

Observations on Pollination in *Bactris*

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Much has been said but little is actually known about the pollination process in most species of wild palms. Schmid (1970b) reviewed the literature on the subject and summarized what was known, but his own study (1970a, b) of pollination in *Asterogyne Martiana* of Costa Rica was the first thorough and reliable contribution to this exciting aspect of palm biology. I went to Costa Rica in the summer of 1970 as a student in the tropical biology course of the Organization for Tropical Studies, hoping to observe the pollination process in some other genera of palms. Suitable material proved to be rather scarce. The tall palms held their inflorescences out of reach and out of sight, and of the smaller palms, few populations contained both male and female flowering individuals. I was fortunate, however, to find two species of the spiny genus *Bactris* (Cocosoideae) in abundant flower and of suitable habit for study. My observations on these palms revealed a pattern of pollination strikingly different from that found in *Asterogyne*.

Two populations of *Bactris* were located in two very different parts of Costa Rica. The first population, occurring at the edge of a large cow pasture on the Finca La Taboga, near Cañas, Province of Guanacaste, proved to be *Bactris guineensis* (L.) H. E. Moore (*Cocos guineensis* L., *Bactris minor* Jacquin). This region has a climate of marked wet and dry seasons. Later in the summer, the Finca was reported to be under several feet of water. The second population was found in a mangrove swamp at the mouth of the Río Rincón on the Osa

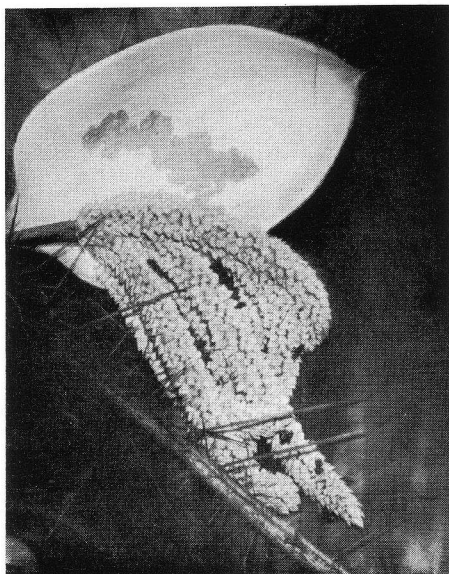
Peninsula, Province of Puntarenas. I have identified this population as *Bactris major* Jacquin (*Pyrenoglyphis major* (Jacq.) Karst.). It is close also to *B. balanoidea* Wendl., which is probably a synonym. In their swamp habitat these palms are subject to constantly moist conditions and share the ground with many land crabs.

The sequence of flowering events was observed in the *Bactris guineensis* population on July 12 and 13, and in the *B. major* population on August 11 and 12. The behavior of insect visitors was noted and samples of the insects were collected and preserved in alcohol. The descriptions and discussion that follow apply only to *Bactris guineensis* and *B. major* although I will often refer to the subject populations as just *Bactris*. The pollination process is generally the same for the two species.

L. H. Bailey (1943) described both species in detail. In features related to flowering and pollination they are essentially alike. Their general habit is as follows. *Bactris guineensis* is caespitose, with many closely-spaced, narrow canes up to 4 m. (12 ft.) tall, while *B. major* is colonial, forming extensive colonies of well-spaced, narrow canes up to 8 m. (25 ft.) in height. Vegetative parts of both species are covered with long, sharp spines. The inflorescences are each enclosed initially by a single thick, spiny, boat-shaped spathe, which later opens out, exposing a bright, cream-colored interior, much in the manner of a typical aroid spathe. The prophyll sheathes the lower part of the flowerstalk, but is inconspicuous.



1. *Bactris major* growing in a mangrove swamp on the Osa Peninsula.



2. Inflorescence of *Bactris major* just prior to opening of the male flowers. Note *Trigona* bees already on the inflorescence.

The flowers of *Bactris* are unisexual and are arranged in triads of a single female flower flanked by two males, with many additional males interspersed between the triads and occupying the extremities of the rachillae. Flowering is strongly protogynous. That is, on one inflorescence, the female flowers all complete anthesis before any male flowers open and shed their pollen. This situation contrasts sharply with that in *Asterogyne* and in most other monoecious palms, in which male flowers bloom before the females. The strict temporal separation of male and female anthesis on an inflorescence decreases the probability of geitonogamy (pollen transfer between flowers on the same plant), and thereby promotes xenogamy (pollen transfer between genetically different individuals), which is necessary to maintain gene flow in the population. Individual stems usually bear no more than one inflorescence in flower at a time.

