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Pollination of *Mabea occidentalis* (Euphorbiaceae) in Panama

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ABSTRACT. The reproductive biology of *Mabea occidentalis* (Euphorbiaceae), an understory tree of tropical moist forests, was studied on Barro Colorado Island, Panama. Morphological and behavioral features of the flowers suggest that *M. occidentalis* is adapted to pollination by bats. These characteristic floral features include maroon and green inflorescences that hang outside of the foliage, nocturnal anthesis, strong musty odor, and many staminate flowers that produce relatively large amounts of pollen and nectar. Nectar concentration and composition fit the chiropterophilous syndrome. The largely self-incompatible inflorescences of *M. occidentalis* are visited nocturnally by small bats (*Glossophaga soricina* and *Carollia castanea*), the red woolly opossum, and noctuid and pyralid moths and diurnally by *Trigona* bees. The relative roles and contrasting foraging strategies of these potential pollinators are discussed. This is the first report of bat pollination for Euphorbiaceae.

Euphorbiaceae, a family of approximately 300 genera and 5000 species (Willis 1973), is predominantly tropical in distribution, yet studies on the pollination biology of its various members have been limited almost exclusively to temperate zone species, primarily *Euphorbia* (Nicotra 1894; Knuth 1899, 1904; Pax and Hoffman 1930; Gramuglio 1953; Krombein 1961; Ehrenfeld 1979). Notable exceptions to this are the studies of *Hevea brasiliensis* by Warmke (1951, 1952) and more recently, work by Armbruster and Webster (1979, 1981, 1982).

Adaptations to pollination by both abiotic and biotic agents occur in the Euphorbiaceae. Wind pollination has been demonstrated (Alex 1957) in *Ricinus*, the castor bean, and hypothesized on morphological grounds for other genera in Acalyphoideae, Phyllanthoideae, and Oldfieldoideae, however, most Euphorbiaceae appear to be pollinated by animals.

Because of the rather open nature of many Euphorbiaceae flowers, it is not surprising that a wide array of visitors are attracted to the easily accessible pollen and nectar. Many of the European *Euphorbia* species are visited mainly by flies, but visits by bees and beetles have also been observed (Knuth 1904). Ehrenfeld (1979) collected 175 species of insects, consisting mainly of bees, large and small flies (Tachinidae and Sarcophagidae), and wasps, from the flowers of *Euphorbia albomarginata* in Arizona and New Mexico.

Open, unspecialized (in terms of pollination syndrome) flowers are limited to neither the "cyathium type" (*Euphorbia*) nor to temperate zone species. In Panama, *Croton panamensis* is visited by a variety of insects including bees (Apidae and Halictidae), flies, and butterflies (Steiner unpubl.). Although unspecialized flowers may be the norm in Euphorbiaceae, specialized types do exist. These include flowers adapted to hummingbird pollination in *Pedilanthus* (Dressler 1957), hawkmoth pollination in *Cnidoscolus* (Perkins et al. 1975), midge pollination in *Hevea brasiliensis* (Warmke 1951, 1952), and bee pollination in *Dalechampia* (Armbruster and Webster 1979, 1981, 1982). No cases of bat pollination have been reported, however. The purpose of this study was to examine the reproductive biology of *Mabea occidentalis* Benth. as a potential example of bat pollination in the Euphorbiaceae.

Mabea occidentalis, an understory tree 4–6 m in height, ranges from Mexico to northern South America (Webster and Burch 1967) and is a common component of the young (ca. 70 yr) tropical moist forest on Barro Colorado Island, Panama. It begins flowering at the end of the wet season (Nov–Dec) and continues until the end of the dry season in late April or early May.

Mabea occidentalis is monoecious with staminate and pistillate flowers clustered in paniculate inflorescences (pseudanthia) that hang down from the tips of branches in the open areas between foliage layers of the canopy. The staminate flowers are maroon and consist of a pedicel, a reduced perianth of only 3–5 small calyx lobes, and a ball of anthers (fig. 1). Staminate flowers are clustered in groups of three, subtended by a green biglandular bract, and born on peduncles that are spirally arranged

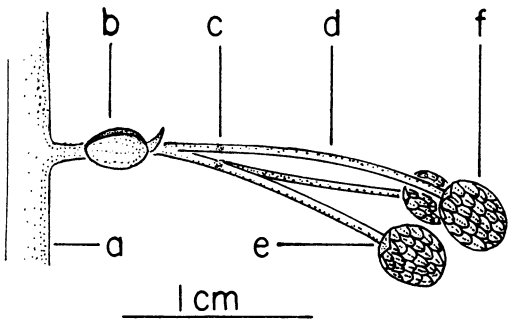


FIG. 1. A cluster of three staminate flowers of *Mabea occidentalis* subtended by a biglandular bract (cf. fig. 2). a. Rachis. b. Biglandular bract. c. Abscission zone. d. Pedicel. e. Calyx lobe. f. Ball of anthers.

around a green central axis (rachis) of the inflorescence (cf. figs. 1–2). Pistillate flowers are solitary at the basal nodes of the inflorescence and, as with the staminate flowers, have no petals or floral disc. There are, however, six small maroon sepals that surround the ovary. The rest of the pistillate flower consists of three fused styles (separated at the apex into three stigma lobes) that form a stylar column (fig. 3). Pistillate flowers usually do not have glands associated with the subtending bracts, but when they are present they are much smaller than those subtending staminate flowers and rarely secrete nectar.

MATERIALS AND METHODS

Study site. This study was conducted on Barro Colorado Island (BCI) located in Gatun Lake, a part of the Panama Canal. Annual rainfall on BCI averages 2750 mm with only 180–260 mm falling during the dry season (mid-Dec to early May); see Croat (1978) for additional information on BCI. Field observations were made primarily on the edge of the laboratory clearing and in the adjacent Allee watershed, between Nov 1979 and Jun 1980. Some observations were made in a less disturbed area of young forest at the junction of Miller and Lake trails. *Mabea occidentalis* voucher specimens have been deposited in DAV.

