Pollination of Androdioecious *Xerospermum intermedium* Radlk. (Sapindaceae) in a rain forest

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Xerospermum intermedium, a fairly common understorey species in the West Malesian lowland dipterocarp forest is androdioecious, with delayed self-compatibility. It flowers annually, and has an extended flowering period, with individuals flowering somewhat asynchronously, presenting small flowers with minimal visual lures. The flowers are visited by an unrestricted array of apparently imprecise opportunistic feeders, predominated by trigonid bees and butterflies. Most of these visitors exhibit low fidelity and forage opportunistically on numerous competing tree species. Presentation of nectar in alternating rhythms between the male and hermaphrodite trees appears to induce pollinator movement between them. Out of such alternating visits between the sexes, a low level of short-range inter-tree pollen transfer by trigonids and butterflies seems to occur. Despite the elaborate system which promotes pollinator movement between the sexes, this species has retained a low level of self-compatibility. The physical barriers to pollinator movement in the understorey, and high interspecific competition for pollinators by a large number of tree species, appear therefore to make it difficult to maintain an obligate outbreeding system. Hence, androdioecism may be one of the explanations for the survival of *X. intermedium*.

KEY WORDS:—Rain forest – androdioecy – nectar pulses – trigonid bees – butterflies – insect movements – pollination – competition.

CONTENTS

INTRODUCTION

The understorey of the West Malesian lowland dipterocarp forest present large physical barriers for pollinator movement. Despite this, dioecious species

predominate in this stratum (Ashton, 1969). This has been argued as evidence for the presence of selection pressures that maintain outbreeding among rain forest trees (Ashton, 1969; later also by Bawa, 1970, 1980). Ashton (1969) also speculated that an unspecialized pollination system, composed especially of abundant insect pollinators, exists that allows for a significant amount of outcrossing, frequent enough to allow gene exchange throughout populations in a continuous habitat. However, there were no studies present on the pollinators, and the nature of pollen transfer, in the climax forests of the Far East as evidence.

Most studies on flower pollination have been made in seasonal tropical rain forests of Central America (Janzen, 1971; Baker, 1973; Linhart, 1973; Frankie, Baker & Opler, 1974; Heithaus, Opler & Baker, 1974; Janzen, 1974; Gilbert, 1975; Janzen, 1975; Stiles, 1975; Frankie, 1976; Frankie, Opler & Bawa, 1976). Some of the conclusions may be applicable to the non-seasonal (perhumid) primary rain forests of the Far East and they do apply to gap-phase of primary forests and seral vegetation in Malaya (Appanah, 1979a). A few representative pollination studies on understorey dioecious species (Bawa, 1974; Bawa & Opler, 1975; Opler, Baker & Frankie, 1975; Bawa, 1979) have been carried out in lowland wet forests in Costa Rica.

The few observations on pollinators in Malaya are not in primary rain forests. Studies on Xylocopids (van der Pijl, 1954; Chua, 1973) are based in secondary vegetation. Burkill's (1919) observations on *Apis dorsata* were made in a botanical garden. Bat pollination (Start, 1974; Start & Marshall, 1976; Gould, 1977, 1978) may be regarded as a gap-phase pollination syndrome (Appanah, 1979a) since these bats dwell outside the mature forests, foraging on forest fringe and mangrove tree species, and only extend their foraging into primary forests during the flowering season (Start, 1974) when they essentially confine their attentions to the canopy.

None of these studies are truly representative of pollination processes within the closed canopy climax vegetation of lowland dipterocarp forests. In view of this, the pollination of a relatively common, apparently dioecious understorey species in the lowland dipterocarp forest, *Xerospermum intermedium* Radlk. (Sapindaceae) was studied. This paper examines the flowering phenology of a population, differences in floral rewards of the different sexes, behaviour and visitation rates of the pollinators to the different sexes, and the potential for inter-tree movement in the understorey.

METHOD OF STUDY

The investigation was conducted in a lowland dipterocarp forest, the Pasoh Forest Reserve in Negri Sembilan, Peninsula Malaysia (Lat. 2° 58′–2° 59′ N, Long. 102° 17′–102° 20′ E).

In the reserve five, 2-ha plots (100 × 200 m) were established (Fig. 1), and trees exceeding 30 cm girth at breast height (gbh) within them were systematically labelled, girthed, identified and mapped (Ashton, 1971). Within these plots, 112 tagged *X. intermedium* trees were examined periodically for flowering (Fig. 2). From initiation of first signs of flowering, the trees were examined at about 10-day intervals with binoculars. A tree climber periodically collected specimens to confirm the observation and sex of the trees. The phenological observations were first made by Yap (1976) from 1974 till 1976 and I followed them till 1978.
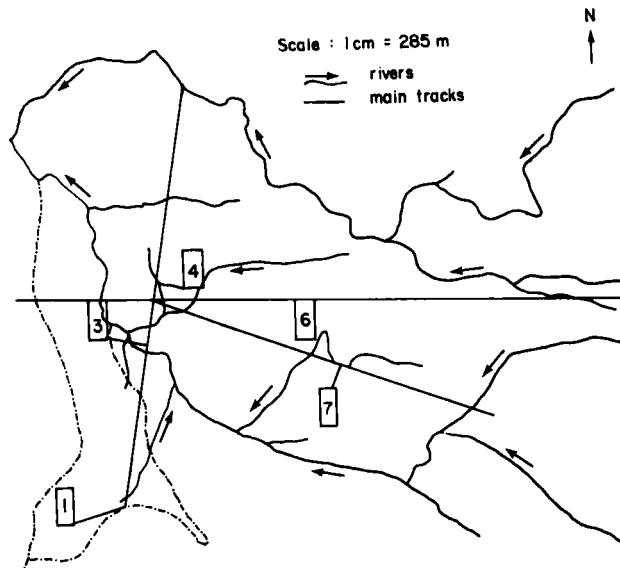
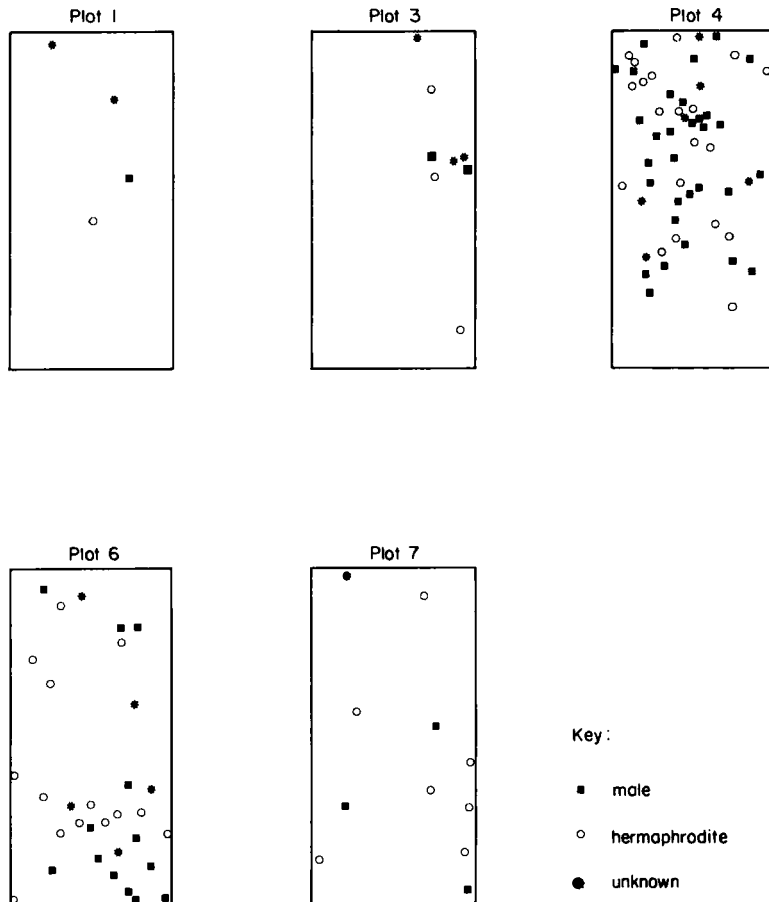Figure 1. Map showing the five 2-ha ecology plots at the Pasoh Forest Reserve.

