Pollination Biology of Saw Palmetto (*Serenoa repens*) in Southwestern Florida

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1. Saw palmetto (*Serenoa repens*) with one inflorescence.

The saw palmetto is a familiar and important component of vegetation in southeastern USA where it is also of economic significance. This paper describes its pollination biology.

Saw palmetto (*Serenoa repens* (Bartr.) Small), a prostrate palm endemic to the southeastern coastal plain of the United States, is common in a variety of habitats from seasonally flooded pine forests to xeric coastal dunes and inland scrub (Tanner et al. 1996). Saw palmetto flower and fruit production is important both ecologically and commercially in the region. Over 300 species of insects have been observed visiting saw palmetto flowers (M. Deyrup, Archbold Biological Station, pers. comm.); some of these flower visitors collect nectar and/or pollen, while others find mates or prey near or on the flowers. Where present, European honeybees (*Apis mellifera*) are prominent flower visitors that produce commercial "saw palmetto honey." Saw palmetto fruits are eaten by many species of wildlife, including black bear (*Ursus americanus*), white-tailed deer (*Odocoileus virginianus*), raccoon (*Procyon lotor*), wild turkey (*Meleagris gallopavo*), northern bob-white (*Colinus virginianus*), gray fox (*Urocyon cinereoargenteus*) and gopher tortoise (*Gopherus polyphemus*; Maehr & Layne 1996). In addition, fruit demand for medicinal use has increased because saw palmetto fruit is used to treat benign prostatic hyperplasia (enlarged prostate; Berry et al. 1984). Since 1996, annual harvests of saw palmetto fruits in Florida have totalled at least 7,000,000 kg (M. Huffman, Plantation Medicinals Inc., pers. comm.).

Saw palmetto flowers are borne on densely-branched, interfoliar inflorescences, 0.5–0.75 m long (Fig. 1). Saw palmettos can produce over five inflorescences at one time, but commonly produce one to three. Each inflorescence contains several thousand individual flowers (Fig. 2). The bisexual flowers are 5–6 mm long, with three white, partially connate petals that are reflexed at anthesis (Fig. 3). Each flower has six stamens and one pistil, with a 3-ovulate, superior ovary. Usually only one ovule matures into a seed (Godfrey 1988).

Although seasonality of saw palmetto flowering and fruiting has been described (Hilmon 1968), very little is known about pollination biology. Knowledge of pollination biology should help land managers maintain biodiversity and natural functioning of ecosystems in which saw palmetto is prominent, while making informed decisions concerning management for wild fruit harvesting. In this study we (1) documented timing of flower bud opening, anther dehiscence, stigma receptivity and nectar production, (2) observed insect visitors to flowers and (3) experimentally characterized some aspects of the breeding system. Saw palmetto exhibits several characteristics consistent with biotic pollination (Faegri & van der Pijl 1979), such as a conspicuous floral display, sticky pollen, floral fragrance and nectar production. Since biotic pollination is usually associated with outcrossing (Proctor 1978), we expected that the breeding system would include at least some outcrossing. This study addressed the following specific questions: 1. How long do flowers function? 2. When is pollination likely to occur? 3. Are insect pollinators required for seed set?

Materials and Methods

Phenology. We conducted all fieldwork at the University of Florida Southwest Florida Research and Education Center, in Collier County, Florida. To characterize timing of bud opening, we observed a total of 16 inflorescences on February 10 and 13, 1998 and March 3 and May 18, 1999. During the afternoon before each observation, we marked mature buds by tying nylon sewing thread around the base of each bud. On observation dates, we checked each marked bud every 20 min from 02:00 to 14:00. We recorded bud opening, presence of nectar in flowers, anther dehiscence and insect visitors to inflorescences. We attempted to collect insect visitors, and sampled pollen loads on collected insects using fuchsin glycerine jelly (Beattie 1971). We also observed insect visitors to five additional inflorescences during March and April 1998. For these inflorescences, we recorded insect visitors for 10 min out of every 30 min, from 09:00 to 16:00.