Spatial distribution of trees. Nearest neighbor distances were measured for the main study clump and Morisita's index of dispersion was calculated (cf. Hubbell 1979) from data of Lang and Knight (unpubl.) for *Mabea* individuals on their permanent 1.5 ha plot on Barbour Trail (BCI).

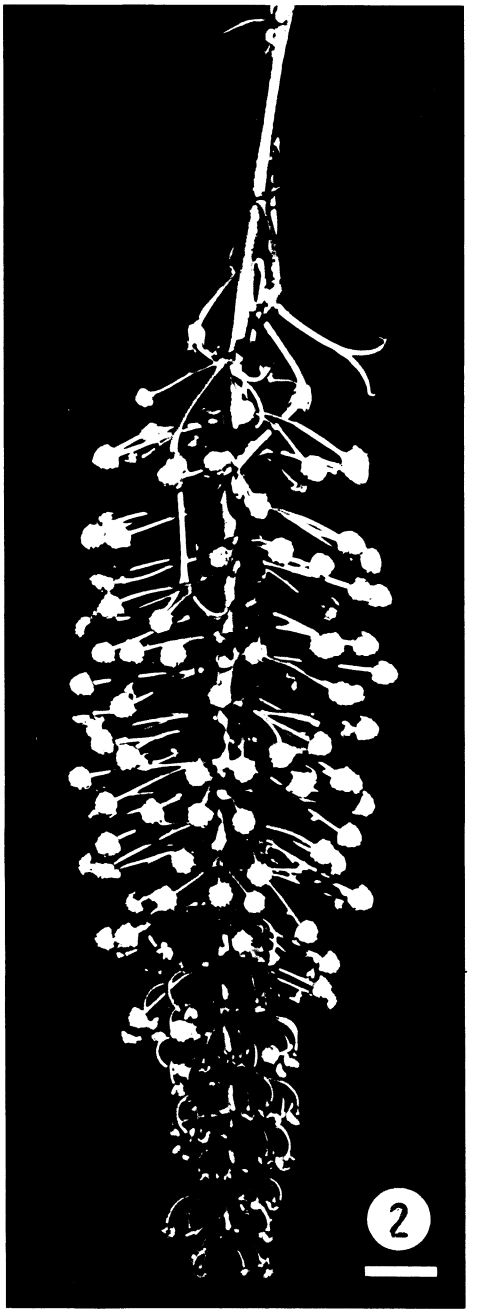


FIG. 2. *Mabea occidentalis* inflorescence at anthesis. Scale = 1 cm.

Phenology. The flowering times of *Mabea* individuals in the study population were deter-

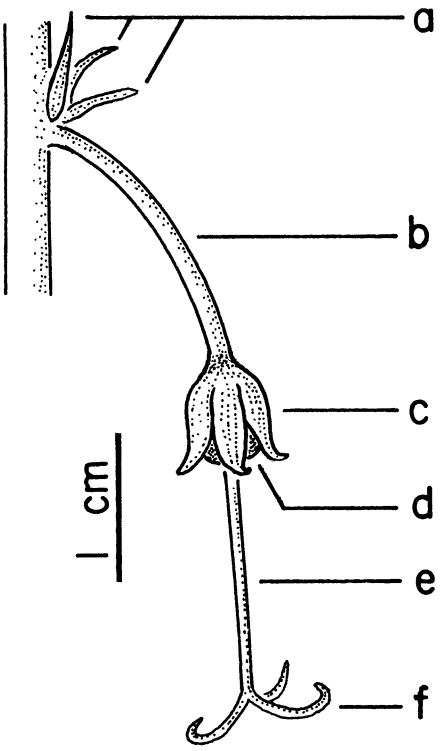


FIG. 3. Pistillate flower of *Mabea occidentalis* (cf. fig. 2). a. Bracts. b. Pedicel. c. Sepal. d. Ovary. E. Stylar column. f. Stigma.

mined by a census of 55 trees at approximately two-week intervals. The number of inflorescences on each tree was recorded at each census.

Floral morphology and behavior. The number of flowers (male and female) was counted for eleven inflorescences from each of thirteen different trees. Intra-inflorescence flowering synchrony, duration of individual flowers and whole inflorescences, and timing of anther dehiscence, stigma receptivity, and nectar secretion of the biglandular bracts were studied. Stigma receptivity was evaluated through timing of cross-pollinations (see breeding systems experiments).

Nectar and pollen. Nectar volume and concentration were measured with calibrated micropipets and a temperature corrected (23°C) Atago hand refractometer, respectively. Glandular bracts on each inflorescence were marked and the entire inflorescence enclosed in bags made from fine-mesh nylon netting. Eight glandular bracts were marked on each of five different inflorescences on five different trees; these were sampled every hour from 1800 to 0500 EST or until nectar production ceased. Only one or two inflorescences were sampled on a single night. The nectar was spotted on Whatman no. 1 filter paper strips in the field and later analyzed by Irene Baker (University of California, Berkeley) using techniques outlined in Baker and Baker (1975, 1979) for proportions of glucose, sucrose, and fructose and for amino acid composition. Counts with a dissecting microscope were made of the number of pollen grains per half anther and anthers per staminate flower for inflorescences from two different trees. Average pollen production per inflorescence per night was obtained by doubling the average number of grains per half anther, multiplying by the average number of anthers per staminate flower, and then multiplying by the average number of flowers presenting pollen per night.