Figure 2. The spatial distribution and sex of *X. intermedium* trees in the five 2-ha ecology plots.

The dehiscence of anthers of male flowers was studied by hourly examination under a binocular microscope of up to 20 flowers, brought down by a tree climber from 06.00 hours onwards. The anthers of the hermaphrodite flowers were apparently indehiscent, and were examined differently. Bagged flowers with morphologically mature anthers were collected, and their stamens were carefully teased out and examined for any breakdown of anther walls and release of pollen. Next, the anthers were softly touched onto a small piece of glycerine jelly (Johansen, 1940) on a glass slide; a cover slip was then applied over the jelly and the preparation gently warmed. The slide was examined under a microscope for any free pollen.

The nectar production of flowers was measured using micropipettes. Numerous inflorescences were isolated from insects, using nylon bags of fine mesh (0.2 mm) a day or two before examination. At hourly intervals from as early as 06.00 hours, up to ten flowers were collected by a tree climber, the flowers being sampled from numerous bags within each tree crown. A $1\mu l$ glass pipette was carefully inserted into the nectary, and the nectar was extracted and measured. Each flower was repeatedly probed for nectar until no more could be obtained. For examining the nectar composition, the nectar collected at peak production times was spotted onto chromatography paper. The dried spots were sealed in plastic bags and sent to Prof. H. G. Baker at the University of California, Berkeley, for analysis.

The number of flowers produced by individual male trees was estimated. This was done by laying m^2 quadrats of nylon nets at intervals in radiating transects from the base of the tree. The fallen flowers were daily collected and counted. The total was estimated by taking the mean number of flowers per quadrat and multiplying this by the area of flower fall shadow. The daily floral production of hermaphrodite trees is not easily quantifiable since the flowers do not absciss immediately after anthesis. The total floral production was estimated by summing the estimation of the total of the number of flowers and fruit initials collected in the quadrats and the number of fruits on the tree counted by a tree climber.

Artificial hand-pollination of hermaphrodite flowers was done. Young inflorescences were isolated using nylon bags and the hermaphrodite flowers with mature stamens were self-pollinated by prying out some of their indehiscent anthers with a pair of forceps, squeezing them softly between two glass slides and applying the anther material over the stigmatic surface. Several young inflorescences prior to anthesis were isolated with nylon bags and left unmanipulated as control. The bags were removed after all the flowers in control had passed anthesis. The number of fruits set was scored.

Extensive collection of flower visitors was made, as far as possible, for several trees spread through the forest. The visitors were caught using hand nets. The Hymenopterans were stored in 90% alcohol while the Lepidopterans were kept in silica gel.

The activity pattern and frequency of visitors to the tree was determined by dividing the flowering crown between an assistant and myself and counting, at suitable intervals ($\frac{1}{4}$, $\frac{1}{2}$, 1 h), all the visible visitors among the flowers for the diurnal foraging period. The visitors were captured randomly at peak activity periods using hand nets. This resulted in capture of most of the visible visitors above the crown. These collections were made from three male and two hermaphrodite trees to determine the frequency of individual visitors.

The foraging behaviour of the visitors was examined closely for feeding

characteristics, damage to flowers, flight and search patterns, between-flower movements and interactions among visitors.

A mark-release-recapture experiment was performed on the danaid butterfly visitors to a male tree. The butterflies were captured with hand nets, and numbers were written with a marker pen underneath both their forewings before release. On four succeeding days, their returns to the tree was observed during peak foraging times.

Owing to the nature of visitation to *Xerospermum* flowers, it was essential to identify the legitimate pollen vectors from among the large spectrum of visitors so that observations could be narrowed to them. The presence of *Xerospermum* pollen on the visitor's body often reveals its pollinatory role. A method was developed of examining the pollen carried by the visitors to make this possible. In it, a small piece (8 mm³) of glycerine jelly tinged with basic fuchsin is cut out with forceps and brushed onto the appropriate part of the killed insect's body several times until most of the pollen is removed. The jelly with pollen is placed on a glass slide, a cover slip applied and warmed over a flame. A second slide is similarly prepared of the pollen from the same part of the insect's body to ensure most of the pollen is removed. The slide is examined for pollen under a microscope with a 10×40 magnification, allowing a quick appraisal of the pollen carried by the vector. Later, the number of pollen grains is counted to estimate the pollen load.

RESULTS

The tree

Xerospermum intermedium is dimorphic, the population consisting of separate male and hermaphrodite trees. The trees can reach a height of about 20 m. The flowers of both sexes are small (hermaphrodite flowers: 3.3–3.6×3.3–3.8 mm; male flowers: 4.6–5.0×2.4–2.6 mm), similar in appearance, cup-shaped and greenish (Fig. 3). The hermaphrodite flower differs from the male flower in having two large ovary lobes flanking the central style, all arising from the base of the flower (Fig. 3). The style rises above the ovary lobes presenting a large, papillate, shiny, stigmatic surface. Both sexes have eight stamens, arranged in four opposite and equal pairs. The anthers of the tallest pair of stamens are adpressed against the sides of the stigmatal surface in the hermaphrodite flower.

Floral biology

Anthesis of male flowers commences in the morning, *c.* 07.00 hours, with the parting of the sepals and petals, and exposure of the anthers. Anther dehiscence is staggered temporally, throughout the morning from about 07.00 to 11.00 hours; the anthers dehiscing progressively in sequence from longest to shortest pairs of stamens.

The apparently indehiscent anthers of hermaphrodite flowers were found to release their pollen to allow self-pollination (see later). So they truly are hermaphrodite. The hermaphrodite flower's functional life lasts for three days. Its anthesis is initiated with the sepals parting by upward protrusion of the style, exposing a shiny and turgid stigma. Onset of anthesis begins mostly after 07.00 hours, with a few late buds even after noon. On the second functional day, the style protrudes out even further. The stigma remains shiny and turgid and apparently receptive. On the third day, the stigma turns soft and brown by late afternoon.
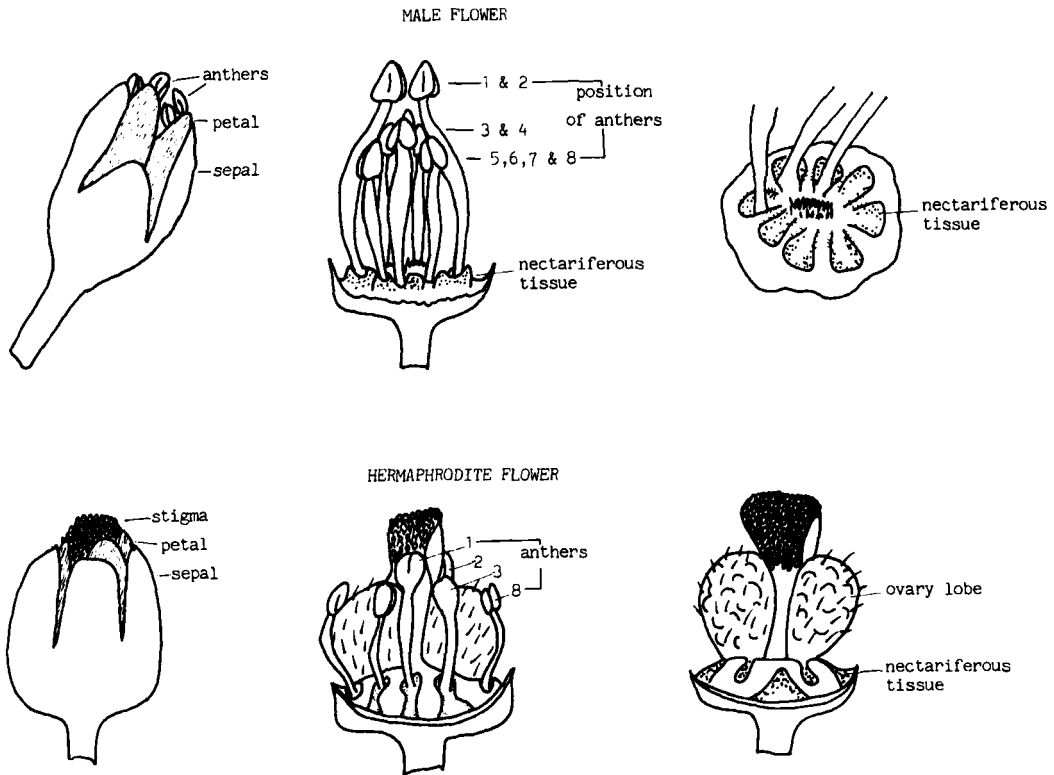
MALE FLOWER

HERMAPHRODITE FLOWER

Figure 3. Male and hermaphrodite flowers of *X. intermedium*.