On February 13, 1998 and May 26–28, 1999 we collected and characterized 1- and 2-day-old flowers. We defined 1-day-old flowers as those that had opened earlier (either pre-or post-dawn) on the collection date, and 2-day-old flowers as those that had opened the day before the collection date. On each date we collected 10, 1-day-old and 10, 2-day-old flowers at 10:30 and 13:30. We observed each of the 160 flowers under a dissecting microscope, and recorded anther dehiscence, presence of pollen in anthers, presence of moisture and/or pollen on the stigma and presence of nectar in the flower. For the 120 flowers collected in 1999 we determined stigma receptivity by applying 3% hydrogen peroxide to the stigmas and watching for bubbling (indicating peroxidase activity and stigma receptivity) under a dissecting microscope (Kearns & Inouye 1993). On May 26, 27 and 28, 1999, we also collected and characterized 3-, 4- and 5-day-old flowers, respectively. We collected 10 flowers at 10:30 and 10 flowers at 13:30 on each of the three days, and recorded the same information that we recorded for 1- and 2-day-old flowers in 1999.

Breeding System. Saw palmetto is a clonal species with branching, prostrate stems and a spreading

Table 1. Insect visitors to saw palmetto (*Serenoa repens*) flowers, activity of visitors, and presence of pollen on bodies of visitors. Insects were observed and collected from five inflorescences in Collier County, Florida during March and April 1998.

Insect Visitors	on rachis	on flowers	nectaring	pollen on body
Orthoptera				
Blattidae 1 sp. indet.		X		
Thysanoptera				
Heterothripidae 1 sp. indet.	X			
Hemiptera				
Largus succinctus		X		
Homoptera				
Flatidae 2 sp. indet.	X			
Coleoptera				
Coccinellidae 1 sp. indet.	X	X	X	
Notolomus basalis	X			X[a]
Diptera				
Plecia nearctica	X	X	X	X[b]
Stratiomyidae 1 sp. indet.		X	X	
Bombyliidae 1 sp. indet.		X		
Dolichopodidae 1 sp. indet.	X			
Ornidia obesa		X		
Syrphidae 2 sp. indet.		X	X	
Physoconops sp.		X		
Muscidae 2 sp. indet.	X	X	X	
Hymenoptera				
Dasymutilla sp.		X		
Camponotus sp.	X	X	X	
Formicidae 3 sp. indet.	X	X	X	X[a]
Formicidae 5 sp. indet.	X			
Polistes metricus		X	X	
Polistes exclamans		X	X	
Meschocyttarus cubicola floridana		X	X	
Colletes sp.		X	X	X
Augochloropsis metallica		X	X	X
Halictidae 1 sp. indet.		X	X	X
Apis mellifera		X	X	X

[a]fewer than 100 grains of pollen present.

[b]pollen amounts varied, but usually fewer than 100 grains present.

growth habit similar to tillering in grasses. At the terminal end of each stem branch is a meristem with a rosette of leaves, hereafter called a ramet. On February 22, 1999 we located 25 saw palmetto ramets of similar height and width that had initiated inflorescences. We verified that each ramet originated from a separate stem, and thus were reasonably confident that the ramets were from different genetic individuals. To characterize the breeding system, we used an experimental design consisting of five treatments: (1) emasculated and open-pollinated (allowed xenogamy, geitonogamy), (2) caged and hand (self)-pollinated (tested for geitonogamy), (3) emasculated and caged (allowed agamospermy, possible geitonogamy), (4) caged (tested for self-pollination without flower visitors), and (5) non-manipulated (hereafter these treatments will be referred to as (1) – (5)). We did not include a caged, cross-pollinated treatment, because we assumed

Table 2. Numbers of fruits and percent fruit set of saw palmetto (*Serenoa repens*) flowers subjected to five treatments to characterize the breeding system (see Methods and Materials for descriptions of treatments). Each of five treatment replicates consisted of 20 flowers within an inflorescence of an individual saw palmetto ramet. # = number of fruits. % = percent fruit set.