Breeding experiments. Inflorescences were bagged prior to stigma receptivity of the pistillate flowers with fine-mesh nylon netting and subjected to one of three treatments: 1) control—113 pistillate flowers from eight different trees left untouched in bags; 2) geitonogamous-pollination—77 pistillate flowers from ten different trees (intra-inflorescence pollen transfer); 3) cross-pollination—138 pistillate flowers from seven different trees. In order to determine the period of stigma receptivity, pollen from a different tree was placed on stigmas: a) 2 days before staminate anthesis (nectar secretion and anther dehiscence), b) 1.5 days before staminate anthesis, c) on the first night of staminate anthesis, d) during the morning or afternoon following the first night of staminate anthesis, e) the second night of staminate anthesis, and f) the third night of staminate anthesis. Fruit set from open-pollinated flowers ($N = 1113$) from six different trees was also monitored.

Floral visitors. Floral visitors were observed for a total of 94.2 hours on 52 different nights between 27 Nov and 2 May. All but 5.5 hours of observation occurred between 27 Nov and 19 Feb. Most observations were made on the edge of the laboratory clearing and in the Allee watershed. A few observations were also made at the junction of Miller and Lake trails.

Observations of bats were made with a head-

lamp attached to a tripod and covered with a red filter or when available with a Javelin Night Viewing Device (NVD) equipped with an infrared light source. Observation time per night was quite variable but averaged 1.9 (±1.4) hours. Mist nets were set around flowering *Mabea* individuals for a total of 24 net hours. Captured bats were identified and pollen samples taken with transparent tape from the head or from fecal samples. Pollen samples were examined under a compound microscope and compared to reference slides for identification. One *Glossophaga soricina* individual was marked with a plastic wing band covered with reflecting tape. Eighteen photographs (taken on three different nights) of bats visiting flowers were taken using a tripod and electronic flash. Charles Rupprecht provided some pollen samples from bats caught as part of a separate bat monitoring project (Smithsonian Environmental Sciences Program).

Observations of floral visits by *Caluromys derbianus*, the red woolly opossum, were made with a headlamp covered with a red filter. The time of visitation, the time spent per inflorescence, the number of inflorescences visited per tree, the manner in which flowers were manipulated, and the extent of interplant movement were recorded. Photographs were made with a 200 mm telephoto lens and a Vivitar 283 electronic flash. Live trapping of *Caluromys* was unsuccessful.

Observations of moths and other nocturnal insects were made with either the NVD or a headlamp with a red filter during night observation periods and during nectar sampling. Many were collected for voucher specimens, but some were only photographed. Visitation behavior was carefully noted to determine whether visits were non-destructive and whether stigmas were contacted.

Most observations of the *Trigona* bee visitors were not made in a systematic fashion, but rather the presence of bees on inflorescences was noted during tree censuses and breeding system experiments at various times throughout the day. After frequent observations of bees on inflorescences were made and after breeding system experiments showed that stigmas were receptive during the day, two experiments were performed to examine the pollinating capability of *Trigona* bees: (1) In order to assess whether diurnal visitors could affect fruit set, night visitors were exluded from inflorescences by bagging during the period of nectar secretion and pollen presentation. Bags were removed early in the morning and replaced late in the afternoon. A total of nine inflorescences (48 pistillate flowers) from five trees were treated in this manner. (2) To determine whether diurnal visitors moved pollen between trees, daytime movement of fluorescent powder between adjacent trees was monitored on one occasion.

Results

Tree distribution. To check the qualitative impression that *Mabea occidentalis* trees are clumped on Barro Colorado Island, Morisita's index of dispersion was calculated for 39 *Mabea* individuals on a permanent 1.5 ha plot of G. Lang and D. Knight. A value of 10.9 was obtained, indicating a clumped distribution (cf. Hubbell 1979). Most of the 12 trees at the main observation site had touching or overlapping canopies with a mean nearest neighbor distance (trunk to trunk) of 2.45 ± 1.02 m.

Floral phenology. Only 37 of the 55 individuals censused in the Allee watershed flowered during this study; it is those trees upon which the percent trees flowering measure is based (fig. 4). The total inflorescences curve is based on 31 of the 37 flowering trees (fig. 4). A few *Mabea* individuals began flowering during the second week in October on BCI; however, as shown in figure 4, the major flowering peak for both the proportion of trees in flower and total number of inflorescences occurred in January and February. Plants in a population on Pipeline Rd., northwest of Gamboa (approximately 10 km from BCI), did not start flowering until mid-November but had a similar flowering peak. Unfortunately inflorescence counts for six of the heavy flowering individuals in the study clump were incomplete for November and December and therefore could not be included. The inclusion of these trees would probably have shifted the flowering peak slightly earlier in the season and caused it to be almost twice as high (i.e., 450 inflorescences). In the census population, the average flowering period for an individual was 3.0 ± 1.2 months (range: 0.5–6.0). The number of inflorescences produced by a given individual is not constant over the flowering period. This is particularly evident

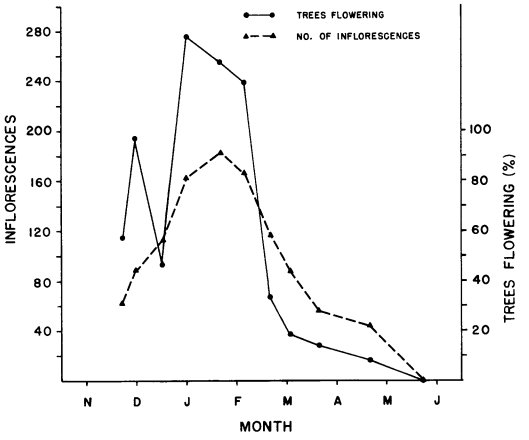


FIG. 4. Proportion of study trees flowering and total number of inflorescences produced by the censused population of *Mabea occidentalis* versus time.