The anthers of the hermaphrodite flower do not dehisce. There is no stomium (slit of dehiscing anther) and the interlocular connective tissue remains undissociated even when the pollen grains mature (Ha, 1978). However controls, with bagged inflorescences to exclude all visitors, showed fruit set (Table 1). Artificially self-pollinated flowers also set fruit (Table 1). It is known that the species has normal embryogenesis (Ha, 1978), ruling out apomictic fruit set and suggesting self-pollination. The anthers of the longest pair of opposing stamens are in direct contact with the stigmatal surface. These indehiscent anthers have a full complement of well developed pollen grains, morphologically indistinguishable from those of the male, that stain in acetocarmine demonstrating their viability. The germinability of pollen in Dyer's pollen mitosis solution with 10% sucrose stock solution was poor in contrast with pollen from male flowers (Appanah, 1979b). Close examination of the anthers showed that, in some of the anthers of the second day and more noticeably third day flowers, the walls break down and a sludge of anther material is left on the stigma. Examination of the surface of the anther walls revealed that some pollen grains ease out of the anther sac on to the stigmatic surface.

Nectar production pattern

In *X. intermedium*, nectar is secreted at the base of the flower by shiny nectariferous tissue borne on the receptacle. In the male trees, the nectar flows in a bimodal pattern with two peak activity periods (Fig. 4A). The first surge in nectar

Table 1. Tests for self-compatibility of *X. intermedium*

| Treatment	Bag number	Tree no. 4515		Tree no. 854	
		28.11.1976 Flowers	2.2.1977 Fruits	11.12.1976 Flowers	3.2.1977 Fruits
Control exclusion bagging	1	22	—	22	3
	2	31	2	34	3
	3	19	—	17	4
	4	17	2	21	2
	5	28	3	26	3
	6	16	3		
	Total	133	10	120	15
	% Fruit set		7.5		12.5
Artificial self-pollination	1	6	2	6	2
	2	4	2	7	2
	3	5	3	6	3
	4	4	3	1	3
	5	4	2		
	Total	23	12	26	10
	% Fruit set		52.2		38.4
Open pollination	A	37	7	33	6
	B	—	—	42	4
	Total	37	7	75	10
	% Fruit set		18.9		13.3
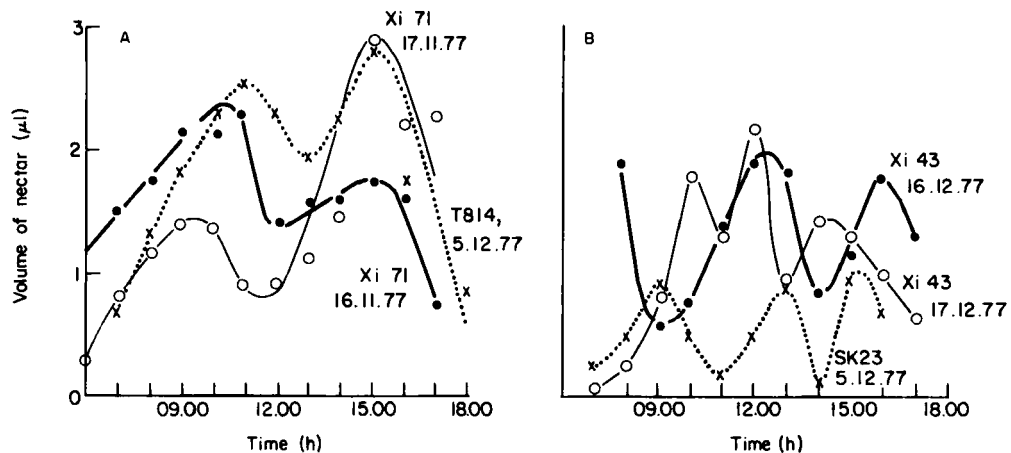
Figure 4. Nectar production of (A) male trees and (B) hermaphrodite trees.

flow reaches its peak at around 09.00–10.00 hours. There is then a decline until noon when it starts flowing again, attaining a second peak at *c.* 15.00 hours before a subsequent decline. The flower remains functional for only one day and usually drops off early the next morning. Nectar production studies on successive days on the same individual revealed constancy in the rhythm. There is also some synchrony in the nectar pulses between individual male trees. The nectar builds up in volume within the bagged flower and, during the non-secretion phase, the volume of the residual nectar actually declines. The average volume of nectar produced by male flowers is 3.5 μl/flower/day ($R=2.6$–4.7 μl).

The functional life of the hermaphrodite flower is three days, during all of which nectar is secreted. Only a small amount of nectar is produced on the first and third functional day. As the second day is the major period of nectar production, systematic monitoring of nectar flow rates were consequently restricted to flowers on their second day of anthesis.

The nectar flow pattern in hermaphrodite trees is loosely trimodal, with three peaks of activity (Fig. 4B). The first surge of nectar flow occurred at around 06.00–09.00 hours, the second around 11.00–13.00 hours, and the final at around 15.00–16.00 hours. The rhythm of nectar flow in three pulses staggered over the day is not, however, clearly distinguishable in all the trees. The average volume of nectar secreted by the hermaphrodite flower is 3.7 μl/second functional day flower/day ($R = 2.4$–5.8 μl).

Comparing the nectar flow pattern of male and hermaphrodite trees, it becomes apparent that the nectar flow pulses alternate between the two sexes of trees, a peak activity period of one sex approximately coinciding with the period of decline of activity in the opposite sex.

Nectar composition

The nectars of *X. intermedium* contain all three sugars: sucrose, glucose and fructose (Table 2A). The proportions of sucrose and the hexoses (glucose and fructose) differ radically between the nectars of male and hermaphrodite flowers. The hexoses are dominant in the male nectars, $s/(g+f) = 0.395$–0.523. Sucrose predominated in the nectars of hermaphrodite flowers, $s(g+f) = 1.13$–1.15.

Analysis of *X. intermedium* nectars show low ninhydrin scores for nectars of male flowers (*c.* 49 nmols/ml) while the hermaphrodite's nectars are more concentrated (*c.* 290–585 nmols/ml) (Table 2B), being 5–12 times more concentrated in amino acids than the male's nectars. The amino acid complements consist of a range of 14 amino acids (alanine, arginine, aspartic acid, glutamic acid, glutamine, glycine, isoleucine, leucine, phenylalanine, proline, serine, threonine, tyrosine, valine),

Table 2A. The proportions of sugars in nectars of *X. intermedium*

Sample number	Sex of flower	Sugars present	Proportion (by weight)	Ratio. $\dfrac{s}{g+f}$
1	male	sucrose(s)	0.283	
		glucose(g)	0.466	0.395
		fructose(f)	0.250	
2	male	s	0.329	
		g	0.440	0.490
		f	0.230	
3	male	s	0.339	
		g	0.479	0.523
		f	0.182	
4	hermaphrodite	s	0.534	
		g	0.305	1.146
		f	0.161	
5	hermaphrodite	s	0.530	
		g	0.347	1.127
		f	0.123	

Table 2B. Spot tests on nectars of *X. intermedium*

Test	Presence of	Samples of male nectars			Samples of hermaphrodite nectars	
		1	2	3	1	2
Ninhydrin score	Amino acid concentration	1(*c*. 49 nmols/ml)	1	1	3–4(*c*. 290 nmols/ml)	4–5(*c*. 585 nmols/ml)
Osmic acid	lipids	nil	nil	nil	nil	nil
p-nitraniline	phenolics	some phenolics	+	+	+	+
Dragendorff	alkaloids	+	+	+	not tested	+
Brom-phenol	protein	trace	not tested	not tested	trace	not tested

qualitatively similar for both sexes. Traces of proteins along with phenolics and alkaloids were detected; this may also be attributable to tissue damage during collection.

