# Chapter 1

**The pollination ecology of chiropterophilous canopy trees, *Parkia speciosa* Hassk. and *P. timoriana* (DC.) Merr. (Mimosaceae) in southern Thailand.**

S. Bumrungsri[1*], A. Harbit[2], C. Benzie[2], K. Carmouche[2], K. Sridith[1] & P. A. Racey[2]

[1]Biology Department, Prince of Songkla University, Hat-Yai, Thailand

[2]School of Biological Sciences, University of Aberdeen, Aberdeen U.K.

[*]Corresponding author.

Address for correspondence:

Biology Department, Prince of Songkla University, Hat-Yai, Songkhla. Thailand.

90112 Phone 66-74-288537      Fax 66-74-212917

E-mail:sara.b@psu.ac.th

**Running title : Pollination ecology of two species of *Parkia***

## Abstract

Although fruit bats are regarded as the principal pollinators of most *Parkia* species, many other visitors have been observed at the flowers. The present study aimed to determine the breeding system of the economically important canopy trees, *Parkia speciosa* and *P. timoriana*, and to identify their pollinators. Inflorescences of both species are comprised of specialised flowers closely packed in a biglobose head, with an average of 2422-3860 flowers per capitulum respectively, 70-75 % of which are fertile. Although structurally hermaphrodite, some fertile flowers are functional staminate, resulting in a polyad:ovary ratio of 4700:1. The stigma is receptive shortly after anthesis which occurs in early evening. Fruit bats, mainly *Eonycteris spelaea*, continuously visit flowering plants from dusk till after midnight. Nocturnal and diurnal insects (moths and stingless bees respectively) visit capitula, mostly at the nectar zone. Pollination experiments carried out in 28 *P. speciosa* and four *P. timoriana* indicated that they are obligate self incompatible. Open pollination resulted in the highest fruit set (58-62%) followed by hand cross pollination (43-45%). Insect pollination resulted in fruit set of 13% in *P. speciosa*. Nectarivorous bats are thus proved to be the most effective pollinators, although not exclusive, for these chiropterophilous plants.

# INTRODUCTION

In tropical lowland rainforest, most species are self-incompatible and spatially isolated from conspecifics, so that selection for long distance pollen transfer is more intense in this species-rich community. Approximately 98-99% of flowering plants in tropical lowland forest are pollinated by animals (Bawa, 1990). Some plants in this community have evolved adaptations to attract specific pollinators, and although most species are also visited by a diversity of insects, some are thought to depend exclusively on bats for pollination (Kress and Beach, 1994; Momose *et al.*, 1998). Such bat-pollinated plants have specific floral traits, the so called 'bat-flower syndrome' with white or cream-coloured, strongly scented, bell or scuttle-shaped flowers which are presented in an exposed position, last only for the single night on which they open, and produce large quantities of pollen and nectar (Faegri and van der Pijl, 1979; Marshall, 1983).

The concept of pollination syndrome implies the specialization of plants to a particular pollinator or a set of pollinators, and it was long believed that specialization is the dominant evolutionary trend in plant pollination systems (Johnson and Steiner, 2000). However, empirical evidence has recently challenged this generalization (Waser *et al.*, 1996; Ramirez, 2004). In addition, some authors have observed that without a sceptical approach, the syndrome might obscure rather than illuminate the pollination system (Heithaus, 1982; Marshall, 1983; Ollerton, 1998). Several other animals, apart from fruit bats, also visit chiropterophilous plants (Grünmeier, 1990; Gribel *et al.*, 1999; Ibarra-Cerdina *et al.*, 2005), some plants were shown to be pollinated by other agents as well as bats. Diurnal visitors are as important as fruit bats in the pollination of *Agave subsimplex* Trel., a chiropterophilous plant from Mexico (Molina-Freaner and Eguiarte, 2003). Similar results were found in columnar cacti (Fleming *et al.*, 2001; Ibarra-Cerdina *et al.*, 2005). The syndrome is therefore best regarded as a hypothesis and field observation and pollination experiments are required before firm conclusions can be reached about the relative importance of different potential pollinators (Ollerton, 1998; Johnson and Steiner, 2000).