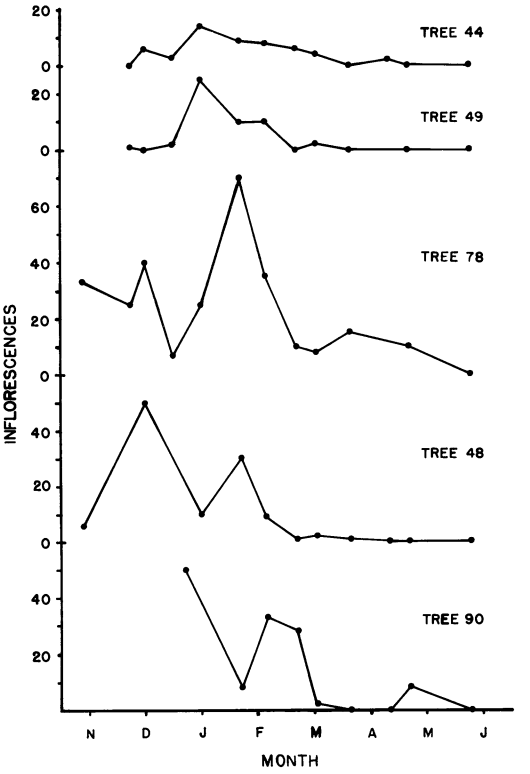


FIG. 5. Pattern of flowering in *Mabea occidentalis* over time for five study trees.

for larger trees that have longer flowering periods. There are usually slack periods between flowering peaks as is evident in the curve of figure 4 and for the five individuals in figure 5.

Floral morphology and development. Each inflorescence of *M. occidentalis* is about 15 cm long and consists of an average of 203.8 (SD = 35.0, $N = 143$) staminate flowers and 4.9 (SD = 1.5, $N = 143$) pistillate flowers. The central staminate flower in the group of three is larger and contains more anthers than the side flowers. The average number of anthers for central flowers from one tree (two inflorescences) was 37.1 (SD = 4.5, $N = 8$) and for side flowers was 29.0 (SD = 4.5, $N = 16$). Before anthesis, inflorescences appear maroon due to the color of the staminate flowers, but as the anthers dehisce, the inflorescences become yellow from the exposed pollen.

Stigma lobe spreading of the pistillate flowers initiates the sequence of flowering for each inflorescence. The three lobes are fully reflexed and receptive about 2 days before and during the entire period of nectar secretion and pollen presentation by the staminate flowers (see breeding system experiments). Therefore, the pseudanthium is protogynous. Pistillate flowers that have not been pollinated abscise 1-2 weeks after the final night of nectar secretion.

The staminate flower clusters present pollen concomitant with nectar secretion by the subtending glandular bracts (cf. fig. 1). Each inflorescence secretes nectar for 2-3 nights with usually one-half to one-third of the staminate flowers reaching anthesis each night, although this can be quite variable. Maturation of the staminate flowers is acropetal, but because the inflorescences hang down, those nearest the pistillate flowers are the first to reach anthesis. Nectar secretion and pollen presentation within each portion of the inflorescence are well synchronized and, for a given glandular bract and staminate flower, last a single night. Staminate flowers abscise above the biglandular bract (fig. 1c) 1-2 days after anthesis. The staminate portion of the inflorescence abscises below the pistillate flowers approximately 2 days after the final night of nectar secretion.

Nectar. Nectar secretion usually begins between 1630 and 1700 EST and can continue until 0700 the next day, however, at least 79% of the nectar is secreted before 2400. Nectar flow peaks for an average *Mabea* inflorescence between 1900 and 2200 and steadily declines

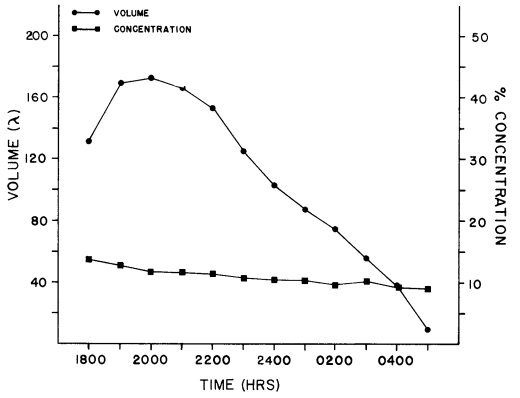


FIG. 6. Mean nectar volume (λ) and concentration [(g sucrose equivalents per 100 g solution)%] versus time in *Mabea occidentalis*. The means are based on the average nectar production of a single glandular bract times the average number of glandular bracts secreting nectar per inflorescence per night.

thereafter (see fig. 6). Nectar concentration starts at about 14% and eventually drops to about 9.5% g sucrose equivalents per 100 g of solution (fig. 6). Each inflorescence produces a mean of 149 mg (SD = 50) sugar per night. The number of inflorescences secreting nectar per night for a given individual is quite variable but is usually less than 20, except for unusually large trees. The strong, musty odor given off by a clump of heavily flowering *Mabea occidentalis* trees can be detected as far away as 50 m. This odor, given off only by the nectar, directly reflects nectar availability.

The proportion of glucose (61.5%) and fructose (29.6%) was much greater than sucrose (8.9%) in the nectar of *Mabea occidentalis*. Only seven amino acids were detected in *Mabea* nectar and only three of these were present in more than trace amounts (1 on a qualitative scale of 1 to 4). Of these, threonine and glutamine scored 2 and serine 3.