Phenology of flowering

Xerospermum intermedium flowers annually. The onset of flowering occurred in various months from July to November, and ended between December to March (Table 3). The length of the flowering season varied annually, from two and a half months in the 1977/78 flowering season to seven months in the 1975/76 flowering season.

The annual intensity of flowering, expressed by the number of individuals coming to flower every season from 1974/75 to 1977/78 is not constant each season (Table 3). There appears to be a rhythmic fluctuation in the intensity of flowering: an intensely strong flowering year in 1974/75, when 66.1% of the 112 tagged individuals (exceeding 30 cm gbh) within the study plots flowered was followed by progressively poorer flowering seasons in 1975/76 and 1976/77. The poorest season of 1976/77 was succeeded by another intense flowering season in 1977/78 when 60.0% of all the individuals flowered. The intensity of flowering appears to be broadly inversely related to the length of the flowering season. The mass flowering seasons of 1974/75 and 1977/78 were short, of four and two and a half months respectively, whereas the poor flowering seasons of 1975/76 and 1976/77 were extended, lasting between six to seven months (Table 3).

The duration of flowering of individual trees for the 1976/77 and 1977/78 flowering seasons is shown in Fig. 6. For both seasons, the male trees flowered for a longer period, from 2–18 weeks ($\bar{X}=5.3$) while the hermaphrodites flowered for one to eight weeks ($\bar{X}=3.5$). There thus appears a difference in the length of flowering between the sexes for both the seasons, the males flowering for a longer duration, indicating a consistent inherent difference in the flowering durations between the sexes.

The flowering is somewhat asynchronous (Fig. 7A, B). There were gaps of 12 weeks and five weeks between the first and last tree starting to bloom during the 1976/77 and 1977/78 flowering seasons respectively. A broad overlap of flowering among the individuals occurred, with a peak in overlap mid-season.

There is no significant difference in the sex ratio of the 112 trees within the study plots; 53 (47.3%) are males, 46 (41.1%) hermaphrodites, and 13 (11.6%) unknown (Fig. 2). The ratio of male:hermaphrodite trees coming into flower varies annually but there is a predominance in the number of males over

Table 3. The annual flowering pattern of *X. intermedium*

Year	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Flowering duration (months)	No. of trees flowering	"₀ of trees flowering	Male	Hermaphrodite	Sex ratio ♂ : ♀
1973/74*			Observations incomplete												
1974/75*										4	74	66.1	46	28	1.70 : 1
1975/76*										7	37	33.0	22	15	1.46 : 1
1976/77										7	23	20.5	16	7	2.25 : 1
1977/78										2½	67	59.8	32	36	0.91 : 1

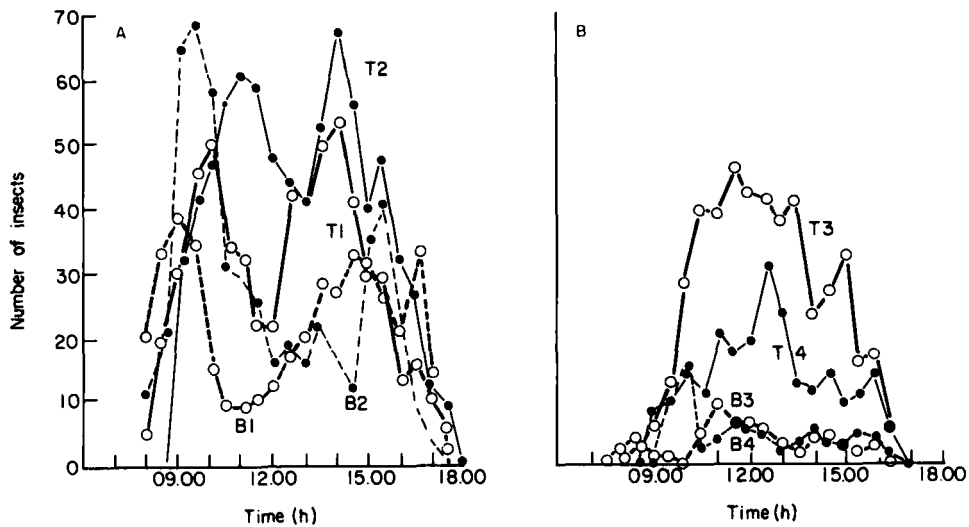* The data for 1974/75 and 1975/76 flowering is from Yap (1976).

Figure 5. The diurnal activity rate of insects visiting (A) male trees and (B) hermaphrodite trees. (T = trigonids, B = butterflies; T1B1 = ♂ tree 730, Date 20-12-1977; T2B2 = ♂ tree 730, Date 24-12-1977; T3B3 = ♂ tree Xi 43, Date 16-12-1977; T4B4 = ♂ tree SK 23, Date 30-12-1977.)
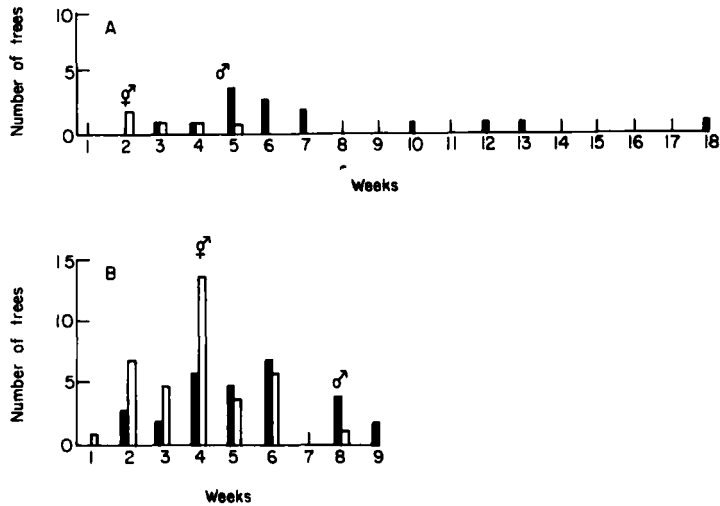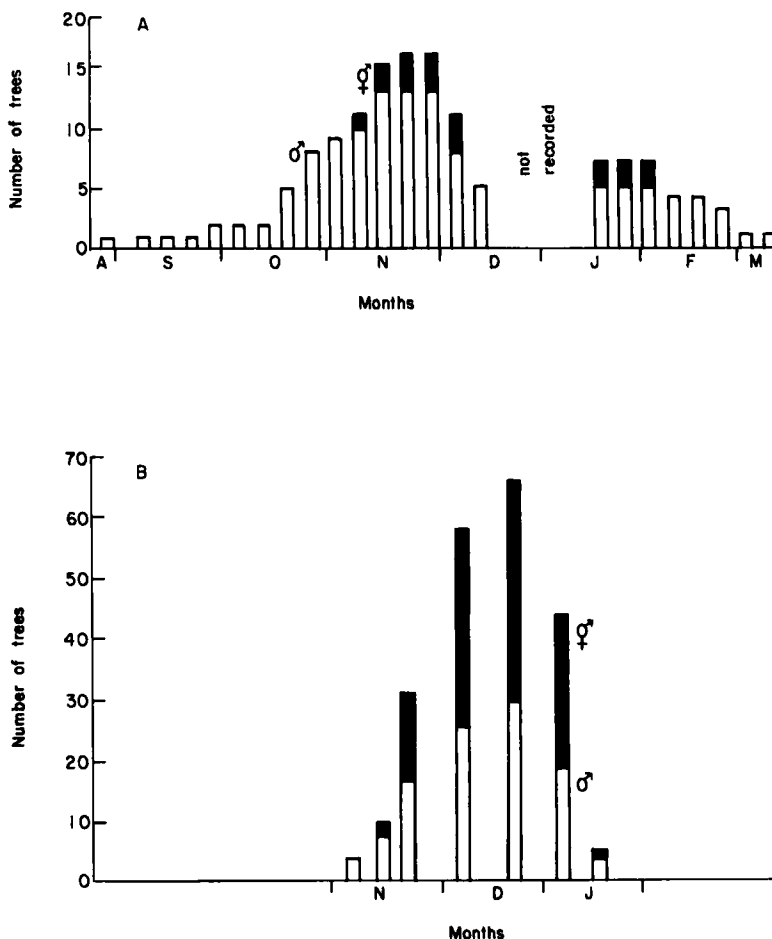
Figure 6. The length (weeks) of flowering of individual male and hermaphrodite trees during the (A) 1976/77 and (B) 1977/78 flowering seasons.

hermaphrodites (Table 3). The data for the four flowering seasons show, excepting for the 1977/78 season when the ratio is almost equal, that a greater number of males flower within the population than hermaphrodites; the difference was at its greatest in the 1976/77 flowering season when the ratio was 2.25 males to a single hermaphrodite. The sex ratio computed for a given time, for the flowering seasons of 1976/77 and 1977/78 (Figs 7A, B) show a general predominance of male trees flowering during the season, they being the first to start flowering and the last to end flowering.

