

Preliminary Observations and Analyses of Pollination in *Coccothrinax argentata*: Do Insects Play a Role?

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1. Habit of silver palm (*Coccothrinax argentata*) in pine rocklands habitat. Note silvery underside of leaves and cream-colored inflorescence.



We examined the reproductive biology of the rare and endemic palm, *Coccothrinax argentata*, in the pine rocklands of southern Florida. In addition to conducting visitor exclusion experiments, we observed five species of insects visiting the flowers of *C. argentata* and found large quantities of *C. argentata* pollen on their bodies. These preliminary results suggest that insects collect pollen from this species and may play a role in its pollination. Understanding the breeding system and pollination biology of the silver palm will facilitate effective management strategies of this rare palm.

Palms have traditionally been associated with anemophily, or wind pollination (Henderson 1986). Delpino (1870) was one of the primary proponents of this theory, relating the “primitiveness” of anemophily to the palm family. Many botanists (Drude 1889, Kerner 1895, Rendle 1904, Cook 1927) continued the myth popularized by Delpino, despite some considerations that palms could be insect- and wind-pollinated (Coulter & Chamberlain 1915, Kugler 1955). The hypothesis of anemophily in palms also arose as a result of their inflorescence and pollen morphology – typically massive inflorescences producing small, inconspicuous flowers and large quantities of pollen. As Henderson discussed in his review, Good (1956) even went so far as to describe palms as the tropical counterparts of catkin-bearing dicotyledons. Later studies maintained that palms are primarily anemophilous in the temperate zone (Baker & Hurd 1968, Stebbins 1974), highlighting the need for field studies that empirically test this assumption. The general hypothesis of anemophily in palms has been abandoned and evidence now suggests that entomophily, or a combination of both may be more common among palms (Dransfield et al. 2008).

Coccothrinax argentata (Jacq.) L. H. Bailey, Florida silver palm (Fig. 1), is a rare palm endemic to south Florida and the Bahamas. It grows in the pine rocklands (Fig. 2), a fire-dependent habitat occurring on outcroppings of limestone, as well as in hardwood hammocks and on coastal dunes. Urban development and long-term fire suppression pose major threats to the pine rocklands, with less than 2% of the original habitat remaining outside of Everglades National Park (Snyder et al. 1990). The range of *C. argentata* extends from southern Florida (northern limit near Boca Raton) to the Florida Keys and the Bahamas (Wunderlin & Hansen 2003), although Davis et al. (2007) identified populations of southern Florida and the Florida Keys to be morphologically distinct.

Little is known of the silver palm's reproductive biology, despite the important role its fruits play in the diet of many animals. Florida's Key deer depend on the fruit as a primary food source, although the deer do not excrete intact seeds and are ineffective seed dispersers (Zona 1997). In contrast, birds, turtles (Liu et al. 2004), and small mammals are considered to be effective seed dispersers of this species. To our knowledge, no study has

2. Pine rocklands habitat. Three palm species dominate the understory: saw palmetto, *Serenoa repens* (foreground, left), silver palm, *Coccothrinax argentata* (background, center), and cabbage palm, *Sabal palmetto* (foreground, right).



been published on the pollination biology of this species, although the few studies that mention its pollination biology suggest anemophily (Zona 1997).

We conducted a preliminary study on the reproductive biology of *C. argentata*, with the aims of elucidating its breeding system and determining if it is strictly wind-pollinated. Specifically, our research addressed three primary questions: (1) Is *C. argentata* self-compatible? (2) Does *C. argentata* set fruit without floral visitation? and (3) Do insects visit inflorescences and which are effective pollinators? The research presented in this paper forms part of a multi-species study on the reproductive biology of three sympatric palms in the southern Florida pine rocklands.

Materials and Methods

Species description. *Coccothrinax argentata* (Arecaceae: Coryphoideae) is a relatively short (stature of mature mainland plants ranges from 0.5–1.8 m) and slow-growing palm. Individuals bear a small, single stem that can occasionally develop into multiple stems. Its leaves are palmate and deeply divided, with induplicate plication and unarmed petioles that do not split at the base.