Pollen. Pedicels of the staminate flowers curve upwards, anthers open, and pollen is exuded between 1800 and 1900 EST. The difference in flower position between those presenting pollen and those still in bud can be seen in figure 5. The number of pollen grains per anther was 267.3 (SD = 12.2, $N = 3$) for one inflorescence. An inflorescence from another tree had a mean of 256 (SD = 36.4, $N = 5$) pollen grains per anther. For the first tree, the average number of anthers per staminate flower was 37.1 (SD = 4.5) for central flowers and 29.0 (SD = 4.5) for side flowers. The average number of staminate flowers per inflorescence was 203.8 (SD = 35.0, $N = 143$), giving a mean of 1.6×10^6 (SD = 0.3×10^6) pollen grains per inflorescence. The number of ovules in *Mabea occidentalis* is always three per female flower (14.7 per inflorescence), so that the average pollen/ovule (P/O) ratio is $1.1 \times 10^5 : 1$ (SD = 0.05×10^5) per inflorescence or about 36,700 ± 1800 : 1 grains per night of anthesis, because only about one-third of the inflorescence presents pollen and nectar on a given night. It is not unreasonable to figure the P/O ratio of the entire inflorescence, because functionally it represents a single blossom (Faegri and van der Pijl 1979) or pollination unit.

TABLE 1. Comparisons of fruit set in *Mabea occidentalis* for cross, geitonogamous, control (bagged but not manipulated), and open pollinations. [a] range: 31.4–53.7.

Treatment	Number of flowers	Flowers setting fruit	% success	Number of trees
Cross	77	71	92.2	7
Geitonogamous	133	5	4.0	10
Control	113	6	5.3	9
Open	1113	493	44.3[a]	6

Cross vs. geitonogamous, $\chi^2 = 167.5$; $P < 0.001$
Cross vs. open, $\chi^2 = 64.4$; $P < 0.001$
Geitonogamous vs. control, $\chi^2 = 0.12$; $P > 0.50$
Geitonogamous vs. open, $\chi^2 = 83.0$; $P < 0.001$

Breeding system. Very little self-pollination occurs in *Mabea* (table 1) even though pistillate flowers hang down among the staminate flowers (fig. 2). Untreated controls and geitonogamous treatments had fruit sets of 5.3% and 3.6% respectively (table 1); this indicates that *Mabea* is self-incompatible within the limits set by both Bawa (1974) and Zapata and Arroyo (1978). The fruit sets of both cross and geitonogamous pollinations are significantly different from fruit set under natural conditions (i.e., open pollination). Table 2 presents the results of time of pollination and fruit set for the 77 cross-pollinated flowers. Because sample sizes for some treatments are small, it is difficult to speculate on the time of optimal receptivity (no significant difference was found between time of pollination and fruit set), but it is possible to see

TABLE 2. Inflorescence age and fruit set in *Mabea occidentalis*. Night 1 is the first night of pollen presentation and nectar secretion (i.e., staminate anthesis). Crosses made during the day (morning or afternoon) were made with pollen left from the previous night. 2.0 days before night 1 vs. night 1, $\chi^2 = 2.6$; $P > 0.10$.

Time of pollination	Fruit set (%)	N
2.0 days before night 1	60.0	5
1.5 days before night 1	85.7	7
Night 1	100.0	13
Day 2	95.2	21
Night 2	93.8	16
Day 3	100.0	6
Night 3	88.9	9

that stigmas of pistillate flowers can be receptive as much as 2 days before staminate anthesis.

VISITORS

Bats. Floral observations began on 27 Nov, however, the first bat visit was not observed until 23 Dec. Between 23 Dec and 19 Feb, bat visits were observed on 18 of 27 observation nights. The most common small (10 g) nectar feeding bat on BCI and primary bat visitor to *Mabea occidentalis* is *Glossophaga soricina* (Glossophaginae). It was the only species photographed and caught carrying *Mabea* pollen; however, another small bat, *Carollia castanea* (Carollinae), was caught by C. Rupprecht and R. Fischer with *Mabea* pollen loads elsewhere on BCI (pers. comm.). The positioning of the pollen (head, face, and forearms) on *C. castanea* suggested that it visits inflorescences by landing and clinging to them. This type of visitation was not seen at my sites; rather, all visits involved a quick (ca. 0.5 second) hover at the inflorescence. This is typical foraging behavior for *Glossophaga soricina* (Baker 1973; Heithaus et al. 1974; Sazima and Sazima 1978). Figure 7 depicts *G. soricina* visiting *M. occidentalis* with its long tongue extended.

Because the red light may have been detected by the bats, whereas the NVD and IR light cannot be detected, the visitation frequency data using these methods are presented separately. Observations were made for different time periods on different nights so only the visitation frequency between 2000 and 2200 hr EST is presented for comparison. The mean bat visi-



FIG. 7. *Glossophaga soricina* visiting a *Mabea occidentalis* inflorescence. Scale = 1 cm.

TABLE 3. Bat visitation (visits/inflorescence/hour) to *Mabea occidentalis* for hour starting as indicated. Based on first 15 minutes of each hour (×4) using Night Viewing Device. Values in parentheses are true values for the entire hour.

	2000	2100	2200	2300	2400	0100	0200	0300	0400	0500
26 Jan	0.0 (2.2)	0.0 (7.8)	6.0	4.0	17.0	27.0	13.0	20.0	9.0	0.0
6 Feb	0.0	2.0 (1.5)	0.0 (1.5)	2.0	2.0	—	—	—	—	—
10 Feb	9.1 (6.2)	1.3 (3.7)	2.7 (2.0)	1.3	8.0	4.0	0.0	4.0	0.0	—