Figure 7. The number of male and hermaphrodite *X. intermedium* trees flowering during the (A) 1976/77 and (B) 1977/78 flowering seasons.

The daily floral production of three male trees was estimated (Fig. 8). Two of the trees (Trees No. 730 and Xi 42) exhibited a common pattern of gradually building up the number of flowers presented per day up to a peak and then declining, the flowering lasting for approximately four weeks. The third tree Xi 41 differed by producing a lower number of flowers per day, maintaining its floral production at about a constant level, without reaching a peak. The estimated floral production of the three male trees was between 282 000–735 000 flowers ($\bar{X} = 496\,000$) over a period of about a month. A hermaphrodite tree (SK 23) produced an estimated total of 88 000 flowers over a period of 40 days, giving an average of 2200 flowers per day. Only trees over 70 cm gbh were sampled for flower production, smaller trees often produced fewer flowers.

The pollinators

The identity and frequency of visitors

Flower visitors in *X. intermedium* are diverse, composed of a wide array of Hymenoptera and Lepidoptera along with lesser numbers of Coleoptera, Diptera,
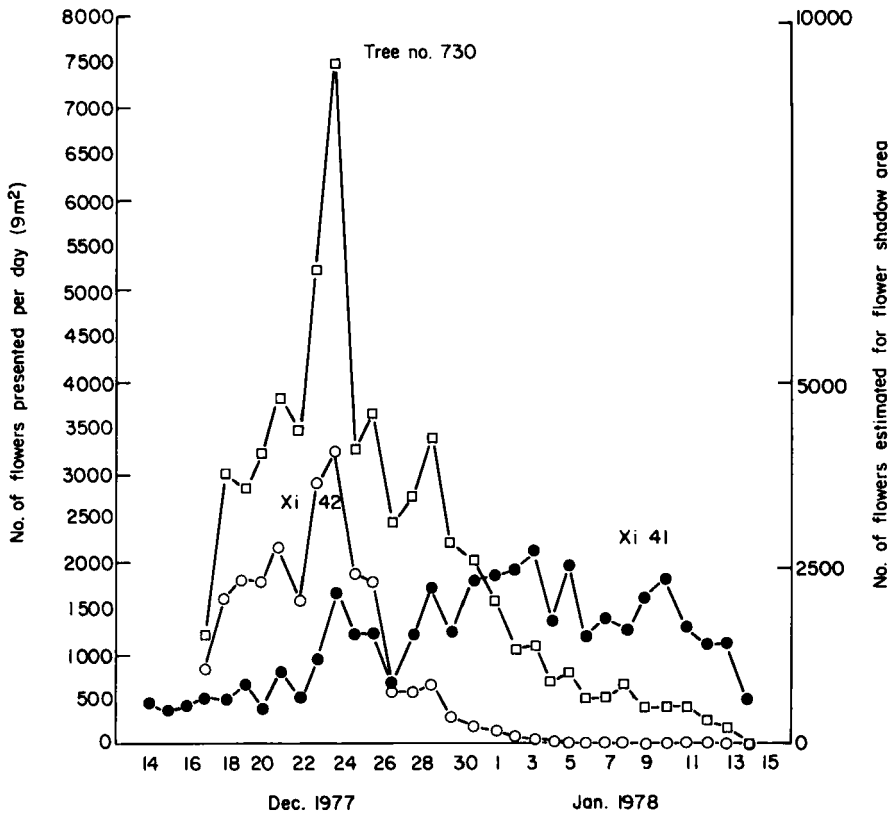
Figure 8. The daily floral production of male *X. intermedium* trees.

Thysanoptera, Orthoptera and Hemiptera (Table 4). The commonest visitors were Meliponid bees of the genus *Trigona; T. moorei* Schwarz and *T. fuscobalteata* Cameron were the most abundant species on both sexes of trees. The composition of these visitors was similar in both sexes of trees. *Apis* species, *Nomia* species and *Xylocopa aestuans* Lepel were only sighted on male trees. The wasp visitors to both the sexes were generally similar.

There was as great a diversity of butterflies as Hymenoptera. The butterfly visitors to the two sexes differed (Table 4). Only seven out of 21 species were common to both the sexes; relatively fewer visited the hermaphrodite in comparison to the male trees. Qualitatively, there is a preponderance of the Danaidae, especially *Euploea* species, visiting the male trees, butterflies being generally uncommon on hermaphrodite trees (see later). The Coleoptera, Diptera and Thysanoptera along with unidentified Orthoptera and Hemiptera were rare.

The male trees received an average of 32.2 butterfly and 34.4 trigonid visitors per count (the average of the number of visitors counted on the tree at $\frac{1}{2}$ h intervals for the diurnal period), these two groups of visitors together constituting 94.1% of all the visitors thus establishing them as the predominant visitors. The hermaphrodite trees received from 2.6 to 3.6 butterfly and 14.1 and 25.1 trigonid visitors per count. Hence, the hermaphrodite trees received not only fewer visitors per count compared with the male trees, but there were also disproportionately fewer butterfly to trigonid visitors. However, these two groups still formed the

Table 4. Identity of insect visitors and their frequency on *X. intermedium* trees

Identity	Male trees*	Hermaphrodite trees
Apidae		
Trigona apicalis Smith	A	—
T. atripes Smith	—	U
T. canifrons Smith	U	C
T. erythrogastra Cameron	U	R
T. fuscobalteata Cameron	A	A
T. geissleri Cockerell	C	C
T. itama Cockerell	A	—
T. moorei Schwarz	A	A
T. nitidiventris (Friese)?	C	C
T. pallidistigma Cockerell	—	U
T. pendleburyi Schwarz	—	U
T. scintillans Cockerell	C	—
T. thoracica Smith	U	C
Trigona sp.	U	—
Apis dorsata Fabr.	R	—
A. florea Fabr.	U	—
A. indica Fabr.	U	—
Anthophoridae		
Xylocopa aestuans Lepel.	R	—
Nomia sp.	R	—
Vespidae		
Stenogaster sp.	U	U
Polistes sp.	U	U
(7 other spp. have not been identified)		
Danaidae		
Euploea algea menestriesii C & R Felder	U	—
E. camaralzeman malayica Butler	U	R
E. diocletianus diocletianus Fabricus	A	—
E. doubledayi evalida Swinhoe	U	—
E. eyndhovii gardineri Fruhstorfer	A	—
E. mulciber mulciber Cramer	A	R
E. tulliolus lederi C & R Felder	U	—
Danaus aspasia aspasia Fabricus	U	—
D. vulgaris macrina Fruhstorfer	C	R
Idea hypermnestra linteata Butler	C	R
I. jasonia logoni Moore	R	—
I. lynceus lynceus Drury	R	—
Nymphalidae		
Euthalia kanda marana Corbet	R	—
Lasippa helidore dorelia Butler	—	C
L. tiga siaka Moore	R	C
Lebadea martha malayana Fruhstorfer	R	—
Terinos terpander Robertsia	R	—
Hesperidae		
Plastingia latoia latoia Hewitson	R	—
P. helena natuna Fruhstorfer	R	—
Lycaenidae		
Jamides elpis pseudelpis Butler	R	—
Nacaduba pavana Singapura Corbet	—	U
Coleoptera		
Dasyvalgus sp.	+	+
Unidentified sp.	+	—
Diptera, Syrphidae	+	+
Thysanoptera		
Thrips sp.	+	+
Hemiptera		
Unidentified early instar	+	—
Orthoptera		
2 unidentified spp.	+	—

* Key:—A—abundant; C—common; U—uncommon; R—rare; ——absent; +—present.

majority of the visitors to the hermaphrodite trees as in male trees. The frequency of wasp visitors remained low in both the sexes.