	Treatment									
	Emasculated, Open-pollinated (1)		Caged, Hand (self)-pollinated (2)		Caged, Emasculated (3)		Caged (4)		Non-manipulated (5)	
Replicate (N=20 flowers)	#	%	#	%	#	%	#	%	#	%
1	3	15	1	5	0	0	0	0	5	25
2	1	5	1	5	0	0	1	5	3	15
3	2	10	2	10	2	10	0	0	4	20
4	4	20	1	5	0	0	0	0	5	25
5	3	15	1	5	0	0	0	0	4	20

that the emasculated, open-pollinated and non-manipulated treatments included xenogamy. We marked 5 ramets for each of the 5 treatments, and marked 20 buds on one inflorescence of each ramet by gently tying nylon sewing thread below the base of each bud, for a total of 100 buds per treatment.

For the caged treatments, we placed cylinders (16 cm diameter) constructed from chicken wire and wrapped twice with white bridal veil (mesh <3 mm diameter) on inflorescences before anthesis began. To help exclude pollinators, we used metal wire to fasten excess bridal veil material on the bottom of each cage around the inflorescence rachis, and applied Tanglefoot (The Tanglefoot Co., Grand Rapids, MI), a sticky material that excludes or traps crawling insects, around the base of the rachis. Each cage covered approximately half of an inflorescence, consisting of 800–1000 buds.

For the hand-pollinated treatments, we monitored buds daily until they opened. Between 08:00 and 10:00 on the day of bud opening, we carefully removed cages and obtained stamens from other flowers on the same ramet with dehisced anthers containing pollen. We then rubbed these anthers over the stigmatic surface of each treated flower until we observed pollen on the stigma using a hand lens. We completed this treatment during the same time period that the emasculation treatment was completed.

We monitored marked flowers until they either fell off or produced fruit. We removed cages and counted all fruits on May 13, 1999, after all fruits began to develop. We recorded fruit set when a

2. Saw palmetto inflorescence containing thousands of flowers.

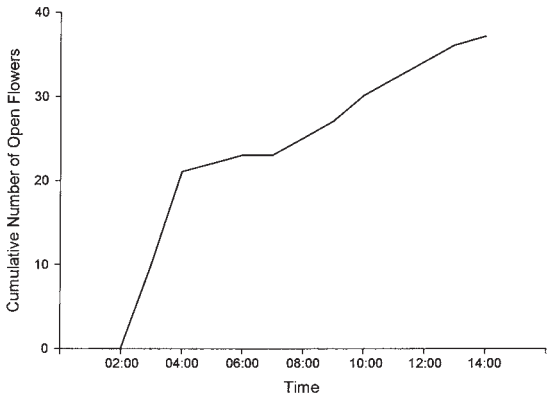
flower's style and stigma had withered but the flower remained attached to the rachilla, and the ovary wall had turned green. We used a Kruskal-Wallis test to test for differences in numbers of fruit set among treatments and performed two planned comparisons. First, to determine if cross-pollination increased fruit set, we compared treatments (4) and (5). Second, to determine if geitonogamy increased fruit set, we compared treatments (2) and (3).

Results

Phenology: Flowers opened asynchronously within an inflorescence over a period of approximately 1 month, with anthesis progressing from the base to the top of the inflorescence. During the 1998 and 1999 12-hr observation periods, a total of 37 marked buds opened. Over half of the buds opened from 02:00 to 04:00. Very few buds opened between 04:00 and 07:00. Buds opened at a faster rate after 07:00, with approximately 40% of buds opening between 07:00 and 14:00 (Fig. 4). Nectar was visible at the base of the gynoecium as soon as buds opened. Anther dehiscence began at 8:00, with the number of flowers with dehiscing anthers increasing rapidly until 11:00 (Fig. 5). Anthers of shaded flowers and later-opening flowers dehisced somewhat later than flowers in the sun or flowers that opened earlier. Median time between dehiscence of the first anther in a flower and dehiscence of all anthers was 2 hrs (range = 40 min–5 hr). Of 26 flowers for which we quantified anther dehiscence, 11 had all anthers dehisce by 14:00.