Coccothrinax argentata produces small, white flowers containing 7–12 twisted stamens and one unilocular carpel, with an inconspicuous uniseriate corolla. Flowers are borne singly along the rachillae. Inflorescences are interfoliar and take about three weeks to expand, finally emerging from a single, silky, pubescent peduncular bract similar in color to the underside of the leaves. The inflorescence is subtended by a peduncular bract and is branched, with many rachillae. Flowers last less than one week, with stigmas and anthers quickly shriveling and drying up thereafter. Anthers become notably twisted after stigma receptivity has passed. Pollen is white, in contrast to the yellow pollen of *Sabal palmetto* and *Serenoa repens*. We observed a strong, sweet odor emerging from the receptive flowers. Flowers open before 08:00, and we observed the highest amount of insect activity and most notable odor between 08:00 and 10:00. Fruits of *C. argentata* are globose, smooth and purplish black at maturity, one-seeded, and measure 0.6–1.2 cm in diameter.

Study site. We conducted our fieldwork in the pine rocklands, an ecosystem endangered by habitat destruction and fragmentation. The pine rocklands in southern Florida are

dominated by the Slash pine, *Pinus elliottii* var. *densa* in the canopy, and native palm species as well as over 250 herbaceous species in the understory (Snyder et al. 1990). Our study area, Navy Wells Preserve (latitude 24.4347, longitude -80.5030), serves as the groundwater recharge area for the Florida Keys water supply (USGS 2004). This large fragment of pine rockland lies just outside of Everglades National Park and is managed by Miami-Dade County. A dirt road bisects the 101.2 ha preserve. In addition to *C. argentata*, two other native palm species are abundant at this site and are fire-adapted: *Sabal palmetto*, cabbage palm, and *Serenoa repens*, saw palmetto. We chose to conduct our fieldwork at this site because it had been recently burned and, like other pine rocklands plant species, silver palm survives and even thrives after a fire (Cooley 2004, Carrington & Mullahey 2006). All field observations and experiments were conducted between February and July, 2008.

Flowering and fruiting phenology. We observed *C. argentata* in bloom at this site from late February through April, although a few individuals bloomed in May. Fruit set occurred from May through the summer months, coinciding with the seasonal rains. Phenological data of *C. argentata* in cultivation at the Montgomery Botanical Center (MBC) in Miami, Florida, suggest similar patterns, with a flowering peak occurring from March through May, although a second flowering peak seems to occur from September through November (Larry Noblick, unpublished data). As we observed at Navy Wells, the MBC populations of *C. argentata* begin to set fruit in June, but continue through December. Although these data reflect *C. argentata* in cultivation, and not growing wild in the pine rocklands, they are still relevant because both habitats share the same climate. Furthermore, these data are useful since phenological data of this species, as well as those of *Sabal palmetto* and *Serenoa repens*, are scarce. We observed that the flowering and fruiting activity of silver palm coincided with that of the other two species, also abundant at this site.

Floral visitors and nectar collection. We conducted pollinator watches on flowering silver palm individuals located throughout the site. All pollinator watches were carried out on sunny and partly cloudy days between 09:00 and 13:00 for twenty 10-minute intervals. Insect appearance and behavior was recorded, noting how long visitors stayed on flowers and if they made contact with the

stigma. The number of visits by different insects was also recorded. Visitors were collected and identified. We also tested for the presence of floral nectar in *C. argentata* using a hand-held light refractometer (Bellingham and Stanley "Eclipse").

Pollen analysis. Visitor specimens were examined using the dissecting microscope to view pollen loads, and pollen was sampled with dissecting needles and fine brushes (cleaned between specimens). Pollen from the insects' bodies was dropped into fuchsin gel on a microscope slide for examination under the light microscope (Dafni et al. 2005). We compared the pollen with known samples in our reference collection to determine what species of pollen were on each insect's body.

Breeding system. To determine the breeding system of *C. argentata*, we performed a pollen limitation experiment using a treatment and control (Kearns & Inouye 1993). The autogamy treatment consisted of bagging peduncular bracts before inflorescences had emerged and leaving the bags on until fruit set. The control plants were not bagged and represented open pollination. Fine nylon mesh (with threads less than 0.1 mm apart), breathable bags that did not permit pollen or insects to enter were used. All plants were tagged, and the date of bagging was recorded.

Fruit initiation was apparent within one month of bagging. The number of fruits per rachilla and per inflorescence was counted, along with the number of flowers and buds. Fruit set was calculated as the proportion of flowers that set fruit per inflorescence.