*Parkia*, one of the most speciose genera of chiropterophilous plants, has a pantropical distribution. Among 35 recognised species, 12 were found in the Indo-Pacific region, distributed from India to Fiji (Hopkins, 1994). Several edible species of *Parkia* including *P. speciosa* and *P. timoriana* (DC.) Merr. are regionally economically

important (Woon, 1994; Aminudin and Latif, 1996) and recent studies suggest that they also have medicinal properties (Jamaluddin, Mohamed and Lajis, 1995; Suvachittanon *et al.*, 1996). Most *Parkia* are assumed to be chiropterophilous, and only a few species are thought to be pollinated by insects diurnally or nocturnally, or by lemurs (Hopkins, 1983, 1984, 1998; Luckow and Hopkins, 1995; Birkinshaw and Colquhoun, 1998; Hopkins *et al.*, 2000). From the uniform biglobose capitula of Asian *Parkia*, fruit bats were postulated to be the principal pollinators (Hopkins, 1994), as was suggested in Africa and South America (Baker and Harris, 1957; Hopkins, 1983, 1984, Grünmeier 1990). The first published report of visit by bats to the flowers of *Parkia* was from Java, in 1929 (Hopkins, 1994). Several authors have observed fruit bats, identified as *Eonycteris spelaea* Dobson, *Cynopterus brachyotis* Muller, and *Pteropus hypomelanus* Temminck visiting the flowers of *Parkia speciosa* Hassk. (Hopkins, 1994). The pollen of *Parkia* was an important component of the diet of *E. spelaea* in Malaysia (Start, 1974; Start and Marshall, 1976). While Hopkins (1994) suggested that the distribution of *Parkia* in the Pacific overlaps that of fruit bats, other vertebrates and a wide array of insects were found to visit *Parkia* throughout their distribution (Hopkins, 1983, 1984, 1994, 1998; Grünmeier 1990). Whether *Parkia* depends exclusively on fruit bats for pollination is important, since fruit bats are declining in abundance in many areas and this may result in pollination failure in these plants, thus reducing crop yields. Although a high pollen:ovule ratio in *Parkia* suggests that obligate outcrossing is likely (Hopkins, 1984) but selfing has been also mentioned (Hopkins, 1983), no intensive field investigation of the breeding system has been undertaken. The present study aimed to determine the breeding system of *Parkia* and to clarify which animals pollinate these plants.

## MATERIALS AND METHODS

*Study species*–From 12 species of *Parkia* occur in the Indo-Pacific region, four of which are found in Thailand : *P. speciosa* Hassk., *P. timoriana* (DC.) Merr., *P. leiophylla* Kurz and *P. sumatrana streptocarpa* Hance. (Nielsen and Santisuk, 1985; Hopkins, 1994). For a detailed description of the inflorescences of two former species see Hopkins (1994) and Nielsen and Santisuk (1985) and Wee and Rao (1980) for *P. timoriana*.

*Parkia speciosa*– is a canopy or subcanopy tree, 35-45m high, with a trunk diameter up to 1m. It is distributed throughout southern Thailand, peninsula Malaysia,

Sumatra, Borneo and Palawan Island in the Philippines (Hopkins, 1994). It grows naturally in a wide range of soil types and topography, and is fairly common in lowland tropical rain forest, especially along streams. This species has a long flowering period (April - October) in southern Thailand. Many trees flower twice a year. Many flower heads are present at the end of hanging peduncles, which are arranged in racemose terminal compound inflorescences mostly at the edge of the tree crown. In the forest, some trees produce as many as 70 capitula a night. Flowering in each tree last for 4-5 weeks. Some trees can produce up to a thousand capitula in one flowering period. Normally, one capitulum per compound inflorescence enters anthesis each night. In one compound inflorescence, up to 12 capitula are present (average±SD, 6.65± 1.90, n= 47). This species is now semi-wild, grown from seed in backyards, or by grafting of selected wild trees which bear a large number of pods.

*Parkia timoriana* –is also a canopy tree, up to 50m high with a large stem diameter, up to 2.5m. This species is distributed from north east India to Irian Jaya. It is found in evergreen primary, disturbed rain forest, moist mixed deciduous, dry evergreen forest on flat and hilly ground (Hopkins 1994). In Thailand, this species is common in lowland as well as in upland evergreen forest. In contrast to *P. speciosa*, this species has a short flowering period, from December to mid January. Trees with more than one flowering period in a year have never been found. In each tree, flowering lasts for four weeks.