This further reduces, but does not eliminate the probability of geitonogamy, since *Bactris* reproduces clonally, and adjacent stems may therefore be genetically identical. Xenogamy ensures gene exchange between clones, and geitonogamy ensures the ability of isolated clones to produce seed. Both processes undoubtedly contribute to the great success of the genus *Bactris*.

The flowering cycle in *Bactris* begins in late afternoon, again sharply contrasting with the situation in *Asterogyne*, in which flowers open early in the morning. The thick, spiny spathe, that tightly encloses the inflorescence prior to flowering, opens rather quickly between 4:30 and 5:30 P.M. The inflorescence then expands and the female flowers all reach anthesis between 6:30 and 7:00 P.M. The calyx and corolla of the female flower are very short and the staminodes much reduced, leaving the apex of the stout and fibrous pistil exposed even in bud.

Table 1. *Data from Bactris guineensis population.*

Time	First day inflorescence	Second day inflorescence
Morning	Spathe tightly closed	Female flowers withered; male flowers unopened, but beetles and flies feeding upon them
4:15 P.M. to 4:30 P.M.		Male flowers open; <i>Trigona</i> bees appear, begin collecting pollen; beetles and flies still feeding
4:30 P.M. to 5:30 P.M.	Spathe opens, inflorescence expands	
5:30 P.M. to 6:00 P.M.		<i>Trigona</i> bees finish collecting pollen and leave; beetles and flies still present in great numbers
6:30 P.M.	Stigmas begin to expand on female flowers; beetles appearing in large numbers to feed on unopened male flowers, many bearing pollen	Male flowers loosen, begin to fall; beetles and flies leave (further activity of flies unknown)
7:00 P.M.	Stigmas fully open, receptive; many beetles present, feeding through the night and presumably contacting the stigmas as they move	

At anthesis, the three stigmatic lobes are reflexed and become slightly sticky. By the next morning, the stigmas are withered and brown.

Between 4:15 and 4:30 P.M. the next afternoon, the male flowers of the same inflorescence all open and the anthers dehisce. The male flowers are somewhat smaller than the females and emit a musky odor. They are conspicuous, with a succulent, cream-colored corolla, short calyx, and six stamens. By 6:30 P.M. the anthers are nearly empty of pollen and the male flowers begin to loosen and fall from the inflorescence. Notice that on any given afternoon the inflorescences in a population are in two distinct phases of flowering. There are new (first-day)

inflorescences, on which the male flowers are unopened and on which the female flowers are approaching anthesis, and there are second-day inflorescences on which the female flowers have undergone anthesis the previous day, and on which the male flowers are now at anthesis. (See Table 1 for a summary of the flowering events.)

Insects usually come to flowers for the purpose of feeding. They may feed on nectar, on pollen, and/or on the tissues of the flower itself. Nectar is apparently not produced by either male or female flowers in *Bactris*. Three lines of negative evidence suggest this: 1) a superficial examination of both kinds of flowers in the field revealed no visible nectar;

2) anatomical studies by Dr. N. W. Uhl (personal communication) showed no evidence of nectaries in the female flowers of two species of *Bactris* (*Bactris* sp., Moore & Parthasarathy 9490, and *B. major* (?), Read 901); 3) no nectar-feeding insects were observed on *Bactris* inflorescences. There were no moths or butterflies, and none of the nectar-feeding flies (including the pollinating syrphids) found by Schmid (1970b) on *Asterogyne*.

Consequently the list of insect visitors to *Bactris* is considerably shorter than that for *Asterogyne*. Altogether, only seven species of insect were collected from *Bactris* flowers at both field sites. Collections were hasty, however, and undoubtedly incomplete, but probably representative of the types present.

The abundant pollen of the male flowers attracts at least three species of *Trigona* bees (Apidae). *Trigona silvestriana* Vachal was collected on *Bactris guineensis*, while *T. corvina* Cockerell and *T. lurida* Smith were collected on *Bactris major*. (Determinations by G. C. Eickwort, Cornell University.) The *Trigona* bees visit only male flowers (on second-day inflorescences) and end their activity before the female flower on the first-day inflorescences reach anthesis. It seems therefore, that they cannot play any role in the pollination of *Bactris*.