Flowers collected 1, 2 and 3 days after opening of buds showed similar timing for anther dehiscence. Virtually all anthers of collected flowers had dehisced during the first day of anthesis. Maximum amounts of pollen were available on anthers immediately after dehiscence, also during the first day of anthesis. Stigma receptivity, however, occurred somewhat later than anther dehiscence, indicating that saw palmetto flowers are weakly protandrous. During the first day of anthesis, stigmas were receptive in only 14% of flowers collected. By the morning of the second day of anthesis, however, over 80% of flowers had receptive stigmas. Proportions of flowers with receptive stigmas continued to be high (70-100%) through the morning of the fourth day of anthesis (Fig. 6). The three-lobed stigma appeared open and moist in receptive stigmas. The lobed stigma

3. Saw palmetto flower buds and open flowers.

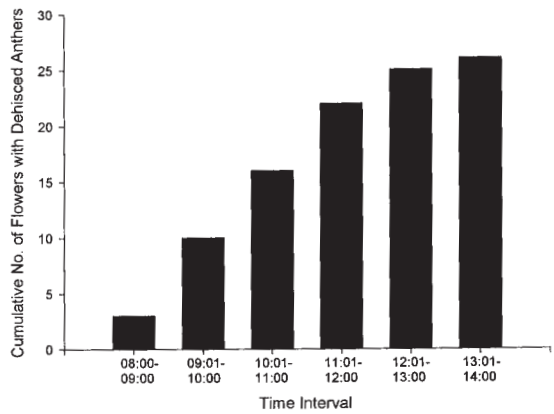


4. Cumulative numbers of saw palmetto (*Serenoa repens*) flowers open over 12-hr time period. Data were pooled from observations of marked buds on 16 inflorescences on February 10 and 13, 1998 and March 3 and May 18, 1999, in Collier County, Florida.

in non-receptive flowers was closed, with one lobe appearing as a hood over the stigmatic surface. Nectar was consistently present in flowers through the second day of anthesis and sporadically present through the fourth day of anthesis. After the fourth day of anthesis, styles, stigmas and petals browned and withered.

Insect Visitors: We observed 34 insect species on saw palmetto inflorescences, representing 7 orders: Orthoptera, Thysanoptera, Hemiptera, Homoptera, Coleoptera, Diptera and Hymenoptera (Table 1). Approximately 80% of the species were in the orders Diptera and Hymenoptera.

5. Cumulative numbers of saw palmetto (*Serenoa repens*) flowers with anthers dehisced from 08:00 to 14:00 during the first day of anthesis. Data were pooled from observations of marked flowers on 16 inflorescences on February 10 and 13, 1998 and March 3 and May 18, 1999, in Collier County, Florida.



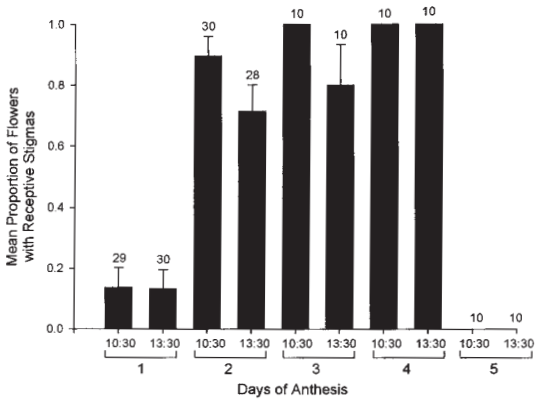
Diptera were common flower visitors, but usually carried no pollen (Table 1). Syrphid flies (Syrphidae) were represented by three species, *Ornidia obesa* and two unidentified species. These flies tended to visit single flowers and obtain nectar quickly while hovering. One of the unidentified species was a common visitor that we observed at four of the five inflorescences. It visited an inflorescence only once or twice during the day, usually during the morning. Muscid flies (Muscidae) were represented by two species. These flies obtained nectar while crawling from flower to flower and usually stayed on inflorescences for several minutes per visit.

Two Diptera species carried pollen on their bodies (Table 1). The first, *Plecia nearctica* (Bibionidae; lovebug) was a very common visitor. Single or coupled individuals actively foraged for nectar, crawled over numerous flowers, or simply lay on inflorescences, sometimes remaining for hours. Lovebugs usually carried pollen (typically <100 grains) on various parts of their bodies. *Physoconops* sp. (Conopidae) also carried pollen. Two individuals were observed with pollen on the ventral surface of their abdomens.

Other Diptera observed and collected were one species each in the families Stratiomyidae, Bombyliidae and Dolichopodidae. Species in Stratiomyidae and Bombyliidae were observed on only one occasion. The Dolichopodidae species was a very common visitor to inflorescences but presumably visited flowers as an insect predator.