*Study sites*–Pollination experiments and the study of pollinator activity on *P. speciosa* was carried out mainly in Trang Horticulture Station, Trang Province and to a lesser extent at Prince of Songkla University (PSU), Hat Yai Campus, Songkhla Province. Nectar was also collected from this species at Bala forest. The horticultural station (7° 30 N, 99° 25'E) is on flat terrain (384 ha) at the elevation of 50 m asl. and maintains plantations of crop plants including *P. speciosa, Cocos nucifera* Linn., *Areca catechu* Linn., *Anacardium occidentalis* Linn., *Aquilaria mallacensis* Lamk., and *Elaeis guineensis* Jacq.. The station are bordered by a small hill (1*0.5km) covered with secondary forest. Large patches of mangrove occur within 10km . On average, the annual rainfall is 2,196 mm, and rain is heaviest in July (350mm). The station is a collection centre for *P. speciosa* in southern Thailand, and includes a number of trees from different localities. Two plantations of *Parkia* cover areas of five ha each comprised of about 600 selected grafting trees, each tree planted in 10

*10 m.. The study plantatations are 8 and 15 years old. Bala Forest (05° 47'N, 101° 49' E) is in Narathiwat Province and is characterised by healthy tropical lowland forest, surrounded with fruit orchards and rubber plantations. Its average annual rainfall is 2,500 mm.

For *P. timoriana*, the study was carried out at on the campus of PSU, Hat Yai Campus, (07° 00.4' N, 100° 30.7' E.) where ten isolated individuals of this species are found. The campus is at the outskirt of Hat Yai City, and at the base of Kor Hong Hill, which is about 6 km long and at an altitude of about 30-140m asl. A large patch of old growth mixed with secondary forest and a rubber plantation covers most of the hill. The 10 year average shows that the climate is hot (average 28.3 °C) and relatively humid (average 72%) with 2,118 mm annual rainfall. The dry season (<100mm rain) lasts for three mo (February to April), whereas rain was heaviest in October-December (for detailed site description see Bumrungsri *et al.*, 2006).

*Floral biology*–Flowers of *P. speciosa* were accessed by an aluminum ladder and towers. In *P. timoriana*, trees are higher, and flowers can only be accessed by towers or climbing gear. Floral biology, including flower opening time, nectar secretion rate, time of anthesis, pollen viability and stigma receptivity were determined. Nectar was collected using a five mL syringe from 30 flowers of *P. speciosa* every hour starting from 1930h until nectar production ceased between 0130-0200h. Sugar concentration in nectar was measured with a pocket refractometer. Pollen viability was investigated by germinating pollen in a 15% sucrose solution at three hourly intervals from 2000h. Pollen from three capitula was germinated for six h, and fixed with formalin acetic acid (FAA) for later examination. Stigma receptivity was examined by immersing it in 3% hydrogen peroxide. Bubbling on the surface of the stigma indicated its receptivity (Kearns and Inouye, 1993). To count the number of pollen grains per anther, each of ten anthers was kept prior to anthesis on a slide. After dehiscence, anthers were mounted with poly vinyl alcohol and pollen grains counted in a microscope. The number of ovules per flower was counted after fixing flowers in FAA for 24h, then transferred to a slide, pressed gently with a rubber eraser and viewed in a microscope.

The total number of flowers was recorded from 18 capitula from four individuals of *P. speciosa* and 15 capitula from three individuals of *P. timoriana*. The percentage of

functional staminate flowers was determined by dissecting 100 randomly selected flowers.

### Abundance and Activity of Visitors

*Nocturnal and diurnal visitors*–Nocturnal visitors were observed using a night shot video (Sony Digital 740E) with an infrared light source. Observations were made on two nights from 1930h-2330h during the peak of flowering of *P. speciosa*. Each capitulum was observed for 10 min, during which visitor taxa and duration of visit were recorded. The percentage occurrence of each taxon was calculated as: number of capitula visited by a taxon*100/total number of observed capitula. Percentage frequency of visits was calculated as : total number of visits by a particular taxon*100/total number of visits by all taxa. The average duration of the visit was also calculated for each visitor.

Diurnal observations were made between 0630-0900h on 42 trees of *P. speciosa* at Trang for three d, during which diurnal insects were recorded visiting 231 capitula . Each capitulum was observed for one min using binoculars and the part the insects visited noted. Insects were collected from flowers using a cloth bag placed over capitula. Pollen found on the insects' body was removed and placed on a glass slide for identification. Captured insects were killed and mounted on a polystyrene platform for later identification.

