico. Rees (1963) found that *C. congonus* Eggers is perhaps the major factor limiting reproductive success in nature by the African oil palm, *Elaeis guineensis* Jacquin.

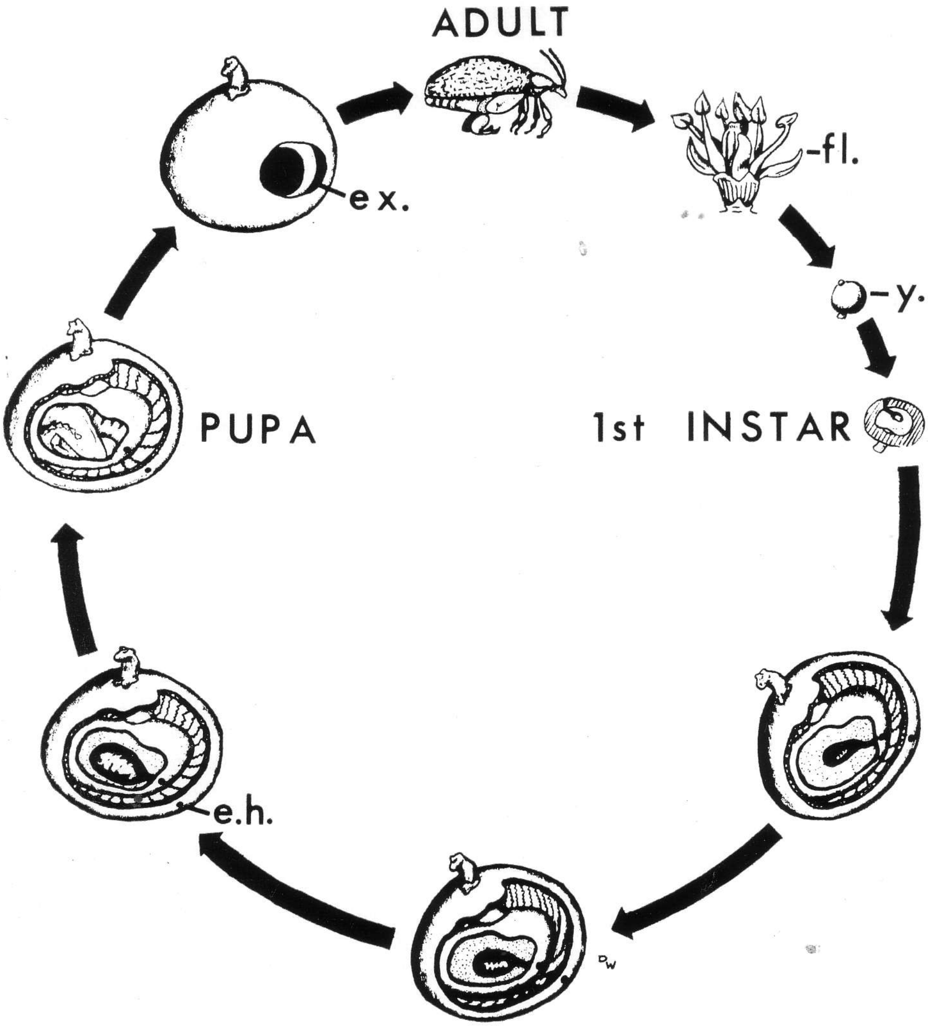
Of more interest was the discovery of *Caryobruchus gleditsiae* Linnaeus, a seed predator, present throughout the range of *S. palmetto*. My attention was first drawn to this insect in the fall of 1970 when seed lots from Smith Island were found to be about 50% infested with larvae.

The adult of the species was described and its range reported to be from Texas to North Carolina by Bridwell (1929). This range corresponds to the natural range of the genus *Sabal* in the United States. Paxson (1961) reported *C. gleditsiae* on *S. minor* (Jacquin) Persoon in Louisiana and Arkansas. First recorded reference to the beetle on *S. palmetto* was by Dury in 1881. Woodruff (1968) reports that the beetle breeds exclusively on palm seeds of several species but mentions nothing of adult feeding behavior.

To understand better the relationship between this insect and the palmetto seed, observations were begun in the summer of 1971 and continued through the summer of 1972.

Field studies revealed that adult beetles apparently take nectar during the flowering period of *S. palmetto* but no evidence of herbivory was seen. The most notable behavior of adults is their nocturnal activity. No adults were ever seen during the daylight hours. Their extreme negative response to light was typified by their evasive behavior in the presence of a flashlight beam during hours of darkness. This made observations of their total activities impossible. I was unable to observe them laying eggs on fruit but did catch them with heads down at the base of the nectiferous ovaries.

Rates of infestation on the 1971 seed crop were determined for all five seed-source populations (Table 3). Average infestation rates varied from 4.0% at Miami to 39.8% at Smith Island.



2. Life cycle of *Caryobruchus gleditsiae*, all views × 2.6: fl., flower of *Sabal palmetto*; y.f., young fruit; e.h., entrance hole; ex., exit hole.