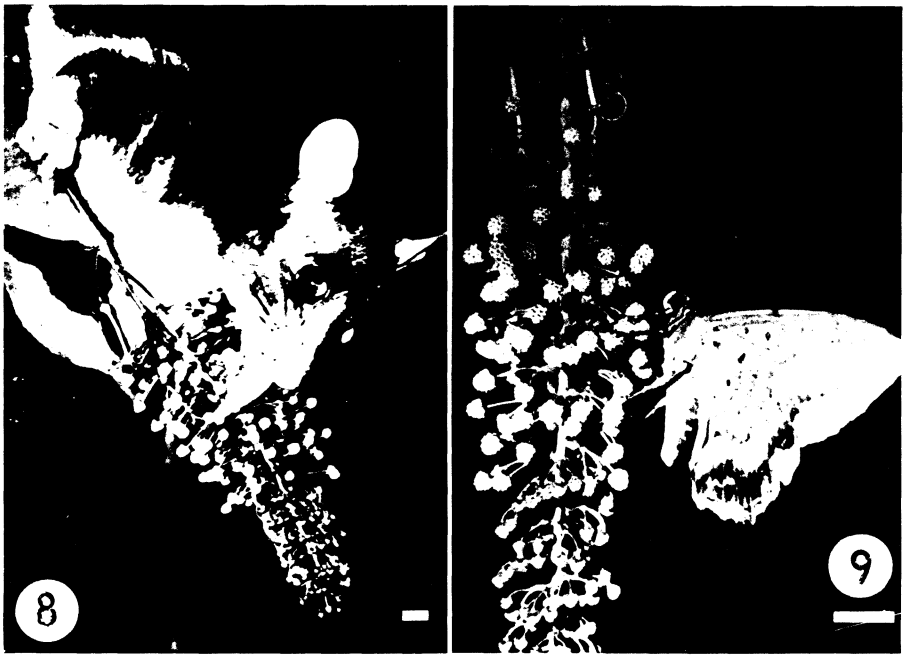
tation frequency for red light observations was 1.7 ± 1.6 (range: 0.0–4.0, $N = 5$) visits per inflorescence per hour with corresponding moth and red woolly opossum visitation frequencies of 0.15 ± 0.22 (range: 0.0–0.5, $N = 5$) and 0.20 ± 0.27 (range: 0.0–0.5, $N = 5$) visits per inflorescence per hour, respectively. For NVD observations the mean bat visitation frequency was 3.4 ± 2.9 (range: 0.0–6.4, $N = 5$) visits per inflorescence per hour and the moth frequency 0.13 ± 0.14 (range: 0.0–0.33, $N = 5$) visits/inflorescence/hour. For each observation type (red light and NVD), on one of five nights no visitors were seen at a tree that had been visited on previous nights. There was no significant difference (one way analysis of variance) in visitation frequency between observation methods or between bat, moth, and opossum under red light. There was, however, a significant difference ($P < 0.05$) between bat and moth visitation frequency using the NVD.

On most nights observations were made between 1900 and 2300 hours, but on two nights they were made between 2000 and 0500. The number of visits per inflorescence per hour for the two all-night observation periods (using Night Viewing Device) is shown in table 3. The numbers in parentheses are the actual number of visits during the hour of observation. The other numbers are based on 15 minute observation periods at the beginning of each hour. These observations show that visitation occurs throughout the night.

Netting around *Mabea* trees was not very successful. Only four captures were made during 24 net hours on four different nights. Three of these were *Glossophaga soricina* individuals and the other was an *Artibeus phaeotis* individual. Only a single individual was caught with pollen, but this individual was captured twice. A head and fecal sample were taken from this individual both times. When first captured, this bat had pollen on its head consisting of 63% *M. occidentalis*, 12% *Trichanthera gigantea* (Acanthaceae), and 25% unknown pollen grains ($N = 8$ grains). Its fecal sample consisted of 95% *M. occidentalis* and 5% *T. gigantea* pollen ($N = 100$ grains). When recaptured, no pollen was recovered from its head, but its fecal sample had 30% *M. occidentalis* and 70% *Pseudobombax septinatum* (Bombacaceae) pollen grains ($N = 100$ grains). The *G. soricina* individual mentioned above was marked with a reflective wing band after its initial capture. Nine days later it was observed at the same site returning four times to the same *Mabea* inflorescences in the course of 1.5 hours of observation.

On five different days during February, at five different locations on BCI, *Carollia castanea* individuals [small bats averaging 1.4 g (Bonaccorso 1979)] were caught carrying large obvious loads of bright yellow pollen on their faces, heads, and forearms (C. Rupprecht, pers. comm.). Pollen samples taken from the heads of these bats (provided by C. Rupprecht) contained only *Mabea occidentalis* pollen. Although the same regular netting project was conducted during Dec 1979 through Mar 1980, only during 11–21 Feb were individuals of *C. castanea* caught carrying pollen.

Red woolly opossum. *Caluromys derbianus* was a common visitor to *Mabea occidentalis* flowers at the main study site (cf. fig. 8). It was most frequently observed during the first part of December when two of the larger trees in the area were at their flowering peaks. During this period, *C. derbianus* would stay in the study area for 2–3 hours at a time, either foraging or grooming. Later in the season, it visited the area only for brief periods one to three times during the evening. During January and February both *C. derbianus* and *G. soricina* were observed visiting the same trees. The visitation behaviors of these two animals is quite different. The red woolly opossum, which is approximately 30 times the size of a *G. soricina* indi-



FIGS. 8-9. Visitors to inflorescences of *Mabea occidentalis*. 8. *Caluromys derbianus* removing nectar. Scale = 1 cm. 9. Noctuid moth removing nectar. Scale = 1 cm.

vidual, removes all of the nectar present on an inflorescence with a single visit, while *G. soricina* removes only a portion of the nectar and returns to the inflorescence more frequently. A more detailed account of the foraging behavior of *Caluromys derbianus* has been published separately (Steiner 1981).