*Fruit bats*–Fruit bats were captured using 2.6*9 or 2.6*6 m mist nets set at the same height as inflorescences at the flowering trees of *P. speciosa* and *P. timoriana*. Sampling began at 1800-1830h and lasted until 2300h. Mistnets were checked every 0.5 h, and when bats were caught, nets were lowered, and the bats carefully removed and placed in a numbered bag. Captured bats were identified following Corbet and Hill (1992), and pollen was collected from their fur. Bats were adapt at avoiding mistnets and only two of more than 60 bats visiting the flowering trees were caught, so that an alternative method to determine species and the relative frequency of visit was used. A set of flowers was photographed with a SLR camera (Nikon FE2 with 70-210 mm lens, flash SB24, SB 50X) and later with a digital camera (Nikon D70, 28-70mm lens, and flash SB-600, Nikon Corp., Japan) when bats visited flowers. Photographed bats were identified from their shape of their rostrum, body size, body color and other morphological features, compared with captured specimens. Photographs which were unclear or did not show diagnostic characters were excluded.

*Pollination experiments*–Since each flower is small and closely packed, the inflorescence or 'capitulum' is treated as a unit of pollination. All experiments were conducted in hermaphrodite capitula only, since a preliminary study carried out in PSU confirmed that they are the only ones that can set fruit (n = 29). All open capitula in sampled trees were checked whether it is hermaphrodite from late afternoon till evening. Several flowers were randomly picked from the fertile flowers, and dissected to locate the style and stigma. The inflorescence was classified as hermaphrodite, if hermaphrodite flowers were present (see result); functionally staminate inflorescences were excluded. The pollination experiments comprised of 1.) open pollination: all potential pollinators were allowed access to the capitula; 2.) spontaneous self pollination: all pollinators were excluded by bagging capitula from 1500-1700h , before anthesis occurred; 3.) insect pollination: capitula were covered with plastic nets (16mm mesh size) allowing access by insects but not bats. Most of the observed insects (bees and moths) were small and could pass through the insect net and access the flower except large moths with wingspan larger than three cm.; 4.) hand-crossed pollination: fertile flowers were rubbed directly with fertile ones from a different tree and bagged; e) self-induced pollination: pollen from a capitulum was rubbed with cotton wool around that capitulum and it was then bagged. Flowers were subjected to cross-pollination and self-induced pollination between 2100-2200h when stigmas were already receptive. Large semi-permeable cloth bags (diameter 20 cm, 35 cm high) with a plastic net inside to stop the flowers touching the cloth were used for bagging capitula. In most sampling trees, three replicates per treatment were conducted, and each sampling tree had at least a replicate of each treatment when few capitula were available. Fruit set was checked 5-7 d after the experiments. A capitulum was scored as set fruit' when green pods were present, regardless of their number. From field observations, unpollinated capitula were shed within three d. Pollination experiments were conducted in 28 trees of *P. speciosa* and four trees of *P. timoriana*. A total of 404 capitula of *P. speciosa* and 93 capitula of *P. timoriana* were included in pollination experiments. In *P. speciosa*, the number of capitula in open, spontaneous self, insect, hand-crossed and self-induced pollination were 98, 85, 76, 75 and 70, respectively, while in *P. timoriana*, there were 31, 13, 16, 21 and 12, respectively.

*Data analyses*–A nonparametric, Kruskal Wallis test, was applied to compare the percent of successful pollinations. Then ANOVA with a Tukey test was used to

compare between those treatments with successful pollination after square root transformation. All values are presented as means ± SD.

## RESULTS

*Floral Biology*–An inflorescence or a capitulum of both *P. speciosa* and *P. timoriana* is comprised of three types of flowers; fertile, nectar secreting and staminodial, closely packed in a biglobose head. The peduncle is thick and long (622 ± 91 mm in *P. speciosa* and 188 ± 70mm in *P. timoriana*). The capitulum is 87.5 ± 8.8 mm long with the largest diameter of 57.6 ± 6.8 mm in the former and 68.5 ± 8.3 and 46.7 ± 6.1 mm in the latter. *P. timoriana* has a much greater number of flowers per capitula, 3,860 ± 393 (range 2997-4189, n = 15) compared to 2422 ± 314 (range 1850-2964, n = 18) in *P. speciosa*. Fertile flowers had the greatest number proportionally followed by nectar secreting and staminodial flowers (*P. speciosa* = 70: 17: 13; *P. timoriana*, 75:20:5).