Statistical analysis. We conducted an independent samples T-test to test for differences in fruit set and number of fruit among the treatment and control. Number of fruit was calculated as the number of fruit produced per inflorescence whereas fruit set was calculated as the proportion of flowers that set fruit per inflorescence. A nonparametric test (Mann-Whitney U) was used because the error variances were significantly different for number of fruit (Levene's test, $t = -7.624$, $df = 22.755$, $p < .001$) and fruit set (Levene's test, $t = -1.706$, $df = 20.030$, and $p < .104$), and transformation was unsuccessful. Normality tests (including histograms and box plots) also showed the data to be non-normally distributed. One reason for this type of distribution could be because of small sample size ($n = 41$). All

statistical analyses were performed using SPSS (Chicago, Illinois, USA).

Results

Floral visitors. Floral visitation peaked from 09:00 to 11:00, and decreased significantly by 13:00. We observed five different species visiting the inflorescences of *C. argentata* including three bees: *Apis mellifera* (Hymenoptera: Apidae), *Megachile georgica* (Hymenoptera: Megachilidae), and *Xylocopa micans* (Hymenoptera: Apidae); flies, *Plecia nearctica* (Diptera: Bibionidae); and ants, *Pseudomyrmex mexicana* (Hymenoptera: Formicidae). During the twenty ten-minute interval watches, we found *Apis mellifera*, the European honeybee, to be the most abundant visitor. Honeybees tended to stay on each inflorescence longer than the other bee species, which tended to forage more quickly and visit a larger number of inflorescences. All visitors made contact with the stigma as they crawled around the flowers and visited the flowers repeatedly, suggesting that they were not just "passing by." During our pollinator watches, we actually observed several of the visitors collecting pollen, notably *X. micans* and *A. mellifera* (Figs. 3–5). Furthermore, we could see ample quantities of pollen on their bodies as they "worked" the flowers (Fig. 6).

During previous fieldwork on wildflower species in the pine rocklands, we and other members of our lab have consistently observed (though have not yet quantified) that palms in bloom recruit visitors disproportionately, leaving nearby wildflowers unvisited. We observed the same phenomenon in our field site: insect activity was concentrated at palm inflorescences, among them, those of *C. argentata*. This pattern may reflect ample nectar with high nectar concentrations in the native palm species of this habitat, notably *Serenoa repens* and *Sabal palmetto*. Though flowers of *Coccothrinax* are fragrant, we did not detect any nectar in the inflorescence using micro-capillary tubes and refractometer. Further anatomical study is warranted.

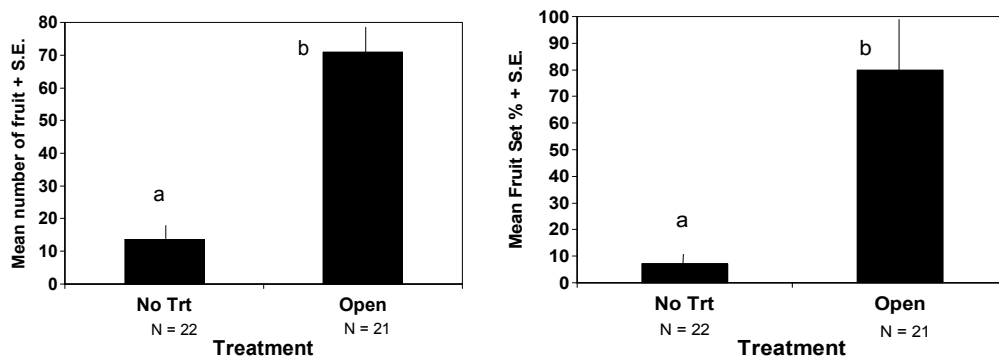
Pollen analyses. Analyses of visitors' bodies under the dissecting microscope demonstrated large quantities of pollen, especially for the hymenopteran species, whose corbiculae or "pollen baskets" allow for pollen storage and hairy bodies promote pollen adherence (McGavin 2001). Slides of pollen sub-samples from the bodies of *X. micans* and *A. mellifera* revealed almost exclusively *C. argentata* pollen grains (>50 pollen grains), except for a few



3 (upper left). Honey bee (*Apis mellifera*) collecting pollen from silver palm flowers. 4 (upper right). Pollen-filled corbiculae on legs of pollen-collecting honey bee. 5 (lower left). Carpenter bee (*Xylocopa micans*) hovering in front of silver palm flowers. 6 (lower right). Carpenter bee collecting pollen from silver palm flowers. Note pollen-covered back and legs.

pollen grains from neighboring wildflowers, presumably Asteraceae. Likewise, a sub-sample of a corbicula from *A. mellifera* consisted entirely of *C. argentata* pollen grains (>100 pollen grains).