Diurnal activity cycle of insect visitors

The visitors exhibited a diurnal foraging pattern. The first visits to the trees occurred from about 08.00 hours onwards; visits ceased completely after 18.00 hours (Fig. 5). The pattern of insect visits to male trees was bimodal, with two marked peak periods of activity: in the morning $c.$ 09.00–10.00 hours and in the afternoon $c.$ 14.00–15.00 hours; these two peaks were separated by a period of low activity around 12.00–13.00 hours (Fig. 5A). The uncommon *Apis* species and wasps did not reveal any rhythm in their activity, appearing at low numbers for most of the anthesis period of the male flowers.

In the hermaphrodite trees, the insects were active for a similar overall diurnal period as in male trees (Fig. 5B). The predominant activity pattern observed was of insects gradually increasing in numbers from early morning, reaching peak numbers between 11.00–12.00 hours, fluctuating at this level for between 13.00–15.00 hours, and declining slowly thereafter (Fig. 5B). This pattern is exhibited in both trees Xi 43 and SK 23 monitored on separate days. The pattern of peak insect activity around mid-day in hermaphrodites broadly coincides with the low insect activity period in the male trees nearby.

The activity pattern in hermaphrodite trees differed from that in male trees in that the peak activity patterns were essentially contributed by trigonid bees alone. The butterflies and wasps did not reveal such patterns of activity and occurred in low numbers at all times.

Foraging of trigonids and butterflies

The bees observed alighted on the flowers in anthesis, or on the compact inflorescence with flowers in anthesis only. They therefore seemed to be capable of distinguishing the flowers in anthesis from the buds and those past anthesis (both male and hermaphrodite flowers) from a distance, for they orientated in the direction of the open flower from as far as 2 m away and were never sighted approaching and alighting on pre- or post-anthesis flowers.

The landing position of the bee on the flower varies with the bee's size. The smaller species like *T. geissleri* Cockerell alight on top of the flowers, most of the ventral body surface contacting the mouth of the flower; whereas the larger species like *T. canifrons* Smith land on the side of the flower if it is isolated, and essentially only its mouthparts, forelegs and the ventral region of the anterior thorax contact the mouth of the flower. When the flowers are in a cluster, the larger bees land on the compact inflorescence and feed on the open flowers while the rest of their body regions are in contact with the other flowers within the inflorescence.

The emphasis seems to be on nectar gathering; the bees separate the petals with their forelegs and mandibles and suck up the nectar. They are never sighted selectively foraging for pollen alone. While the bees are foraging for nectar in male flowers, pollen adheres on to the body parts. At intervals, the bees halt their feeding and start combing their body of pollen with their legs, packing the pollen into a small grey-white pellet in the corbiculae.

On the hermaphrodite flowers the bees forage only for nectar. The anthers of these flowers do not dehisce and the bees did not break them. The bees either alight on top of the open flower, or on its side as they do in male flowers; their

mouthparts, legs and most of the thorax and to a lesser extent the abdomen come into close contact with the broad surface area of the stigma, enabling the transfer of pollen from their body to the papillate stigma surface.

The butterflies are avid visitors to the flowers, feeding assiduously on them. The danaids appear to recognise the inflorescence visually, and initiate directional flights to them from at least 4 m away. Unlike the trigonids, which seemed capable of distinguishing flowers in anthesis from the rest and orientated directly towards these rewarding flowers, the danaids gave no indication of differentiating the different stages of the flowers. They approach the inflorescence and hover over them before landing exclusively near flowers in anthesis and feeding from them alone, indicating that they have the ability to differentiate the rewarding flowers from the rest only when in close proximity.

Upon landing on the inflorescence, the butterfly inserts its proboscis repeatedly into the base of the flower and sucks up the nectar. From one landing on the inflorescence, it was seen to feed on three or four flowers, without moving its position, by extending its proboscis and exploring into the flowers for the nectar. It would crawl amongst the inflorescence to reach flowers further off. Alternatively, it would also take short flights, enabling it to orientate itself in a different position on the inflorescence before resuming feeding. While feeding, its proboscis, thorax, abdomen and legs came into extensive contact with the surface of the flowers.

Flight paths of butterflies

Observing the movements of butterflies between a male and a hermaphrodite tree, separated by about 10 m at the base, showed low frequency of movements, mainly of danaids, from the male to hermaphrodite tree, this being slightly more frequent around noon. They only remained at the hermaphrodite tree for brief intervals, making quick forays to a few flowers and then moving off, flying around the vicinity and occasionally visiting the flowers again or even returning to the male tree.

In one case an *Idea* species was observed to visit a hermaphrodite tree after feeding on a male tree more than 100 m away. The visit lasted for approximately seven minutes during which it visited a few flowers and explored around the tree before leaving.

A mark-release-recapture experiment on butterflies

A mark-release-recapture experiment on the commonest species of butterflies visiting a male tree was performed. The rate of return to the tree was low and dropped rapidly in successive days. Of the 59 marked butterflies, seven were sighted on the second observation day, two on the third day and three on the fourth day. Among the butterflies, the *Idea* species show a high percentage of return suggesting they have relatively high fidelity to the resource site. An individual *E. mulciber* (marked no. 10) was remarkable in that it returned to the tree for up to four days after being marked.

Body pollen of visitors

The size of the pollen loads, their variety, and their distribution over the bodies of the visitors was examined (Tables 5 A–D and Fig. 9). The sizes of the pollen loads of trigonid bees visiting male trees varied greatly and up to 32 000 pollen grains of a single species were carried by a bee (Table 5A). The pollen carrying
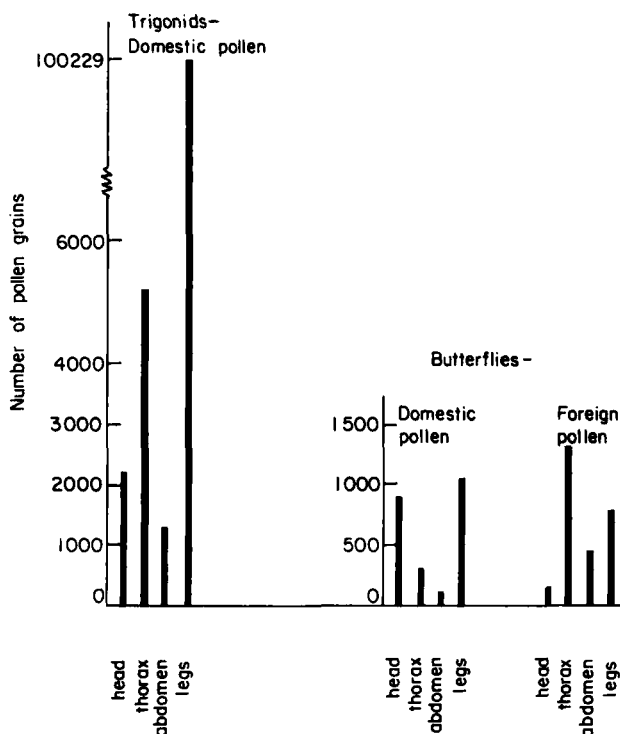
Figure 9. Distribution of body pollen of visitors to male *X. intermedium* trees.

capacity of the different species seems to be dependent on the bee's size, the larger species such as *T. thoracica* and *T. erythrogastra* generally having bigger pollen loads; at the other extreme is the small bee, *T. fuscobalteata* which as a rule is almost barren of body pollen. The mean pollen load of the 30 bees examined was approximately 3600 pollen grains per insect.

