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Pollination Ecology of the Two Wild Bananas, *Musa acuminata* subsp. *halabanensis* and *M. salaccensis*: Chiropterophily and Ornithophily¹

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ABSTRACT

The two Sumatran wild bananas, *Musa acuminata* subsp. *halabanensis* and *M. salaccensis*, belonging to the different sections *Musa* and *Callimusa* respectively, have contrasting flowering traits corresponding to their different pollination syndromes: *i.e.*, chiropterophily and ornithophily, respectively. The *M. a. halabanensis* flowers, on pendent inflorescences with dark purple bracts, produced jelly-like nectar of 22–25 percent sugar concentration primarily at night, and were pollinated by the nectarivorous pteropodid bats, *Macroglossus sobrinus*. In contrast, the *M. salaccensis* flowers, on erect inflorescences with purplish pink bracts, produced dilute nectar of 18–21 percent sugar concentration primarily in the daytime, and were pollinated by the nectarivorous nectariniid birds, *Arachnothera longirostris* and *Aethopyga siparaja*. The flowering span of each female flower was 24–40 hr, while that of the male flowers was < 12 hr. Open flowers of both species contained significantly less outcrop of nectar than bagged flowers. Fruit weight and seedset of open *M. salaccensis* flowers were significantly more than those of bagged flowers and were significantly less than those of hand-pollinated flowers.

MUSACEAE, IN A BROAD SENSE, is composed of seven genera: *Musa*, *Ensete*, *Phenakospermum*, *Ravenala*, *Heliconia*, *Strelitzia*, and *Orchidantha*, all of which have nectar-rich flowers. *Heliconia* endemic to South America, South Pacific Islands, and Eastern Malaysia are pollinated by hummingbirds in South America (Linhart 1973, Stiles 1975, Kress 1983), and by macroglossinae bats in the South Pacific Islands (Kress 1985). *Strelitzia* endemic to South Africa is pollinated by nectariniid birds (Frost & Frost 1981). In contrast, *Musa*, widely distributed in continental South East Asia and in the Malaysia tropics, are chiropterophilous (Start & Marshall 1976, Nur 1976, Gould 1978, Payne *et al.* 1985) or ornithophilous (Nur 1976). Pollination syndromes of the other genera have not yet been clarified.

There are two wild bananas in West Sumatra: *M. acuminata* and *M. salaccensis* (Hotta 1989a, b). *M. acuminata* is composed of three subspecies, one of which is subsp. *halabanensis*. These two species have different basic chromosome numbers

and belong to different groups: section *Musa* and sect. *Callimusa*, respectively. Inflorescence structures and flower phenology preclude pollen transfer within the same inflorescence. The flowers align linearly on inflorescences, with female flowers at the basal part, and male flowers at the apical part. Anthesis proceeds from basal to apical flowers linearly within the inflorescence (Fig. 1). The objective of this paper is to compare the pollination biology of these two wild bananas.

MATERIALS AND METHODS

Field research was carried out in the orchard at Ulu Gadut (0°55'S, 100°29'E) east of Padang, West Sumatra (430–450 m in altitude) from 27 November 1987 to 22 January 1988. The major part of the Ulu Gadut region is covered by primary tropical rain forest and orchards in which fruit trees, *e.g.*, *Durio zibethinus*, *Garcinia mangostana*, and *Lansium domesticum*, were planted. Both of the *Musa* species form thick stands along streams with *Achasma macrocheilos*, *Hornstedtia* sp. and many tree species which belong to secondary forest elements, *e.g.*, *Macaranga trilolata*, *Villebrunea rubescens*, *Pternandra caerulea*, *Saurauia* sp. etc.

¹ Received 10 August 1989, revision accepted 18 September 1990.