We found pollen grains to be slightly oblong with minor edges. They are medium-sized, averaging 20–30 μm in diameter and 5–10 μm smaller than pollen of the other two palm species at the study site.



7 (left). Mean and standard deviation of number of fruit produced by *C. argentata* at Navy Wells after pollinator exclusion experiment. "No Trt." refers to the pollinator exclusion treatment and "Open" refers to the control. Treatments with different letters represent significant differences ($p < .05$) using a Mann-Whitney U test. 8 (right). Mean and standard deviation of percentage fruit set of *C. argentata* at Navy Wells after pollinator exclusion experiment. "No Trt." refers to the pollinator exclusion treatment and "Open" refers to the control. Treatments with different letters indicate significant differences ($p < .050$) using a Mann-Whitney U test.

Breeding system and fruit set. The bagged autogamy treatment produced significantly fewer fruit ($Z = -5.251$, $p < .001$) and lower fruit set ($Z = -5.468$, $p < .001$) than the control open pollination (Figs. 7 & 8). The fact that the bagged flowers set some fruit indicates that the species is self-compatible. However, since this fruit set was still significantly lower than the open pollinated plants (Fig. 9), it may be that fruit set is better with pollen from other individuals and the plants are facultatively xenogamous.

Our pollinator watches and analyses of visitors' pollen content lead us to believe that the inflorescences from which visitors were excluded probably set fruit as the result of self-pollination within the bags, perhaps moved by the wind. The bags that we used, a very fine nylon mesh, would not have allowed pollen to pass through them, but wind and other things may have jostled the flowers and moved the pollen.

Herbivory. While removing bags to count fruit, we noticed that several of the inflorescences had been damaged by herbivores and the bags were full of frass. Furthermore, during our pollinator watches, we also noticed the following herbivores on the leaves and inflorescences of *C. argentata*: the echo moth, *Seiractia echo* (Lepidoptera: Arctiidae), the banana weevil, *Pachnaeus litus* (Coleoptera: Curculionidae), and the cabbage palm caterpillar, *Litoprosopus futilis* (Lepidoptera: Noctuidae). Carrington and Mullahey (2006) observed *L. futilis* on saw palmetto and noted that it uses other Florida palm species,

including the silver palm, as a host. The caterpillars live inside the peduncular bracts, consuming the buds and immature flowers and sometimes even the entire inflorescence. The authors cited heavy damage and occasional mortality of saw palmetto inflorescences caused by *L. futilis*. Throughout our fieldwork, we also monitored significant damage to inflorescences of saw palmetto and sabal palm, presumably caused by the cabbage palm caterpillar given that we commonly observed its presence on these species. We noted that the silver palm inflorescences were damaged less by *L. futilis* than were the inflorescences of the more common palms.

Discussion

We set out to answer three primary questions: (1) Is *C. argentata* self-compatible? (2) Does *C. argentata* set fruit without floral visitation? and (3) Do insects visit inflorescences and which are effective pollinators? The results from our bagging experiment suggest that *C. argentata* is self-compatible and can set fruit without floral visitation, given that the autogamy treatment did set fruit. However, bagged inflorescences exhibited significantly lower fruit set than the control, highlighting the importance of insects and, perhaps, pollen from other individuals for pollination. We have not eliminated the possibility of agamospermy, but think it unlikely as many bagged inflorescences set no fruit at all.

The results from this study are preliminary, for we have only studied one population of silver palms for less than half a year. However, they

provide evidence that *C. argentata* is more than just wind-pollinated. Five species, representing three orders of insects, were observed visiting the flowers and collecting pollen. Furthermore, when analyzed under the dissecting microscope, visitors' bodies (notably *X. micans*, *A. mellifera* and *M. georgica*) carried large quantities of pollen. A majority of pollen grains carried by insect visitors to the flowers was pollen of *C. argentata*.