Hymenoptera contained the most species of insect visitors, the most numerous visitors, and virtually all of the presumed pollinator species (Fig. 7). The most common insect visitors were ants (Formicidae), represented by *Camponotus* sp. and eight unidentified species. Three out of four species that we observed nectaring carried pollen (typically < 100 grains) on their bodies (Table 1).

Vespidae was represented by three species: *Polistes metricus*, *Polistes exclamans* and *Meschocyttarus cubicola floridana*. These common visitors obtained nectar and crawled over numerous flowers, but carried no pollen on their bodies (Table 1). However, four bee species – *Colletes* sp. (Colletidae), *Augochloropsis metallica* and an unidentified species in Halictidae, and *Apis mellifera* (Apidae) – were potential pollinators. All of these species carried large loads (> 100 grains) of *Serenoa* pollen (Table 1). *Apis mellifera* visited most frequently, approximately every 30 min to 1 hr at all five inflorescences. *Colletes* sp. and the halictid species were observed regularly at two inflorescences.



6. Mean proportions of saw palmetto (*Serenoa repens*) flowers with receptive stigmas. Flowers were collected May 26–28, 1999. Error bars represent standard errors of means. Numbers above histogram bars indicate sample sizes of flowers collected. Flowers were collected at 10:30 and 13:30 on days 1–5 of anthesis, as noted below histogram bars.

Other species that we observed visiting flowers were a cockroach (Orthoptera: Blattidae), a true bug (Hemiptera: Largidae: *Largus succinctus*) and a beetle (Coleoptera: Coccinellidae); none of these species carried pollen (Table 1). We observed the cockroach at night on one occasion. A thrips species (Thysanoptera: Heterothripidae) and two planthopper species (Homoptera: Flatidae) were common at inflorescences but were not observed visiting flowers. *Notolomus basalis* (Coleoptera: Curculionidae) was common on inflorescence branches. Although we did not observe it visiting flowers, a collected individual had fewer than 100 grains of *Serenoa* pollen on its body (Table 1).

Breeding System. Median fruit set ranged from 0 in treatment (4) to 20% in treatment (5) (Table 2). A Kruskal-Wallis test showed differences in number of fruits produced among treatments (χ^2_4=18.58, $p < 0.001$). Treatment (5), with cross pollination, had higher fruit set than treatment (1), without cross pollination ($0.01 < p < 0.025$). Although no difference in fruit set was detected between treatments (2), with 100% hand pollination (geitonogamy) and (3), without hand pollination ($p > 0.1$), failure to detect a difference may have been due to small sample size.

Discussion

Phenology of anthesis, behavior of insect visitors and results of experimental manipulation of flowers indicated that *Serenoa* has a facultatively xenogamous breeding system. Because *Serenoa* is a clonal species, however, apparent xenogamy may in fact be pollination from genetically identical ramets. Whereas addition of a hand-cross-pollination treatment may have helped distinguish between xenogamy and geitonogamy, much more work would be required to characterize genotypes of ramets.

Anthesis lasted approximately 4 d, with weak protandry promoting xenogamy or geitonogamy. Although pollination is possible throughout anthesis, probability is highest on the second day. At this time stigmas are most likely to be receptive, and nectar is most likely to be present as an attractant for potential pollinators.

Although *Serenoa* flowers were visited by a wide variety of dipterans and hymenopterans, the primary pollinators appeared to be bees. Bees carrying large loads (> 100 grains) of *Serenoa* pollen regularly visited flowers of every inflorescence observed. In addition to carrying large pollen loads, bees promoted xenogamy by visiting inflorescences of many different *Serenoa* ramets, and by crawling over numerous flowers of each inflorescence. Through this activity, bees not only may pollinate two-day-old flowers while obtaining nectar, but also may pollinate older flowers with receptive stigmas, but without nectar. This behavior is equally likely to result in geitonogamy and self-pollination.