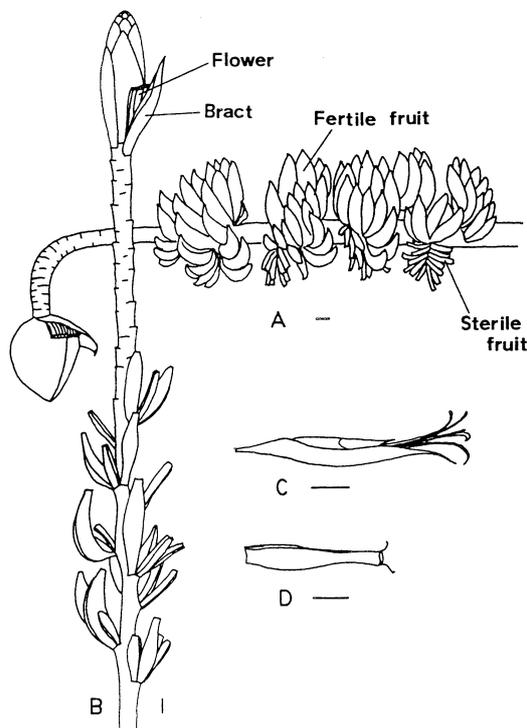


FIGURE 1. Inflorescences and male flowers of *Musa acuminata halabanensis* (A, C) and *Musa salaccensis* (B, D). Scales denote 1 cm.

MUSA SALACCENSIS.—Observations on phenology, nectar production, pollinator behavior, and fruit and seed-set were made in the stand of *M. salaccensis* along a stream (ca 40 m × 60 m, containing 63 colonies of *M. salaccensis*).

Nectar samples were taken by 50- μ l "Micro-cap" calibrated capillary tubes. Volume in the tubes was measured to the nearest millimeter, and the nectar was transferred in the field directly to a Bellingham and Stanley pocket refractometer to measure sucrose equivalents of sugar concentration.

Three male-stage inflorescences and one female-stage inflorescence were bagged with nylon netting to exclude flying visitors. Marked flowers of the bagged and unbagged (= open) inflorescences were drained several times daily without destruction to determine the rate of nectar production and the standing crop of the nectar.

We observed the diurnal pattern of vertebrate pollinator visits to inflorescences from a blind hut for a total of 32 hr (20 hr in the daytime and 12 hr in the nighttime) in December 1987. Within 18 m of the blind hut, we could see 14 inflorescences, 12 and 2 of which were at the male and female

stage, respectively. During the observation, we also measured the air temperature, moisture, and illumination at intervals of 30–70 min. Insect visitors were captured by net for identification.

To determine the factors affecting fruit-set and seed-set, some female flowers were categorized as bagged flowers: flower buds bagged with nylon netting; diurnally open flowers: flowers bagged only during the night from the time of anthesis to flower wilting; hand-pollinated flowers: flower buds bagged and hand-pollinated with pollen taken from another plant; and open flowers: flowers kept open to pollinator visits. The opening of these female flowers occurred during 10–14 December 1987.

On 22 January 1988, all the fruits originating from the treated flowers were harvested, and the wet weight and the number of fertile seed per fruit (*i.e.*, seed-set) were measured and counted. To determine the frequency distribution of seed-set of open flowers, we also harvested the fruits for which anthesis had occurred several months before.

MUSA ACUMINATA SUBSP. *HALABANENSIS*.—Observations were made in a small stand of *M. a. halabanensis* (ca 10 m × 10 m, containing 10 pseudostems of *M. a. halabanensis*).

An inflorescence was bagged with nylon netting, and the volume and sugar concentration of the nectar in the bagged and open male flowers were measured. The flowers were destroyed to obtain these measurements.

We observed the temporal pattern of the vertebrate pollinator visits to inflorescences from a blind hut for two days (6 hr in the daytime and 2.5 hr in the nighttime) in January 1988. Insect visitors were netted for identification.

Bird and bat specimens, caught in nylon mist nets set within the stand of the two *Musa* species, were preserved in methanol for identification. These pollinator specimens were preserved in the Department of Biology, Andalas University, Padang, West Sumatra.