In both species, up to 70 capitula open in a night, and flowering of each tree generally lasted for 4-5 weeks. In both species, the open capitulum is yellowish, although their capitula differ in coloration before the flower opens. It is light greenish yellow in *P. speciosa* and reddish brown in *P. timoriana*. Pollen is released in polyads, comprised of about 16 grains, and there are 64.8 ± 4.54 polyads per anther in *P. speciosa*. Anthers are basifixed and there are ten stamens in each flower. The style is long, tipped by a cup-shaped stigma. In *P. speciosa*, an ovary contain 16-19 ovules (average ± SD = 17.14 ± 0.91, n=21). The number of ovules in an ovary of *P. timoriana* appears to be comparable with those in *P. speciosa*. Fertile flowers are structurally hermaphroditic but some were functionally staminate, characterised by short pistils, with the stigma curled inside or exposed outside the flower tube, but not beyond the anthers. In hermaphrodite flowers, the style generally elongates to exsert the stigma beyond the anther shortly (1 h) after anthesis. Two h after anthesis, the style extends 1-2 mm beyond the anther, so that the capitulum appears like a yellowish ball covered in short spine-like styles. However, this can vary between trees. In some *P. speciosa* trees, the stigma exserts beyond the anther as early as late afternoon while in *P. timoriana*, the style exserts shortly after anthesis. In a capitulum, fertile flowers are either functionally staminate, or hermaphroditic, or a mixture of both. In the case of *P. speciosa*, a wide range, from 15-100% (average 62%, n = 6 ),

of hermaphroditic flowers are present in hermaphrodite capitula whereas it is 6-93 % (average 41.5%, n = 9) for *P. timoriana*. The proportion of hermaphrodite capitula to functional staminate capitula ranged between 1:3-1:6 (average 1:4.5, n=3 trees, 121-649 capitula/tree). In *P. speciosa*, the hermaphrodite capitulum is randomly present in a compound inflorescence (n = 36 trees), as also observed from fruit setting, but in *P. timoriana*, it is mostly present after the middle part of a compound inflorescence (n = 4 trees). Thus, both *Parkia* were andromonoecious, with functionally staminate and hermaphrodite capitula in the same tree. Both species are protandrous, and the stigma is receptive shortly after anthesis (0.5h).

### *Parkia speciosa*

On the day that flowers open, staminodial flowers expand their staminode in the morning. The time that fertile flowers open varied between trees, and opening was generally complete between 1700-1830h. Anthesis occurs at 1930-2015h when it is dark. The stigma is receptive at 2000-2100h. Nectar secretion started at about 1930h and become copious at 2000h. Nectar secretion volumes were highest at 2000-2100h, after which production steadily decreased until it almost ceased (<0.1 mL) at 0130-0200h. Total nectar volume was 7.7 ± 2.1 mL per night (range 4.0-11.1, n = 29). Nectar concentration was at its maximum in the early evening (14.2%) and then gradually decreased (Fig. 1.). Secreted nectar accumulated at the basal zone between nectar secreting flowers and fertile flowers. Nectar is initially produced as milky drops and became transparent later. The flower produces a faint but noticeable odour before nectar is secreted and then a strong fruity odour during nectar secretion.

Each capitulum functions for one night, and flowers start to be shed in the morning. In some areas, all pollen was removed before dawn, although in others pollen was collected by bees in the morning. Where present, numerous white styles are clearly visible, exserted from hermaphroditic flowers. The functional staminate capitula drop off in the afternoon, whereas hermaphrodite ones either remain attached to the peduncle for several days or longer if fruit is setting. Eighty-five percent of pollen grains germinate at the early evening just after anthesis, whereas about 50% are still viable 24 h later. However, the germination percentage is much lower on the second morning (17%) (Fig. 2.).

### *Parkia timoriana*

Flowers opened completely at about 1700h. Anthesis occurs between 1835-1850h, the stigma is generally receptive at 1900h, but in some trees as late as 2030h. Nectar secretion started at about 1745h, and secretion volumes were highest at 2000-2100h, when they averaged 3.3 mL. Secretion had reduced to <0.2 mL at 0100-0200h. The total nightly nectar volume was $12.4 \pm 3.5$ mL (range 5.1-17.9, n = 30). Nectar concentration was at its maximum early in the evening (15.2%) till 2200h, and gradually decreased (Fig. 3.). As in *P. speciosa*, functional staminate capitula dropped off the following afternoon. In *P. timoriana*, pollen appear to have shorter longevity, and the germination percentage of pollen was <10% at 27-33h after anthesis. Pollen from nectar flowers is also able to germinate, and 50% germinated at 1930h.