Moths. Visits to *Mabea* flowers by moths were observed on 26 of 45 nights between 27 Nov and 19 Feb and on five additional nights in April. Most of the moths observed, collected, or photographed were noctuids (fig. 9), the rest were pyralids. At least thirteen different species were observed, but only seven species were collected (six Noctuidae and one Pyralidae). The size of the moth visitors was quite variable. For those collected, wingspans ranged from 3.0 to 10.5 cm, but a few observed specimens had wingspans as large as 15-20 cm. Between 27 Nov and 19 Feb, the major flowering period, 57 moth visits were recorded. These visitors were separated into four relative size classes: extra large (>12 cm), large (7-12 cm, cf. fig. 9), medium (4-7 cm), and small (<4 cm) based on field estimations. The relative proportions were 4, 24, 22, and 50%, respectively. If moth visits during April, the tail-end of the flowering season (XL—0, L—25, M—58, and S—18%), are included, the overall percentages are XL—3, L—24, M—35, S—38.

The average time spent by a moth on an inflorescence was 1.87 ± 0.82 minutes ($N = 14$). On one occasion (29 Apr) a large moth remained on a single *Mabea* inflorescence for over 2 hours, while smaller moths sporadically landed on the other side of the inflorescence. Most of the moth visitors to *M. occidentalis* were small and did not move around much on an inflorescence and, as a result, rarely contacted stigmas. At trees where bats were visiting flowers, moth visits were eight to 136 times less frequent than bat visits. During a photographic session in April, ten visits were made to one inflorescence by four species of moths over a 3-hour period, yet no flowers were pollinated.

Other nocturnal visitors. Other nocturnal insect visitors were seen occasionally on *Mabea* inflorescences including a large cerambycid, *Brasilianus plicatus* (Olivier), observed twice, two unidentified beetles, two katydid species (Tettigoniidae), and a cockroach. All of these except the katydids fed nondestructively on pol-

len exposed on the staminate flowers. The katydids ate the staminate flowers and biglandular bracts as well as the pollen. At the very end of the flowering period (May), the nocturnal bee *Megalopta* (Halictidae) was observed collecting pollen on 2 nights. The rarity of floral visits by these insects and their visitation behaviors make it very unlikely that they play any significant role in the pollination of *M. occidentalis*.

Bees. Two species of *Trigona* bees, *T. fulviventris* and *T. fuscipennis*, were regularly observed visiting *Mabea* flowers, two species, *T. tetaira* and *T. dorsalis*, were occasionally seen, while *T. cupira* and *T. domiciliorum* were observed only once. *Trigona fuscipennis* was observed on inflorescences throughout the flowering season ($N = 31$ at 11 trees), but *T. fulviventris* was observed only through the first week in January ($N = 10$ at 4 trees). *Trigona tetaira* was observed only four times at two different trees, while *T. dorsalis* was seen two times at two different trees.

All three species collected pollen from staminate flowers and visited most frequently in the early morning and late afternoon. This corresponds to activity patterns observed for *T. fulviventris* and *T. fuscipennis* by S. P. Hubbell (pers. comm.) and Gilbert (1973) in Costa Rica. In the morning the *Trigona* spp. would glean pollen left from the previous night, while late in the afternoon, they would force open anthers before they could dehisce naturally. In most cases the robbing did not damage the anthers or noticably reduce the amount of pollen exposed at anthesis, but in a few cases destruction of the anthers and depletion of pollen were quite obvious. This was observed by visually comparing bagged, damaged and undamaged inflorescences from the same tree at anthesis. In all cases, the most heavily damaged inflorescences were robbed by *Trigona fuscipennis* individuals.

The foraging behavior of *T. fuscipennis* and *T. fulviventris* on *Mabea* was quite different, beyond differences in pollen robbing. *Trigona fuscipennis* usually foraged in groups with as many as nine bees on a single inflorescence, while *T. fulviventris* usually foraged singly or with no more than two or three bees on an inflorescence. Similar differences in foraging behavior have been described for these two species in Costa Rica (Johnson and Hubbell 1975).

In the course of pollen collecting, *Trigona* bees were occasionally observed to contact the stigmas of pistillate flowers. Fluorescent powder placed on the staminate flowers on one inflorescence was collected by *Trigona fuscipennis* and transferred to the stigma of another inflorescence on a tree approximately 4 m away.

Of the nine inflorescences from five different trees (48 flowers) that had night visitors excluded by bagging, four inflorescences from three trees set 15 fruits, a fruit set of 31.2%.

Wasps. Much less commonly observed were three vespid wasp species [*Polybia occidentalis* (Olivier), *Stelopolybia panamensis* (Camaron), and *Stelopolybia* sp.], the only other diurnal floral visitors. They visited inflorescences mainly in late afternoon for newly secreted nectar, although occasionally they were seen in the morning collecting nectar left over from the previous night. Pollen was not actively collected or passively transferred by these wasps.

Discussion

The morphological and behavorial features of the flowers of *Mabea occidentalis* including exposed inflorescences, nocturnal anthesis, maroon and green coloration, strong musty odor, and relatively large amounts of pollen and nectar all fit the syndrome of bat pollination as described by Faegri and van der Pijl (1979). The nectar characteristics of *M. occidentalis* (i.e., low number and concentration of amino acids and low proportion of sucrose relative to glucose and fructose) are also typical of bat-pollinated flowers (Baker 1978; Baker and Baker 1975, 1979, in press).

The staminate and pistillate flowers in *M. occidentalis* are integrated into a single pollination unit or pseudanthium. Because pistillate flowers hang down among staminate flowers (fig. 3), a substantial amount of selfing (actually geitonogamous pollen transfer) would be expected were *Mabea* self-compatible. Self-compatibility is apparently the rule for monoecious species (East 1940; Godley 1955; Thomson and Barrett 1981), however, there are additional exceptions to this rule in Euphorbiaceae and other families (Thomson and Barrett 1981).