RESULTS

M. SALACCENSIS.—Bracts of female and male flowers began to open in early morning; 80 percent ($N = 10$) of female and 90 percent ($N = 10$) of male flowers began to open between 0300 and 0800 hr. Perianths of most female flowers fell down by the morning of the third day, and most male flowers fell by the evening of the first day.

Diurnal changes in nectar production rate (μ l/hr) and sugar concentration of bagged female and

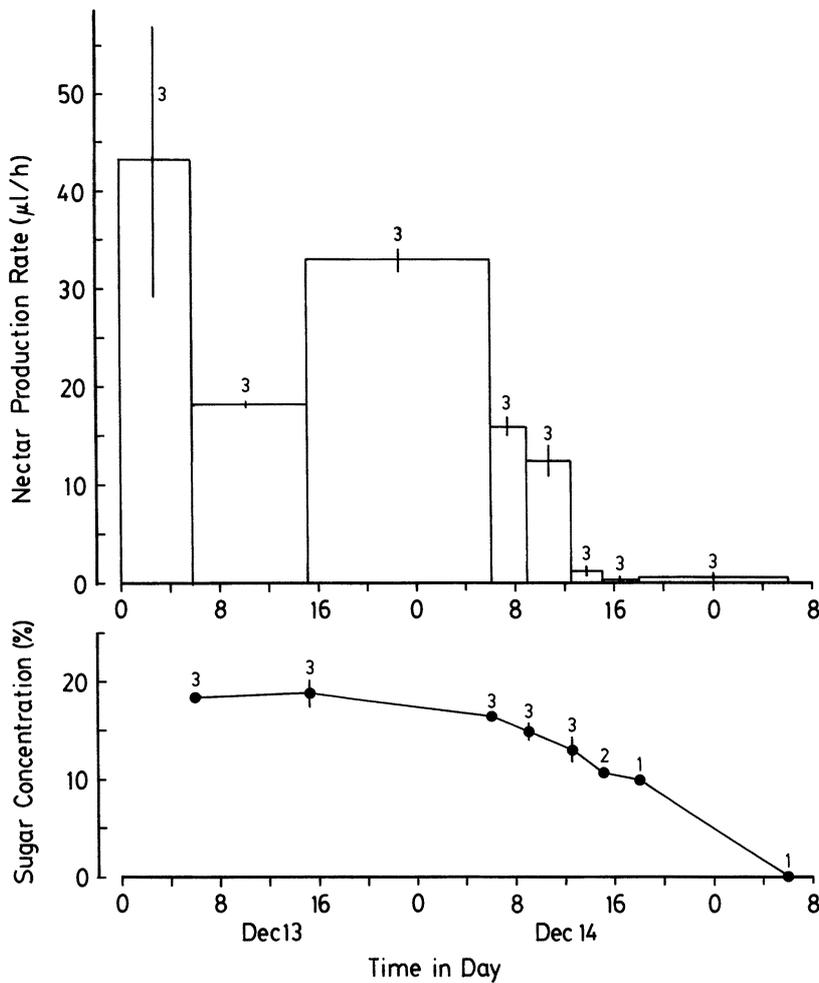


FIGURE 2. Changes in nectar production rate ($\mu\text{l/hr}$) and sugar concentration (%) of female *Musa salaccensis* bagged flowers. The rate before 6000 hr is estimated assuming that nectar production started at 0000 hr. The bars indicate standard deviations. The numbers of flowers inspected are shown above.

male-flowers are given in Figures 2 and 3, respectively. A bagged female flower contained $260.0 \pm 97.2 \mu\text{l}$ (mean \pm SD) ($N = 3$) nectar at 0600 hr just after anthesis, and then continued producing nectar at a rate of $17\text{--}33 \mu\text{l/hr}$ until noon of the next day (Fig. 2). The sugar concentration of the nectar was 18–19 percent on the first day and gradually decreased. A bagged male flower contained $22.5 \pm 15.9 \mu\text{l}$ (mean \pm SD) ($N = 6$) nectar at 0730 hr and continued producing nectar at a rate of $17.2\text{--}18.8 \mu\text{l/hr}$ until 1550 hr (Fig. 3). During this period, sugar concentration of the nectar was kept at 18.8–20.4 percent.