### Abundance and activity of visitors

*Nocturnal and diurnal visitors*–Infrared digital video observations on 30 capitula of 18 individuals of *P. speciosa* showed that nearly all were visited by at least one nocturnal visitor. From a total 252 visits, bats showed the highest percentage frequency (58%) followed by moths (33.3%) and giant honey bees (*Apis dorsata* Fabricius) (8.7%). Likewise, most of sampled capitula were visited, by moths(77.4%) mainly in the family Arctiidae and bats (67.7% occurrence) whereas about half of them were visited by giant honey bees. Visits by bats were transient (average 2 s) while moths and bees stayed longer ( average 24.7 and 28.4 s, respectively). Moth often landed on fertile flowers whereas most bees visit nectariferous flowers. However, very little pollen was found on the body of moths but was present on all voucher specimens of bees. From additional field observation, moths are the major nocturnal insect visitors to flowers on dark nights while during light nights, giant honey bees frequently visited capitula especially the nectar-secreting flowers of *P. speciosa*.

Diurnal observations made on 289 capitula in 62 trees of *P. speciosa*, indicated that in about half of all capitula that visitors were observed. The majority of insect visitors were stingless bees (*Trigona* spp.) (74.4%), followed by dwarf honey bees (*Apis florae* Fabricius ) (13.5%), while Asian honey bees (*Apis cerana* Fabricius), flies, unknown insects and moths were minor visitors (1.5-4%). Most stingless bees (75.6%) visited nectar-secreting flowers, while all other insects observed (except moths) did so. Half of the moths visited hermaphrodite flowers. The pollen of *Parkia* was identified

from the bodies of stingless bees. Other vertebrate visitors are loris (*Nycticebus coucang* Boddaert ), olive-backed sunbird (*Nectarinia jugularis* Linn.), house gecko (*Hemidactylus* sp.) but they are nectar thieves rather than pollinators.

*Fruit bats*–Fruit bats were observed at the flowering trees of *P. speciosa* and *P. timoriana*. Bats arrived at the flowering *P. speciosa* after 2000h and at *Parkia timoriana* after 1930h. Groups of bats (5-15), identified from photographs as *E. spelaea*, approached inflorescences from any direction and visited well exposed capitula as well as those hidden under leaves. The pattern of visits reflected both solitary foraging and flock foraging - a few bats continuously moved around the trees whist a group of many bats intermittently visited flowers for ten minutes, and then disappeared in a pulse fashion. Bats landed on capitula briefly, for 1-2 seconds, occasionally for five seconds. When approaching a flower, bats landed head upright, feet gripping fertile flowers, their mouths at nectar secreting flowers, and their wings covering the whole capitulum with their thumb claws at staminodial flowers. As a consequence, pollen from fertile flowers dusted the chest, abdomen and wings. Sometimes two bats collided with each other when approaching flowers. In *P. speciosa*, far fewer bats visited flowering trees, compared with *P. timoriana*, although occasionally, up to 30 bats visited *P. speciosa* during a short period. Visits by bats were very frequent and continuous throughout the night till 0200h when nectar secretion ceased.

Although mistnets were set at flowering trees of both *Parkia*, only a few bats were captured. Seven bats in two species were captured at flowering trees of *P. speciosa*. These were *Eonycteris spelaea* ( two mature males, a non-reproductive female, a lactating female, and two juvenile females) and a lactating female *Cynopterus brachyotis*. Pollen of *Parkia* was found on the body and in the faeces of captured bats. A juvenile *E. spelaea* was caught at the flowering trees of *P. timoriana*. In addition, all photographs taken showed that *Eonycteris spelaea* is the only bat visitor to both *P. speciosa* (100%, n = 154 photos from 8 trees) and *P. timoriana* (100%, n = 54 photos from 3 trees). *E. spelaea* can be recognised from its very short chocolate brown hair, relative naked ear without any white rim, large eyes and long slender snout. Occasionally, the long tongue was also seen when the bat licked nectar. This bat often

emits high pitched 'tseets' during flying. When clinging on capitula, the length from head to feet is almost equal to the length of the capitulum.

*Pollination experiments*–There were significantly different pollination successes among treatments (p<0.001) (Fig. 4.) Open pollination has the greatest pollination success with 62.2 % of sampled capitula (n = 98) setting fruit in *P. speciosa*, and 58.1% in *P. timoriana* (n = 31). Cross pollination was the next most successful with 45.3 % setting fruit in the former and 42.9% in the latter, which was not significantly different from open pollination (p > 0.05) in both species. Insect pollination resulted in 13.2% fruiting in *P. speciosa* only and was significantly different from open and hand cross pollination (p<0.001). The low pollination success from self induced pollination (1 in 70, 1.4%) and self pollination (1 in 85, 1.2%) suggests that it could have resulted from accidental contamination of pollen from other trees, as in one plantation, anthesis was earlier (1930h) than at another (2015h). In one capitulum with self induced pollination, two pods were set and remained on the tree for three d. They fell later but the receptacle remained green for a few weeks later. In *P. timoriana*, flowers subjected to open pollination and cross pollination set fruits whereas the others set no fruit.