The remaining four species of insects collected were found feeding in the tissues of the male flowers. Of these, there were one species of drosophilid fly and three species of small beetles. The beetles include one species of flower beetle (Nitidulidae) and two weevils (Curculionidae). The beetles feed by chewing into the tissues of the unopened male flowers, and may feed on pollen when they reach the interior. They appear on the inflorescences soon after the flowers are exposed by the opening of the spathe. This may be as much as 24 hours before

the male flowers open. The beetles are apparently attracted by the musky odor given off by the fresh inflorescences (by the unopened male flowers?). On the second day, at the time that the male flowers are open and shedding pollen, the beetles begin to leave the inflorescence and move to one of the newly opened inflorescences. The bulk of this movement occurs in early evening, after the bees have finished collecting the pollen and the male flowers are beginning to loosen and fall from the inflorescence. This coincides with the beginning of anthesis of the female flowers on the new inflorescences. (See Table 1.)

The drosophilid flies occur with the beetles on the second-day inflorescences, perhaps feeding on plant juices released by the feeding activity of the beetles. The flies do not occur in my samples taken from first-day inflorescences in the evening; perhaps their food is not available until the next day. Under these circumstances, it seems unlikely that they play any role in pollination of *Bactris*, but more information is needed about their habit and pollen-carrying capacity before anything definite can be said about them.

It appears then, that of all the insect visitors to the flowers of *Bactris*, only the nitidulid and curculionid beetles can play any role in pollination. These insects appear in great numbers on the second-day inflorescences up to the time that the male flowers release their pollen. Subsequently, they appear in great numbers on the new inflorescences at about the time that the female flowers are becoming receptive. Beetles taken from these inflorescences and examined microscopically are found to carry pollen grains of *Bactris*, and only *Bactris*, among the hairs of their bodies. The beetles are small (less than 3 mm. in length), and can carry only a few grains each, but literally hundreds of them make

the trip from an old to a new inflorescence each evening. Only one pollen grain is theoretically needed to fertilize each of the 30 to 50 pistils that will develop into fruit on an inflorescence. Pollen must be transferred inadvertently, as the beetles land on, or walk over the sticky stigmas of the female flowers.

The possibility of pollination by wind should be given some consideration here, since palms have been traditionally regarded as wind-pollinated (see review in Schmid, 1970a). Knuth (1904) suggested specifically that several species of *Bactris*, including *B. major*, are wind-pollinated. However, two factors make wind-pollination in *Bactris* unlikely. First is the fact that wind is usually absent from the wooded natural habitat of the two species studied. Only at the artificially cleared Guanacaste site was there any breeze that might have carried pollen through the air. Second is the fact that the pollen-shedding period of the male flowers on the second-day inflorescences ends before the female flowers on the first-day inflorescences reach anthesis. Male and female flowers would have to attain anthesis simultaneously if wind-pollination were to be effective.

If we accept the hypothesis that *Bactris* is beetle-pollinated in the manner outlined above, then a number of peculiar morphological and phenological features of the plants can be explained. The female flowers, for example, are extremely fibrous (Uhl, personal communication) and are apparently unpalatable to the beetles. They are scarcely touched as the succulent male flowers become riddled by the voracious insects. Since the female flowers also produce no nectar and no pollen, and are not conspicuous in any way, they have no way of attracting insects to themselves. It seems that the male flowers must be the bait to attract the beetles to the inflorescences on which the female flowers are receptive to pol-

len. It follows then that the female flowers must open before the males on a particular inflorescence, so that the unopened males can be present as the attractant. The reversal of the order of flowering from that in most other monoecious palms can thus be directly related to the peculiar means by which *Bactris* attracts its insect pollinators.

The pollination mechanism in *Bactris* is very efficient. The female flowers need not produce any attractant of their own, and can concentrate their energy in their chief function of producing fruit. The male flowers perform a triple duty, of attracting insects to the inflorescences on which female flowers are receptive, then 24 hours later investing the same insects with a load of pollen, and finally, by falling soon from the inflorescences, forcing the insects to leave at just the right time to be attracted to a new inflorescence where they begin the cycle anew. The abundance of heavy infructescences in both *Bactris* populations attests to the success of the system.

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