Standing crop of floral nectar of open flowers was compared with that of bagged flowers. The

difference of nectar volume between open and bagged 8- and 32-hr-old female flowers (which opened 8 and 32 hr before sampling, respectively) was significant (8-hr-old bagged: $431.9 \pm 95.5 \mu\text{l}$ ($N = 3$), open: $53.3 \pm 25.1 \mu\text{l}$ (6); 32-hr-old bagged: $574.9 \pm 18.1 \mu\text{l}$ (3), open: $15.8 \pm 25.5 \mu\text{l}$ (3), t -test, $P < 0.001$, $df = 7$; $P < 0.001$, $df = 4$, respectively). The difference of nectar volume between open and bagged 6-hr-old male flowers was also significant (bagged: $116.8 \pm 46.0 \mu\text{l}$ (6), open: $22.6 \pm 19.7 \mu\text{l}$ (5), $P < 0.005$, $df = 9$). These results show that nectar of open flowers was almost depleted by flower visitors in the morning, several hours after the anthesis.

Open flowers were visited by birds, tree shrews,

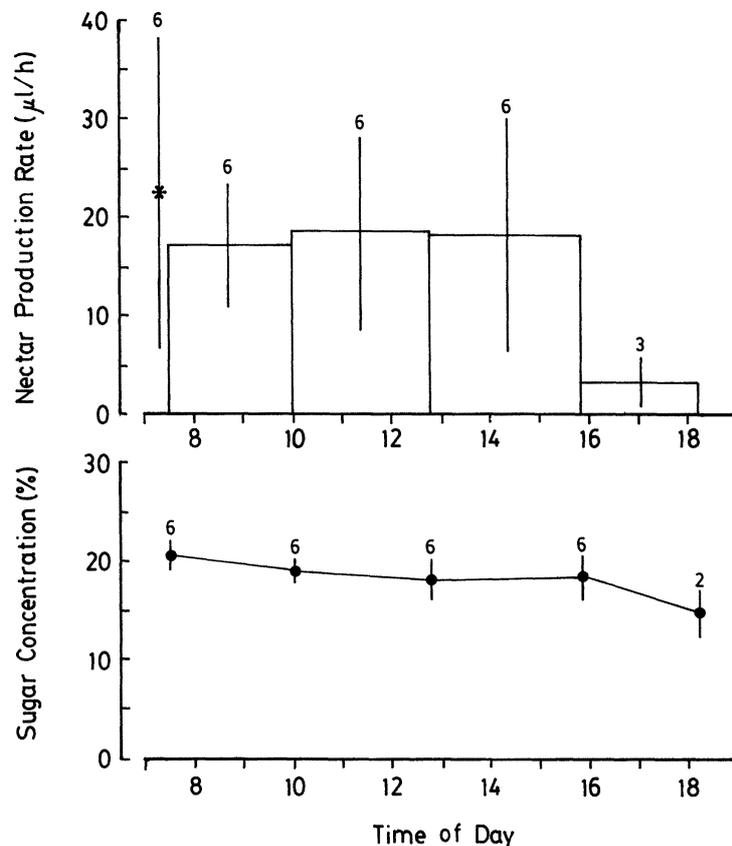


FIGURE 3. Changes in nectar production rate ($\mu\text{l}/\text{hour}$) and sugar concentration (%) of male *Musa salaccensis* bagged flowers. The asterisk indicates the standing crop of nectar at 0730 hr. The bars indicate standard deviations. The number of flowers inspected are shown above.

and various insects (Table 1). The intact flowers, however, were visited only by nectariniid birds and tree shrews. Insects listed in Table 1 visited only the flowers which had been visited by the vertebrate visitors. Perianths of these flowers were damaged or plucked by the vertebrate visitors so that insect visitors could approach the nectar at the bottom of the sturdy flower tube while they did not touch either the anther or the stigma. Thus, the vertebrates, especially the two nectariniid birds, were recognized as effective pollinators. A tree shrew (*Tupaia* sp.) also foraged banana flowers (but very rarely) and was possibly an occasional pollen vector.