Cross-pollination produced the highest average number of fruit per capitulum (mean 9.0 ± 6.5, range 1-27 pods, n=30) compared to open pollination (mean 6.1 ± 4.4, range 1-19, n= 62) and insect pollination (mean 4.2 ± 3.2, range 1-11, n=11). The observed mature pods per synflorescense in natural conditions is 1-15 pods (5.6 ± 3.0, n= 81)

For *P. speciosa*, open pollination can be mostly partitioned into bat and insect pollination and the contribution of insect pollination to open pollination success can be calculated as: (% of insect pollination / % of open pollination) x 100 = (13.2/62.2)x 100 = 21.22 %. Therefore, bat pollination accounts for about 80% of the fruit set in open pollination treatments, and insects for 20% .

## DISCUSSION

*Floral Biology*–*Parkia speciosa* and *P. timoriana* present many features of the chiropterophilous floral syndrome including robust exposed flowers which open for one night, have a strong fruity or musty odour and a large quantity of pollen and

dilute nectar (Faegri and van der Pijl, 1979). Compared with other sections in this genus, *Parkia* has some characters typically associated with bat-pollination including specialization of flower type, increased amount of secretory tissues in nectariferous flowers and basifixed anthers (Luckow and Hopkins, 1995; Hopkins, 1998). In addition, the pendant inflorescence, the nectar ring, the staminoidal fringes over the nectariferous flowers and the production of polyads probably represent specializations to bat-pollination, though they are also present in some other Mimosoideae (Luckow and Hopkins, 1995). The strong foetid or fruity floral scent of these *Parkia* may imply the presence of sulphur compounds (Pettersson and Knudsen, 2001), characteristic of many chiropterophilous plants (Knudsen and Tollsten, 1995; Bestmann *et al.*, 1997) and Gmelin, Susilo and Fenwick (1981) indicated that *P. speciosa* is able to synthesise such compounds. The floral scent was strongly apparent during the first hours after anthesis which is also the time of highest nectar secretion.

Although functionally staminate capitula are not present in all species of *Parkia* , their presence was suggested as a strategy to increase the pollen:ovule ratio (Hopkins,1984; Grünmeier, 1990). In the case of *P. speciosa*, this ratio is calculated as follows : in a capitulum, there are 1.13 million polyads (64.8 polyads per anther *10anthers*1747flowers); there are 1083 ovaries, since 62% of 1747 flowers are hermaphrodite (0.62*1747), and since there are 4.5 male capitula to one hermaphrodite capitulum, the polyad:ovary ratio is 4703 :1. This ratio is about twice that reported in *Parkia nitida* Miq. in the neotropics (Hopkins, 1984). In addition, Wongchana, Wunnachit and Bumrungsri (2006) reported a higher average number of polyad per anther in *P. speciosa* (111.03 ± 4.25), and they found that the ratio between male capitula and hermaphrodite one was 3:1. Increasing the pollen:ovule ration could benefit a particular plant for several reasons. Since fruit bats have a large contact surface area compared to the stigma, some pollen will be lost and excess pollen is necessary to ensure pollination (Heithaus *et al.*, 1974). Likewise, pollen will be partially lost since nectarivorous bats normally ingest pollen by grooming their fur or consuming it directly from anthers (Marshall, 1983). In addition, these bats usually visit different plant species during a single night, for example, pollen from up to five species of plants were found in the faeces of *E. spelaea* in a night (Bumrungsri *et al.*, unpublised manuscript; Kitchener *et al.*,1990). Hence, pollen may not always be deposited on a conspecific stigma, although bat plants can reduce this waste if pollen

makes contact with different parts of the bat's body (Howell, 1977). Thus, nectarivorous bats are regarded as inefficient pollen vectors since they deposit less pollen onto the stigma than they lose or consume (Fleming and Sosa, 1994). Another reason for the presence of the male capitulum is that since fruit production is energetically expensive, plants can lengthen their flowering period and maintain regular visits of pollinators by producing less expensive functional staminate capitula (Hopkins, 1984). This can particularly explain why *P. timoriana*, which flowers once a year, produces functional staminate capitula in the first half of synflorescence.