The pseudanthium of *Mabea occidentalis*, with a pollen/ovule ratio of 36,700:1, can be viewed as a xenogamous floral unit based on its high pollen/ovule ratio (cf. Cruden 1977). Although

many bat-pollinated flowers are characterized by the production of large amounts of pollen (Faegri and van der Pijl 1979), P/O's for these species have not been reported.

There are approximately 50 species of *Mabea*, all but two of which occur exclusively in South America (Jablonski 1967). Nothing has been reported previously regarding the pollination of other species with the exception of *M. fistulifera* (Torres de Assumpçao 1981). The inflorescences of *M. fistulifera*, which are about the same size as those of *M. occidentalis*, also produce large amounts of pollen and nectar and appear to be pollinated by diurnal monkeys (Torres de Assumpçao 1981). The possibility of nocturnal anthesis and pollination, however, has yet to be ruled out (Torres de Assumpçao 1981). Jablonski (1967) characterized *Mabea* as wind-pollinated but provided no data to substantiate his claim. An examination of herbarium specimens of 28 species revealed 21 species with characteristics suggesting bat pollination and seven with reduced inflorescences, much smaller staminate flowers, and bracteal glands that were reduced or absent, suggesting pollination by pollen collecting insects or wind.

The evidence for "trap-lining" by bats consists of a pattern of regularly spaced visits by one species throughout the evening to plants that produce small numbers of flowers nightly over relatively long flowering seasons (Baker 1973; Heithaus et al. 1974; Sazima and Sazima 1975, 1978; Gould 1978). Quick visits (less than 1 second) in which only a portion of the available nectar is removed and constant but different directions of arrival and departure to flowers are two additional components of this syndrome. None of the above studies, however, have demonstrated that the same individual bat returns at regular intervals to a given flower. My observations, although from but a single bat on a single night, show that *Glossophaga soricina* does return to the same flower or inflorescence at intervals.

Mixed pollen loads (i.e., from more than one species) are commonly carried by flower visiting bats (Alvarez and Gonzalez Q. 1970; Heithaus et al. 1975; Howell 1977), so it is not surprising to find mixed fecal loads from the *Glossophaga soricina* visitor to *Mabea occidentalis*. Heithaus et al. (1975) found that 42.3% of the pollen loads they examined from flower visiting bats were mixed, with as many as six pollen types represented on some individuals. They suggested, therefore, that bats exhibit rather low flower constancy, however, they did note that some bat species showed greater constancy (fewer mixed loads) than others. Howell (1977) felt that bats are more effective pollinators than the pollen load (Heithaus et al. 1975) and fecal (Alvarez and Gonzalez Q. 1970) analyses suggested, because these studies failed to look closely at spatial partitioning of pollen on the bat's bodies or temporal partitioning of bats by the plants.

It is interesting that *Carollia castanea* individuals were caught carrying *Mabea* pollen loads, because they are regarded as frugivorous (Fleming et al. 1972; Gardner 1977; Bonaccorso 1979) and have not previously been recorded as flower visitors. This may, however, be due to misidentification of *C. castanea* as the related *C. perspicillata*, which has been frequently caught carrying pollen and seen visiting flowers (Heithaus et al. 1975; Sazima and Sazima 1978). The pollen loads of *Carollia castanea* contained only *Mabea* pollen, which suggests that *Carollia* forages opportunistically on *Mabea* and does not visit other flowers. *Carollia castanea* has been characterized as a groundstory frugivore (Bonaccorso 1979) that feeds primarily on *Piper* fruits. The abundance of flowering *Mabea* individuals with strong smelling nectar in the *C. castanea* foraging stratum probably accounts for utilization of this resource during February. The abundance and pattern of pollen deposition (face, head, and forearms) indicates that *C. castanea* may land on *Mabea* inflorescences to remove nectar rather than hover as does *Glossophaga soricina*. Because *C. castanea* is very capable of removing fruits while hovering (Bonaccorso pers. comm.), it seems likely that *C. castanea* lands on inflorescences, because it does not have the long tongue and elongated snout of the Glossophaginae (e.g., *Glossophaga*) and is, therefore, less efficient at harvesting nectar on the wing.

Both dye movement and fruit-set data show that inter-tree pollen transfer can be effected by *Trigona* bees. These bees might best be viewed as "back-up" pollinators for flowers that fail to get pollinated by nocturnal visitors. If flowers are pollinated at night, *Trigona* visitation may be superfluous. The potential for diurnal pollination following nocturnal anthesis has been observed in other primarily bat-

pollinated species including *Carnegiea gigantea* (McGregor et al. 1962), *Ceiba acuminata* (Baker et al. 1971), and *Passiflora mucronata* (Sazima and Sazima 1978).

The long visitation time, low visitation frequency, and low probability of pollen deposition all argue against a major role for moths as pollinators of *Mabea occidentalis*, yet in the absence of other visitors they could be important. The energetic requirements of noctuid and pyralid moths should, because they are settling moths, be low and easily met by visits to relatively few inflorescences. Therefore, little inter-tree pollen flow would be expected. Additional evidence against adaptation to pollination by moths can be obtained from an analysis of *Mabea* nectar. Baker and Baker (1975, 1979, in press) and Baker (1978) have found correlations between pollination syndromes and nectar composition, particularly with respect to sugars and amino acids. For flowers adapted to pollination by settling moths, only 7% had nectar with sucrose to glucose and fructose ratios as low as *Mabea* nectar (less than 0.1), while 33% of the Neotropical bat-pollinated flowers had hexose dominant nectar (S/G+F < 0.1) and the rest were hexose rich (S/G+F < 0.5). Bats, therefore, appear to have provided the strongest evolutionary force in shaping the floral characteristics of *Mabea occidentalis*, even though they are by no means the exclusive pollinators.

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