Arachnothera longirostris, a nectariniid bird, has a long, curved bill. The lengths of the culmen and the wings of the females were, respectively, 38.5 ± 3.7 mm (mean \pm SD, $N = 8$) and 60.0 ± 2.6 mm ($N = 8$). Those of males were 39.9 ± 0.6 mm ($N = 2$) and 69.2 ± 1.4 mm ($N = 2$). Another nectariniid, *Aethopyga siparaja*, has a thin, slightly

curved bill. The length of the culmen and the wing of one female specimen were 12.8 mm and 57.0 mm, respectively.

Bird behavior on banana plants was categorized into three major patterns: collecting nectar, chirping, and "transit." When the bird visitors collected nectar, they first perched on the bract, and then inserted bills into the perianths, and sucked up the nectar. Because an inflorescence possesses several open flowers at a given time, the birds generally checked all the flowers of each inflorescence when visiting. Usually, they successively visited several inflorescences at the observation site. The durations of nectar collection per inflorescence were 6.79 ± 3.02 sec (mean \pm SD, $N = 14$) in *Ar. longirostris*, 6.53 ± 4.41 sec ($N = 40$) in males of *Ae. siparaja* and 28.0 ± 35.9 sec ($N = 6$) in females of *Ae. siparaja*. Neither bird species foraged in flocks. When the male *Ae. siparaja* searched for a mate, it perched on the twigs of trees at the observation

TABLE 1. Visitors to *Musa* spp. inflorescences.

Class	Order	Family	Species	<i>Musa</i>		
				<i>salaccensis</i>	<i>a. halabanensis</i>	
Mammalia	Chiroptera	Pteropodidae	<i>Macroglossus sobrinus</i>		+	
	Scandentia	Tupaidae	<i>Tupaia</i> sp.	+	+	
Aves	Passeriformes	Nectariniidae	<i>Arachnothera longirostris</i>	+		
			<i>Aethopyga siparaja</i>	+		
Insecta	Hymenoptera	Apidae	<i>Trigona laeviceps</i>	+	+	
			<i>T. minankabau</i>	+		
			<i>T. apicalis</i>		+	
		Vespidae	<i>Polybioides raphigastra</i>	+		
			Formicidae	<i>Odontomachus rixosus</i>	+	
				<i>Aenictus dentatus</i>	+	
	Lepidoptera	Hesperiidae	<i>Ancistroides nigrita</i>	+	+	
			<i>Erionata thrax</i>	+	+	
	Diptera	Stratiomyiidae	?	+	+	
			Drosophilidae	<i>Drosophila</i> sp.		+
	Dermaptera	Blattaria	Pygidicramidae	<i>Challia</i> sp.	+	
			Blattellidae	<i>Blattella</i> sp.	+	+
				<i>Blattella</i> sp.	+	

site and chirped for a few minutes (106.3 ± 40.3 sec, $N = 8$). The behavior of birds flying over or hopping from one branch to another across the observation site was named "transit."

Figure 4 shows the diurnal pattern of pollinator visits to inflorescences on 19 January 1988. On 19 January, when it was raining off and on, *Ar. longirostris* visited the flowers in the morning, and *Ae. siparaja* visited in the afternoon when *Ar. longirostris* were absent. Both species were apt to forage at different times of day also on 21 January (a day without rain). Although no direct aggressive interaction was observed, such diurnal foraging segregation between species may be related to competitive exclusion of one species by the other.