The distribution of pollen on the body of the bee (Fig. 9) shows some pollen adhered to the head; the abdomen has the least amount on it; a large part is distributed on the thorax but the majority of the pollen is found on the legs. The corbicular loads were found to have 4800–31 200 grains compacted together in the pellet. A tiny trace of foreign pollen, derived from nine plant species was present on trigonid bees visiting male trees. The ratio of domestic to foreign pollen was 2870 : 1 (Table 5A).

The pollen loads of butterflies visiting male trees differed from the trigonid bees (Table 5B). The butterflies' pollen loads were much smaller; the largest number on an individual was 763 grains ($\bar{X} = 110$ grains). Among the butterflies, *Idea* species carried bigger pollen loads then *Euploea* species.

The distribution of domestic pollen on the bodies of the butterflies differed from that on trigonids. In the butterflies, most of the pollen is concentrated on the legs and the head region, including the proboscis, with minute amounts on the thorax and scarcely any on the abdomen (Fig. 9).

A significant feature of the pollen loads of butterflies visiting male *X. intermedium* trees was the presence of large amounts of foreign pollen, constituting more than seven foreign species, and making up 51.4% of the total pollen load on the

Table 5A. Pollen loads of trigonid visitors to male *X. intermedium* trees

Species	No. of bees sampled	No. of domestic pollen grains	Total	Mean	No. and type of foreign pollen	Total	Mean
T. thoracica	3	11 150, 1215, 302	12 667	4222	15L, 2A	17	
T. moorei	5	2052, 3, 1683, 9, 54	3801	760	9H, 1I, 1K, 3A	14	
T. apicalis	6	10 604, 631, 215, 15 446, 316, 17 420	44 632	7438	1J	1	
T. itama	5	10, 431, 217, 1, 355	1014	202	1A, 5B	6	
T. canifrons	4	6318, 5120, 1421, 111	12 970	3242	—	—	
T. scintillans	1	395	395	395	—	—	
T. nitidiventris	1	5	5	5	—	—	
T. erythrogastra	3	31 766, 1570, 79	33 415	11 138	—	—	
T. fuscobalteata	2	147, 23	170	85	—	—	
Total*	30		109 069	3636		38	1.27

* Ratio of domestic to foreign pollen is 109 069 : 38 = 2870 : 1

Table 5B. Pollen loads of butterfly visitors to male *X. intermedium* trees

Species	No. of butterflies sampled	No. of domestic pollen grains	Total	Mean	No. and type of foreign pollen	Total	Mean
E. eyndhovii	8	48, 56, 52, 7, 116, 93, 90, 24	486		80A, 6B, 1E, 19?	106	
E. diocletianus	4	30, 79, 22, 26	157		1165A, 1B, 15?	1181	
E. mulciber	3	36, 13, 53	102		1003A, 51B, 1C, 3D	1058	
E. tulliolus	3	92, 19, 46	157		100A, 40M, 3X	143	
I. hypermnestra	3	763, 557, 80	1400		153A	153	
Total*	21		2302	109.6		2641	125.7

* Ratio of domestic to foreign pollen is 2302 : 2641 = 1 : 1.15

Table 5C. Pollen loads of trigonid visitors to hermaphrodite *X. intermedium* trees

Species	No. of bees sampled	No. of *X. intermedium* pollen grains	No. and type of foreign pollen grains
Trigona canifrons	3	76; 0; 0	824G, 113I; 0; 13G
T. thoracica	6	23; 2; 0; 0; 0; 0	2M, 1N; 0; 1M; 0; 1A, 3M; 0
T. erythrogastra	3	0; 27; 0	0; 0; 0
T. atripes	7	0; 0; 0; 0; 0; 0; 0	3P; 27G; 0; 0; 0; 0; 0
T. geissllerri	6	0; 0; 0; 0; 0; 0	0; 0; 0; 0; 0; 0
T. moorei	4	6; 0; 0; 0	0; 0; 0; 0
T. nitidiventris	1	0	0
T. pallidistigma	1	0	0
T. pendleburyi	1	0	0
T. fuscobalteata	12	0; 0; 0; 0; 0; 0 0; 0; 0; 0; 0; 0	609G, 3H; 15H; 0; 0; 0; 0; 15H; 0; 8L, 10Q; 0; 0; 0
Total	44	134	1648
Mean		2.85	35.06
Ratio		1	12.3

Table 5D. Pollen loads of butterflies visiting hermaphrodite *X. intermedium* trees

Species	No. of butterflies sampled	No. of *X. intermedium* pollen grains	No. of foreign pollen grains
Idea hypermnestra	2	1501; 1488	3; 29
Euploea mulciber	1	23	2
E. vulgaris	1	3	0
E. diocletianus	1	27	9
Lasippa helidore	1	0	0
L. tiga siaka	3	1; 0; 0	6; 0; 8
Unidentified sp.	1	0	5
Total	10	3043	62
Mean		304.3	6.2
Ratio		49	1

butterflies sampled (Table 5B). Pollen of unidentified species A proved to be the predominant pollen species, even exceeding slightly the total domestic pollen load. The rest of the pollen species occurred only in scarce amounts.

Moreover, the distribution of foreign pollen on the bodies of the butterflies differed radically from the distribution pattern of *X. intermedium* pollen (Fig. 9). The thorax was the site for most of the foreign pollen, especially of species A, in contrast to the greater presence of domestic pollen on the legs and proboscis.

Examination of wasps and beetles captured on male trees showed the majority of them to have *X. intermedium* pollen in very low amounts.

In an examination of 47 trigonid bees, consisting of 10 species, visiting hermaphrodite trees (Sk 23 and Xi 43), only five (11%) had *X. intermedium* pollen on their bodies, indicating that they had foraged on a male tree prior to being captured on the hermaphrodite tree (Table 5C). Only two bees had pure *X. intermedium* pollen loads, the rest of the bees carrying pollen contaminated with foreign pollen to varying degrees. The bees carrying *X. intermedium* pollen were *T. thoracica*, *T. canifrons*, *T. erythrogastra* and *T. moorei*. The mean *X. intermedium* pollen load per bee was very low, three grains per bee only, though the size of the load

ranged up to 76 grains. Out of 47 bees examined, 11 carried foreign pollen comprising nine different plant species; the ratio of *X. intermedium* to foreign pollen was 1 : 12.3. Pollen of unidentified plant species G, constituting the major species of foreign pollen, was found on four bees. Foreign pollen grains of species A and M, found on three bees, were also common to bees visiting male tree no. 730.

Of the small sample of butterfly visitors to hermaphrodite trees examined for body pollen (Table 5D), only the *Idea* species had high *X. intermedium* pollen loads, suggesting that they arrived after foraging on the male tree. The *Euploea* and *Danaus* species showed the presence of low amounts of *X. intermedium* pollen on their bodies. The presence of only a low level of foreign pollen, the ratio of *X. intermedium* to foreign pollen being 49 : 1, distinctly differs from the pollen loads of butterfly visitors to male trees which have high foreign pollen contamination.

Of the wasp visitors to hermaphrodite trees examined for body pollen, some were positively carrying *X. intermedium* pollen. Foreign pollen was found on the bodies of wasps visiting hermaphrodite trees just as on male trees. All carried very small loads.