The life cycle of this insect is incompletely understood but has a peculiar bimodal nature. There is a long-term univoltine generation (Fig. 2) which begins with egg laying on small immature fruits on the tree. The eggs are white, ellipsoid, and less than 1 mm. long. The first instar apparently hatches rapidly, tunnels its way into the seed, and establishes itself in the endosperm. At this point, development of the larva stops or at least slows down considerably. Whether this is a diapause or quiescence and what the trigger factor is are unknown, but it is an obligate phenomenon. The larva must stop growing because the immature fruit does not contain enough energy for the insect to complete development to adult stage. During late summer and fall, while the larva lies dormant, the fruit and seed mature in size and the endosperm hardens. At this time, even though sufficient energy is stored up in the seed, cold weather apparently enforces continuance of the dormant state since the larva overwinters in the seed. Development resumes in spring followed by emergence of adults.

Timing of the development sequence in nature is unknown, but adults were observed emerging from mature fruits still on trees in early July at Smith Island. Emergence probably occurs earlier, especially in the southern portion of the range. This is supported by the fact that adults began emerging from infested fruits in the laboratory after about one month of storage at room temperature (22° C).

The second reproductive mode of this insect is multivoltine and occurs on mature, dispersed fruit. Egg laying is accomplished on fruit on the ground, and development of larvae is uninterrupted so long as climatic factors are favorable. This activity occurs primarily in late spring and summer on the fruit crop from previous years.

The utilization of the seed by the beetle is remarkably efficient. The larva converts the entire endosperm and embryo into larval tissue, then uses the seed coat as a pupal case. The emerging adult bursts the seed coat and cuts a nearly perfectly circular escape hatch in the epicarp of the fruit. Multiple egg laying is common on the dispersed fruit but never more than one adult matures in one seed. Ultimate size of the adult beetle is directly proportional to the size of the seed.

Adults reared on dispersed fruits could, theoretically, result in 100% predation, especially in the area immediately surrounding the parent tree (Janzen, 1972). In some locations such may well be the case. A survey of a plot 1.0 meter square at the Ft. George site in July 1972 revealed that of 610 dispersed fruits 561 or 92% were, or had been, infested with *C. gleditsiae*. This compares with only 4% infestation of predispersed fruit at the same location in December 1971.

Seed samples from Ft. George south showed lower predispersed infestation rates than those locations to the north (Table 3). The reason for this may be the presence of a tiny braconid wasp, *Heterospilus* Haliday (new species to be described by P. M. Marsh), which is parasitic on the larval stage of *C. gleditsiae* in predispersed fruits. This wasp was discovered emerging from stored seed and was found only in seeds from Ft. George south. No evidence of wasp attacks on larvae in dispersed fruits has been found, possibly because the ovipositor is incapable of penetrating the mature seed. Another parasitic wasp, *Eupelmus cyaniceps* Ashmead (Eupelmidae) has been found on *C. gleditsiae* in fruits of *S. minor* in Louisiana (Paxson, 1961).

Heterospilus n. sp. has characteristics of an efficient parasite: a sex ratio of 10 females to one male, and ability to rear as many as 30 young on a single beetle larva. Such a parasite could play a major role in limiting numbers of a host insect, as it apparently does on that portion of the population of *C. gleditsiae* which lays eggs on immature fruit.

A most perplexing question is how predispersed fruit escape with as little predation as they do when dispersed fruits are so heavily infested. Clearly, the interrelationship between *Caryobruchus gleditsiae*, the braconid wasp, and *Sabal palmetto* is complex and will require considerably more investigation to understand fully.

Escape of Seed

Sabal palmetto reveals distribution patterns in dry forest situations similar to those of many species in tropical forests; i.e., widely and randomly scattered. Janzen's (1970) theory on distribution of rain forest species may apply to this case. Fruit falling on dry ground is subject to considerable predation by beetles. This is especially true near the tree where most fruit falls and insects are attracted in greater numbers. Any seed which is carried to areas away from seed-bearing trees would have a greater probability of escaping predation. The activities of small mammals or birds appears to accomplish this in *S. palmetto.* Seedlings in these remote areas would also be more likely to escape destructive insect activities associated with larger trees. Survival of one such seedling could then start the cycle over and further increase the chance for slow outward migration over land. This certainly seems to be borne out by the distribution patterns of *S. palmetto* which I observed in the maritime forests of Smith Island and at Ft. George.

On the other hand, seeds falling into water seem to escape predation by the beetles. This may explain the great density of trees commonly found along creek banks, on the shores of salt and fresh water marshes throughout the range, and in alluvial floodplains of many rivers in Florida. A key to the escape of these water-borne seeds may be in their frequent covering by sand and organic debris. I was able to observe this phenomenon at Ft. George where dispersed seeds were covered with sand and debris washed in by storm tides during late winter of 1971–1972. These seeds were uncovered in the survey of a second plot 1.0 meter square in July 1972. Of 753 seeds, 514 or about 68% had escaped by burial. Of the 188 exposed seeds, 173 or 98% had been attacked by *Caryobruchus gleditsiae.* In a similar fashion, Wilson and Janzen (1972) found that some fruits of *Scheelea rostrata* (Oersted) Burret, a Costa Rican palm, escaped predation by *Caryobruchus buscki* Bridwell when covered by forest floor litter.

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