Table 2 shows the comparison of fruit weight and seed-set among 4 treatments of flowers: open, diurnally open, bagged, and hand-pollinated flowers. Bagged flowers only produced sterile fruits, weighing 2.54 ± 0.49 g (mean \pm SD) and containing almost no seeds (only 2 fruits among 7 contained 2 seeds each). Fruit weight and seed-set of open flowers were larger than those of bagged flowers (fruit weight: t -test, $P < 0.05$, $df = 15$; seed-set: $0.1 > P > 0.05$, $df = 15$). On the other hand, fruit weight and seed-set of open flowers were not significantly different from those of diurnally open flowers (fruit weight: $P > 0.2$, $df = 15$; seed-set: $P > 0.2$, $df = 15$). This result suggests that the flowers were pollinated in daytime.

The fruit weight and seed-set of open flowers, however, were significantly less than those of hand-

pollinated flowers (fruit weight: $P < 0.01$, $df = 12$; seed-set: $P < 0.001$, $df = 12$). The frequency distribution of seed-set of 5 open inflorescences was bimodal: the frequency of 0, 0–10, 10–20, 20–30, 30–40, 40–50, 50–60, 60–70, 70–80, 80–90, and 90–100 seed-set were 22, 16, 7, 5, 8, 9, 13, 17, 13, 17, and 3, respectively. These results suggest that fruit-set and seed-set were pollinator limited. Note that the seed-set of above-mentioned open flowers (38.2 ± 30.9 , $N = 39$) was larger than that in Table 2 (9.7 ± 12.0 , $N = 10$). Disturbance by observers might decrease pollinator visitations to the study site during the observation period (Table 2) compared with those during the observer-free period.

MUSA ACUMINATA SUBSP. *HALABANENSIS*.—Bracts of male inflorescence began to open between 1700 and 2000 hr and the bracts and the flowers fell until 1000 hr the next morning.

Nectar volume of a bagged male flower at 2000 hr (just after the anthesis) and at 1000 hr (when the flowers had fallen in nylon netting) were 60.0 ± 10.3 μ l (mean \pm SD) ($N = 29$) and 139.0 ± 36.6 μ l ($N = 30$), respectively. Assume that the flower stopped nectar production at 0600 hr, the mean rate of nectar production between 2000 hr and 0600 hr on the next day was 7.90 μ l/hr. The nectar was jelly-like in contrast with the water-like nectar of *M. salaccensis*, and the sugar concentration was 22.5–24.8 percent (2000 hr: $22.5 \pm 0.4\%$, $N = 19$; 1000 hr: $24.8 \pm 0.7\%$, $N = 13$).