The most prominent insect in this study was the European honeybee (*Apis mellifera*), a likely function of nearby (< 1 km) apiaries. Where honeybees are sparse or absent, native bees are likely the primary pollinators (M. Deyrup, Archbold Biological Station, personal communication). Although we observed little or no pollen on bodies of most flies and wasps, they may cross-pollinate *Serenoa* flowers. Behavior of other insects that remain primarily on one inflorescence (e.g., lovebugs, ants) occasionally may result in geitonogamy or self-pollination.

We conclude from the results of experimental manipulation of flowers that while both geitonogamy and xenogamy are possible, insects are required for effective pollination of *Serenoa* flowers. Treatments (2), (3) and (4) showed that geitonogamy is possible but results in low or only occasional fruit set. The comparison between treatments (1) and (5) demonstrated that xenogamy increased fruit set to normal levels. Three possible explanations for fruit set in treatment (4) are apomixis, pollination of flowers by thrips, and geitonogamy *via* gravity or wind. A caged treatment using insecticide to exclude thrips would help to clarify the mechanism (Baker & Cruden 1991, Kearns & Inouye 1993).

7. Hymenopteran visiting saw palmetto flowers.

Subtle differences in breeding systems exist between *Serenoa* and related, co-occurring palm species. *Sabal etonia* Swingle ex Nash has weakly protandrous, primarily bee-pollinated flowers similar to those of *Serenoa*. Timing of flower opening and anther dehiscence also were similar, but unlike *Serenoa*, anthesis in *Sabal etonia* lasted only 1 day (Zona 1987). *Sabal palmetto* (Walter) Lodd. ex Schult. also has primarily bee-pollinated flowers, but the flowers are protogynous and function only for 1 day (Brown 1976). *Sabal minor* (Jacq.) Pers. has weakly protogynous, primarily wasp-pollinated flowers that function for 1 d (Ramp 1989). *Rhapidophyllum hystrix* H. Wendl. & Drude is usually dioecious, has self-compatible flowers, and is reportedly pollinated by a species of *Notolomus* (Shuey & Wunderlin 1977).

Percentage fruit set for *Serenoa* in this study is low when compared to other palm species (Brown 1973, Ramp 1989), but is comparable to natural *Serenoa* fruit set from other sites. Fruit set from six ramets monitored in two other southwestern Florida sites during a concurrent study ranged from 2-39%, and averaged 18% (M. Carrington, University of Florida, unpublished data). *Serenoa*'s low fruit set may be the result of a preponderance of pollination by geitonogamy among different genetically identical ramets.

Because *Serenoa* shares pollinating species (notably *Apis mellifera*) with at least the two other bee-pollinated palms, competition for pollinators could occur. However, *Serenoa* has a longer flowering season than either *Sabal etonia* or *Sabal palmetto* (personal observation), its inflorescences are longer-lived (Zona 1987, personal observation), and its flowers are longer-lived (Brown 1976, Zona 1987). All of these characteristics should increase the likelihood that *Serenoa* flowers will receive intraspecific pollen. In addition, we identified only *Serenoa* pollen on insects visiting *Serenoa* flowers, suggesting that constancy of flower visitors was high.

As a result of demand for saw palmetto fruits for medicinal use, interest in fruit harvesting and in establishing commercial plantations has increased.

Results from this study indicate that insect pollination of flowers is an essential component of managing saw palmetto for fruit production. To encourage insect visitation to flowers, land managers should not use insecticides in managed areas during flowering and should reduce or suspend insecticide use in areas adjacent to saw palmettos. Although placing apiaries in or near saw palmetto areas during flowering may increase fruit set, introduced honeybees may out-compete native bee species, thus reducing rates of pollination for other native plant species (Corbet 1991).

Establishment of plantations has been virtually non-existent in the United States, and probably is not needed in the Southeast where extensive areas of wild saw palmettos occur. Where saw palmetto is cultivated in greenhouses, nurseries or plantations, however, this study has shown that opportunities may exist for self- or cross-pollination of flowers *via* hand-pollination.

Annual saw palmetto flowering and fruiting are significant ecological events that attract hundreds of insect species, and provide food for bird and mammal species, most notably the rare Florida black bear. Land managers will face increasing challenges to provide human benefits (i.e., wild fruit picking, enlarged prostate treatment) while conserving biodiversity and ecological phenomena. This study, through reporting on the natural history of flowering and pollination, is a contribution toward this end.

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