DISCUSSION

Despite the failure of the anthers of the hermaphrodite flowers to dehisce, control bagging and selfing experiments showed fruit set suggesting, in the presence of normal embryogenesis, the species to be self-compatible. Hence, *X. intermedium* is truly androdioecious. The sex ratio of the total sampled population in this species, which is close to unity, conforms to Fisher's (1930) theoretical argument for such a ratio in a random mating population. However, the male trees flower more frequently, and the sex ratio of male to hermaphrodite trees in flower each season generally leans towards males. A staminate dominant flowering ratio contrasts with Kaplan's (1972) and Lloyd's (1974) evidence that seed set is maximized when the proportion of pistillate plants equals or exceeds staminate plants. This deviation may be due to the constraints imposed by the physical barriers of the understorey on inter-tree pollen transfer. That the understorey of the primary forest may impede pollinator movement seems so from the paucity of large pollinator fauna within the understorey, most of them foraging above the canopy (Appanah, 1979a). Hence, a greater number of flowering males can in these circumstances increase the chances of pollen transfer to the hermaphrodite tree. Furthermore the male trees produced a greater quantity of flowers (almost six times that estimated for hermaphrodite trees), they were consistently the first to bloom, flowered for the longest duration and were the last trees to terminate flowering. Such a flowering pattern would ensure the continuous availability of pollen and maximize the chances of pollen transmittal to the hermaphrodite trees. Again, the functional life of the hermaphrodite flower, extended for three days, increases its opportunity for receiving pollen. In conclusion, the flowering pattern described seems well adapted to promote pollen transfer from male to hermaphrodite trees.

The main floral reward for the principal flower visitors appeared to be nectar. The nectar flowed in pulses, roughly alternating between the two sexes, a peak secretion period of one sex coinciding approximately with the period of decline of the opposite sex. The activity pattern of the insect visitors to the two sexes of trees echoed rather closely this rhythm of nectar pulses. In the male trees, insect activity

was bimodal, with the two peaks occurring in the morning and afternoon, coinciding with the periods of nectar flow. In the hermaphrodite trees, nectar flow appeared to be in three ill-defined pulses, but the insect activity seemed to peak once, at mid-day, this being the period of decline in activity of both nectar flow and insect activity in the male trees and the time of a rather consistent surge in secretion among hermaphrodite trees.

Hence, the provisioning of nectar, as a floral attractant, in rhythmic alternating pulses between the two sexes appears to provide the impetus for nectar foragers to shift between the trees, effecting pollen transfer. Bawa & Opler (1975) suggest that it may be by temporal variation of production of floral rewards between the two sexes of dioecious species in Costa Rica that inter-plant movement of pollinators may be effected. The situation in *X. intermedium* is somewhat comparable to that in the monoecious species, *Cupania guatemalensis* (Bawa, 1977), also Sapindaceae. In that species the visitors are thought to alternate between the male and female flowers apparently in response to spatial and temporal heterogeneity in the presentation of floral resources.

Another factor that may promote inter-tree movement of pollen vectors between the sexes is the qualitative difference in the consituents of the nectars. While *X. intermedium* nectars have a complement of 14 amino acids, qualitatively similar for both sexes, their concentrations differ. The nectars of hermaphrodite flowers were 5–12 times more concentrated than that of male flowers. This may be selectively advantageous in hermaphrodite flowers as they do not freely release pollen, a major source of amino acids for flower visitors even though the principal vectors actively collected little. More interesting is the disparity in the proportions of sugars between the nectars of the two sexes. The hexoses were dominant in the male flowers, and sucrose in the hermaphrodite flowers. Similar disparities in nectars of other dioecious species are known (Percival, 1961; Baker, pers. comm.). An interpretation of the biological significance sought for is elusive (see Wykes, 1952; Furgala, Gochnauer & Holdaway, 1958). However, it is not impossible that the differences in the nectars between the two sexes may promote inter-tree movement of pollinators.

An elaborate system thus appears to exist in *X. intermedium* which promotes inter-tree movement of the pollinators between the two sexes. Under the prevailing conditions, it was not possible to directly observe the inter-tree movement of such small insects as trigonid bees. However, the presence of conspecific pollen on the visitors to the hermaphrodite trees, whose anthers do not dehisce, provides proof that they have been foraging on male trees previously. Although the number of trigonid bees and butterflies were about equal on the male trees, the trigonid bees predominated among the visitors to hermaphrodite trees, suggesting their possibly greater role as pollinators. The conspecific pollen loads on the trigonid bee and butterfly visitors to the hermaphrodite trees differed however. The *Trigona* species had small, much more contaminated pollen loads while the danaids had bigger and purer conspecific pollen loads. This suggests individual butterflies are potentially capable of pollinating more hermaphrodite flowers than would individual bees. The rarity of butterfly visits to hermaphrodite trees nevertheless reduces their pollinatory role, and suggests that the principal pollinators are *Trigona* species. Only a few *Trigona* species, such as *T. thoracica*, *T. canifrons*, *T. erythrogastra* and *T. moorei* have been identified as pollinators based on the evidence of conspecific pollen on their bodies. Similarly, only a few species of butterflies, *Idea*

hypermnestra, *Euploea mulciber*, *E. diocletianus* and *Danaus vulgaris* visited hermaphrodite trees with conspecific pollen on their bodies. Most of the other *Trigona* species, butterflies, wasps and beetles may then be regarded as opportunists that merely exhaust the floral rewards without providing the benefit of pollination. However, this identification is based only on a small sample size and others may yet prove to be pollinators.

Among the principal *Trigona* visitors, what causes some species to be mere opportunists while others are acting as pollinators is unknown and can only be conjectured. A bee, while making short searching flights may discover one flowering *X. intermedium* tree. The pulsing nectar flow can induce the bee to leave the tree to seek other floral resources during a decline in nectar production. Out of numerous such movements by the bees, a few may result in discovery of *X. intermedium* trees of the opposite sex. The spatial distribution of the trees, which is usually clumped with the sexes randomly distributed, increases the chance that movements between trees of opposite sexes will occur. The extended flowering season also enhances the occurrence of such inter-tree movements. doubtless, numerous inter-tree movemtns by the bees are taking place, but most seemed to be interspecific opportunistic foraging visits as evidenced by the wide variety of foreign pollen ($>$ 20 species) found on the visitors. Only a few of the bees seemed to have made the appropriate inter-tree movements, providing a low level of outcrossing in the species.

Under the circumstances described, it is possible to envisage mainly short-range pollen transfer, principally by the bees and probably between trees growing in a clump, since these bees of the understorey are not known to undertake long-range horizontal dispersion. The few tropical studies on the dispersal ranges of the trigonid bees suggest that they are restricted (Bawa & Opler, 1975). However, nothing is known about how far a given *Trigona* moves laterally in the rain forest. Although recent studies reveal *T. erythrogastra* to forage up to 1100 m to some *Elaeis* palms outside the forest (Appanah, 1979b), it is not known whether they would do so over such distances within the understorey of the forest. Such circumscribed foraging suggested for *Trigona* species is known in *Apis* (Free, 1960, 1962) and is prevalent among bumblebees (Free, 1968).

Certain butterflies are suggested to be lesser yet significant pollinators of *X. intermedium* on the basis of their rarer visits to hermaphrodite trees, albeit with larger and purer conspecific pollen loads. However, examination of the pollen loads of *Trigona* and butterfly visitors to male trees indicated the latter to have greater levels of foreign pollen on their bodies contrary to the situation in hermaphrodite trees. The mark-release-recapture experiment suggests high mobility of a large number of butterflies with low constancy to the site, though a few of the marked individuals regularly returned to the tree for several successive days. On the whole, the butterflies seem generally to possess lower fidelity than trigonids, and appear to be mere opportunistic feeders. The butterflies' greater mobility and lower fidelity suggest such inter-tree 'traplining' (Janzen, 1971) may be only temporary.

In retrospect, movement of the pollen vectors between conspecific trees is low, probably due to the physical barriers impeding such movements within the understorey, this further exacerbated by the interspecific competition for the pollinator fauna by a large number of tree species. Such competition for pollinators must prove extemely detrimental to obligate outbreeders such as dioecious species.

Levin (1972) has speculated on the role competition for pollinators may have played in promoting autogamy. Self-compatibility in *X. intermedium* could have been selected for as a consequence of competition for pollinator services, in conjunction with the physical barriers impeding pollinator movement in the understorey. However, the failure of the anthers to dehisce normally suggests inhibition of self-pollination. The retention of partial self-compatibility in *X. intermedium* allows it to maintain high seed production in the face of difficulties in maintaining an obligate outbreeding system. Hence, androdioecism which has been assumed rare or absent (see Bawa, 1980) may be one of the explanations for the fairly common occurrence of *X. intermedium* in the understorey of a lowland dipterocarp forest.

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