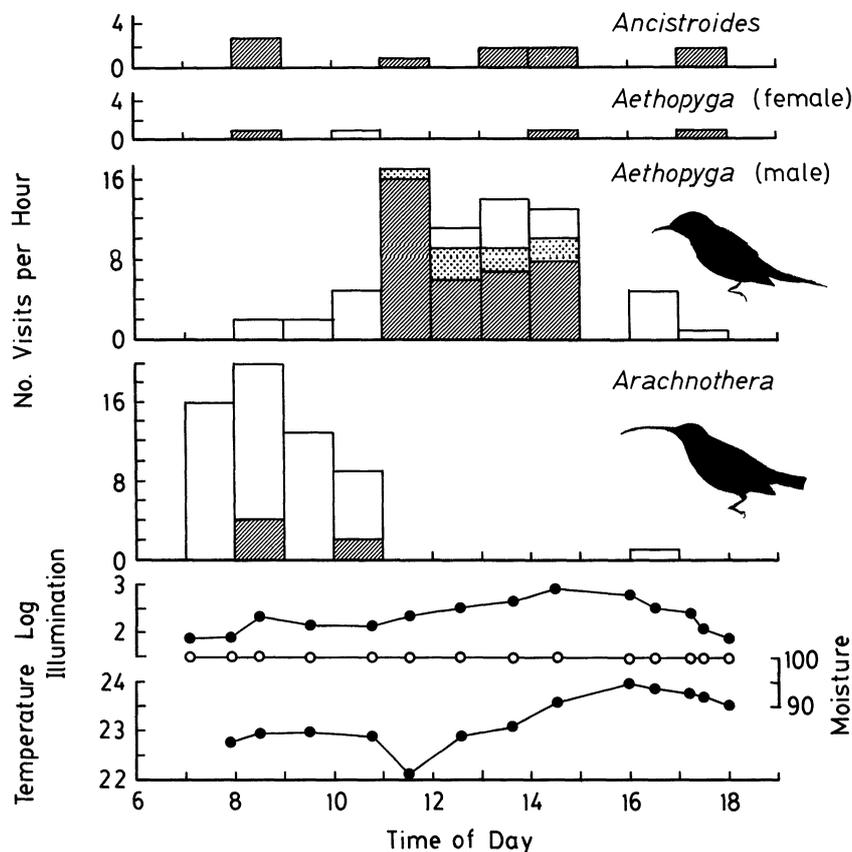


FIGURE 4. Diurnal pattern of pollinator visits to *Musa salaccensis* inflorescences and changes of log illumination (lux), air temperature ($^{\circ}\text{C}$) and moisture (%; open circle) on 19 January 1988. Pollinators visited inflorescences for collecting nectar (shaded), chirping (dotted) or transit (open column). Silhouettes of *Arachnothera longirostris* and *Aethopyga siparaja* are also drawn.

The nectar volume and sugar concentration of an open flower at 1000 hr were $2.3 \pm 3.4 \mu\text{l}$ ($N = 21$) and $16.1 \pm 3.0\%$ ($N = 3$), respectively, and were significantly less than those of a bagged flower at 1000 hr (nectar volume: t -test, $P < 0.01$, $df = 49$; sugar concentration: $P < 0.01$, $df = 14$).

TABLE 2. Comparison of fruit weight (g) and seed-set per fruit among 4 treatments: open (daytime and night), diurnally open, bagged, and hand-pollinated *Musa salaccensis* flowers.

Treatment	N	Fruit weight		Seed-set	
		Mean	SD	Mean	SD
Open	10	6.21	3.77	9.7	12.0
Diurnally open	7	7.93	2.85	15.3	11.9
Bagged	7	2.54	0.49	0.6	1.0
Hand-pollinated	4	12.83	1.43	62.0	15.9

An inflorescence in male-stage was visited by the nectarivorous bat, *Macroglossus sobrinus* three times between 1930 and 2030 hr on 20 January 1988. They perched on the bract and licked the nectar with their long tongues, then soon flew away. On the bract which fell, we found many claw marks made by the bats. In the daytime the female flowers, which had probably already been visited by bats the night before and damaged, were visited by many insects (Table 1).

The frequency distribution of seed-set of open inflorescences was bimodal: the frequency of 0, 0–50, 50–100, 100–150, 150–200, 200–250, 250–300, 300–350, 350–400, 400–450, 450–500, 500–550, and 550–600 seed-set were 135, 42, 17, 19, 22, 13, 27, 35, 35, 15, 3, 5, and 1, respectively. Of 298 female flowers, 135 produced sterile fruits weighing 3.19 ± 0.96 g (mean \pm SD). The mean seed-set of each fruit bunch was variable

TABLE 3. Comparison of characteristics of *M. salaccensis* and *M. a. halabanensis*.

Characteristic	Characteristic state	
	<i>M. salaccensis</i>	<i>M. a. halabanensis</i>
Inflorescence orientation	erect	horizontal (female part) and pendent (male part)
Perianth tightness	tight	loose
Bract color	purplish pink	dark crimson
Flower color	green	whitish yellow
Perianth length (male flower)	23–28 mm	42–47 mm
No. open flowers/bunch	3–8	15–40
Anthesis	early morning	evening
Female flower longevity	24–40 hr	24–40 hr
Male flower longevity	<12 hr	<12 hr
Nectar production	diurnal	nocturnal
Rate of nectar production	17–19 μ l/hour	7.9 μ l/hour
Sugar concentration of nectar	18–21%	22–25%
Pollinators	nectariniid sunbird	pteropodiid bat

and independent of its order in the bunch. These patterns of fruit-set and seed-set may suggest pollinator limitation.