Studies on other Coryphoid genera provide evidence of entomophily. Henderson (2002) described two contrasting pollination systems for this subfamily, weevil pollination and bee, fly and wasp pollination, although exceptions exist. Dufay and Anstett (2004) found that *Chamaerops humilis* engages in a nursery pollination mutualism with the weevil, *Derelomus chamaeropsis*, whereby females are pollinated by "deceit." *Cryosophila* and *Rhapidophyllum* are also weevil-pollinated (Shuey & Wunderlin 1977, Henderson 1984). Several species of *Licuala* are pollinated by flies, wasps, and bees; Halictidae and Apidae appear to be the most efficient pollen collectors and pollinators (Barfod et al. 2003). Similarly, Zona (1987) identified bees, including *Megachile* spp., *Augochloropsis metallica*, *Xylocopa micans*, and *Apis mellifera*, as the most important pollinators of *Sabal etonia*. It is worth noting that in our fieldwork, we observed several of these genera pollinating *C. argentata* and all of these genera also pollinating *S. palmetto* (Khorsand Rosa & Koptur, unpublished data). Thus, entomophily may be more common among the Coryphoids than anemophily.

It is likely that *C. argentata* is insect- and wind pollinated, or amphiphilous (Lewis et al. 1983). The combination of biotic and abiotic pollination does occur in other genera of Areaceae including *Cocos*, *Phoenix*, *Elaeis* and *Attalea*, although wind may play a larger role in fruit set than insects (Scholdt & Mitchell 1967, Syed 1979, Lewis et al. 1983, Anderson et al. 1988, but see Dransfield et al. 2008). In a comparative study of the pollination biology of *Attalea speciosa* (as *Orbignya phalerata*) in open pasture and secondary forest, Anderson et al. (1988) found that wind supplements insect pollination, and the combination of these two syndromes permits for adaptability to a broad range of ecological conditions. In open pastures, anemophily may result in higher fruit set than entomophily. Thus, habitat may influence the proportion of transferred pollen grains and the pollination mechanism.



9. Silver palm bagged for pollinator exclusion. Note control (unbagged) infructescence full of unripe fruit, in contrast to treatment (bagged) infructescence with fewer fruit.

Even if *C. argentata* is amphiphilous, wind may not provide an effective means of pollen transport among isolated conspecifics, consequently lowering seed set (Koptur 1984). Thus, insects may play a key role in maintaining genetic diversity of *C. argentata*. Although native bees may act as important pollinators of rare plants, non-native bees, such as *A. mellifera*, may still contribute significantly to the reproductive success of *C. argentata* in isolated fragments. Honeybees can colonize isolated and small fragments because the entire colony can fly tens of kilometers (Gould & Gould 1988).

In the absence or reduction of native bees in fragmented habitats such as the pine rocklands, honey bees may also act as key pollinators because they are able to pollinate flowers that do not fit the "insect pollination syndrome" better than other insects. Although the flower morphology of this species (like that of many other palm species) does not fit the insect-pollination syndrome, honey bees may visit flowers to satisfy their resource needs

and even adapt to the small flowers if competition with other pollinators is low. Thus, flower morphology can be misleading, and pollination syndromes may not accurately reflect the ecological circumstances of the specific location in which the species grows.

Finally, anemophily has been traditionally associated with large quantities of small, dry, smooth pollen grains that are spread individually or in small groups (Dafni 1992). The pollen morphology of *C. argentata* from our analyses leads us to question this long-standing assumption. Our results corroborate the wind-pollination hypothesis given the smooth, dry surface of pollen grains and the large quantities of pollen dispersed as individual units. However, pollen grains are medium sized and are transported on insects' bodies. Other palm genera such as *Cocos* have relatively large pollen grains (Lewis et al. 1983), and are now considered to be pollinated by wind and insects (Dransfield et al. 2008). According to Henderson (1986), several studies provide evidence that in addition to wind, insects and nectarivorous bats collect pollen from *C. nucifera* (Start & Marshall 1976, Cock 1985). Thus, like flower morphology, pollen morphology does not necessarily indicate the pollination vector.

The silver palm was originally assumed to depend on abiotic pollination, and although wind may play a part in its breeding system, our study demonstrates that insects, including bees, can adapt to the flower morphology for resource exploitation. This study, though preliminary, exemplifies how we can challenge traditional assumptions about pollination mechanisms by coupling data collection and analysis with field observations.

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