DISCUSSION

The two wild bananas, *Musa acuminata* subsp. *halabanensis* and *M. salaccensis*, exemplified the respective pollination syndromes; *i.e.*, chiropterophily and ornithophily. This confirms the earlier observations made by Nur (1976). He provided information on pollinators of 7 wild species and 4 cultivars of bananas, including *M. a. halabanensis* and *M. salaccensis*. Although most of his work was done in a botanical garden, he observed bat visitation to *M. a. halabanensis*, and nectariniid bird and tree shrew visitation to *M. salaccensis*. This study documents these patterns more precisely with information on nectar production and phenology in a more natural environment.

Comparison of characteristics of the two bananas shows the broad differences in inflorescence orientation, coloration, perianth length, floral phenology, and nectar production (Table 3). The contrasts can be clearly attributed to foraging behavior, morphology, and nocturnal and diurnal activity patterns of the bats and birds.

The inflorescence orientation and perianth tightness prevent potential alternative vertebrate visitors (birds to *M. a. halabanensis* and bats to *M. salaccensis*) from visiting. Without such prevention, the vertebrates could visit flowers of either alternative banana species because the stands of the two bananas exist at close range and the open flowers (especially the female ones) do open during day and

night irrespective of their caloric value. The bracts on horizontal or pendent inflorescences of *M. a. halabanensis* appeared to be hard to perch on for nectariniid birds without sharp claws (like bats). The slippery surface prevents nectar extraction from the flowers. The macrogrossine bats, on the other hand, may hardly insert their tongues, between the hard perianths which are tightened together, into the intact *M. salaccensis* flowers.

Bracts and flowers of *M. a. halabanensis* are dark crimson and whitish yellow, respectively, and inconspicuous to the human eye; those of *M. salaccensis* are bright pink and green, respectively, and stand out clearly from the surrounding green vegetation. Although most megachiropterans must orient to food sources by sight or smell, bright colors are not necessarily visual cues for those nocturnal, colorblind foragers (Kress 1985); visual conspicuousness is the key factor for attracting diurnal birds. The contrasting timing of anthesis and nectar production is obviously correlated with the nocturnal and diurnal activity patterns of the respective pollinators.

Some of the differences in floral characteristics between *M. a. halabanensis* (section *Musa*) and *M. salaccensis* (sect. *Callimusa*) are applicable to those between section *Musa* and sect. *Callimusa* distributed in the West Malaysian area (Hotta 1989a). Taxa belonging to sect. *Musa* have glaucous dark crimson bracts and nocturnal flowers while the *M. salaccensis* group of sect. *Callimusa* have erect inflorescences, brilliant bracts, and diurnal green flowers.

Finally, we discuss the effects of the breeding system and the pollination syndromes on the reproductive success of *Musa*. In contrast with the

prevalence of self-compatibility of neotropical *Heliconia* (Kress 1983), *Musa* developed a monoecious breeding system, *i.e.*, a structurally self-incompatible system. Monoecious *Musa* has some tactics to decrease the risk of not being visited by available pollinators. Female flowers of *Musa* have a longer flowering time than male flowers. *Musa* has blooms consistently all year maintaining attractiveness to vertebrate pollinators. There are more male flowers than female flowers in a *Musa* population. These traits might promote the availability of pollen on birds' or bats' bodies and keep the constant attractiveness of the individual plant with a lower cost of nectar. Nevertheless, seed-set of *Musa* was pol-

linator-limited, suggesting severe competition among nectar plants for available vertebrate pollinators.

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