Anthesis in late afternoon or at dusk and protandry is reported in several species of *Parkia* in the neotropics (Hopkins, 1984) and Africa (Baker and Harris, 1957; Grünmeier, 1990). Both Grünmeier (1990) and Hopkins (1984) indicated that styles of these species elongate beyond the anther by 2300h or after 2400h respectively which is much later than in both *P. speciosa* and *P. timoriana* in the present study, and after peak fruit bat activity, although Grünmeier (1990) reported that visits to *P. bicolor* A. Chev. continued until dawn. When the style is exserted beyond the anther, it is better placed to receive pollen from pollinators, and there is less chance for it to be contaminated with pollen from the anthers below. This may explain why hand cross pollination was less successful than open pollination, as it was carried out after just after the stigma becomes receptive and styles still not obviously elongate. Theoretically, the plant should coincide stigma receptivity with anthesis and peak pollinator activity (which presumably is also the time of highest nectar secretion rate). From the present study and that of Grünmeier (1990) on *P. bicolor*, we suggest that the time for which the style elongates beyond the anther should be associated with the duration of nectar availability. Those species in which the style elongates beyond the anther later, will secrete nectar for longer as a means of attracting effective pollinators. Further investigation to determine timing of stigma receptivity in other *Parkia* species is required. Grünmeier (1990) reported that before 2400h, the stigma of *P. bicolor* remained inside flower tubes whereas the anthers begin to drop off at the time that the style was elongating.

***Breeding system and effective pollinators***–The present study is the first intensive investigation on the breeding system of *Parkia*. It is clear that *P. speciosa* and *P. timoriana* are obligate self incompatible plants. A further investigation to

examine how self incompatibility is achieved in these plants is required. The high pollen:ovule ratio suggests obligate outcrossing (Cruden, 2000), which is common among tropical forest plants (Bawa, 1974; Heithaus *et al.*, 1974; Kress and Breach, 1994). This breeding system provides a higher quantity and quality of fruit set (Bawa, 1990; Lim and Luders, 1998; Gribel *et al.*, 1999). The results of the pollination experiments from the present study strongly confirm suggestions from previous researchers that fruit bats are the effective pollinators, although not exclusively, of most species of *Parkia* (Baker and Harris, 1957; Hopkins, 1984; Grünmeier, 1990). This result partly support Hopkins (1984) who came to the *a priori* conclusion that most species of *Parkia* are bat-pollinated because the flowers are chiropterophilous, the bats behave in the way likely to cause pollination, and other potential vectors are unlikely to transfer pollen.

Fleming and Sosa (1994) suggested that nectarivorous bats are legitimate and effective pollinators of many tropical plants as they deposit pollen on conspecific stigmas, and contribute significantly to successful fertilisation. In the present study, the nectarivorous bat, *E. spelaea*, is the ultimate pollinator of *Parkia* since it visits when the flower's sexual organ is in optimal condition to receive pollen. It makes brief but frequent visits for nectar by landing upright on a capitulum and dusting its thorax and abdomen with pollen, which is then transferred to another capitulum. A recent study confirmed that most of netted bats at the flowering trees of *P. speciosa* were *E. speleae* (Sripaoraya, 2005). Sripaoraya (2005) reported that the mean number of visits per night of *E. spelaea* to *P. speciosa* and *P. timoriana* was 98 and 112 times/capitulum, respectively and the highest visit frequency occurs when nectar production is at a peak. *E. spelaea* is also a reliable pollinator for these trees as it regularly visits flowers despite the availability of other food plants. *Parkia* is one of the major food sources of *E. spelaea*, as indicated from faecal analysis, accounting for 17-74% of its diet (average 34%) in every month throughout the year (Bumrungsri *et. al.*, unpublised manuscript). Nectar of both species of *Parkia* were reported to contain high content of crude protein, calcium, and Sodium (Sripaoraya, 2005). *E. spelaea* was reported to feed on plants of 31 species in Malaysia, with pollen of *Durio, Parkia, Artocarpus, Eugenia, Duabanga* and *Sonneratia* contributing more than 90% of the diet (Start, 1974; Start and Marshall, 1976). With its capacity for long distance foraging, up to 38km (Start and Marshall, 1976), *E. spelaea* is an effective pollen

vector for these self incompatible plants, and thus, potentially responsible for gene flow over a large area. However, more information on the foraging behaviour of this bat, as well as pollen-mediated gene flow of these plants is required. Hopkins (1994) indicated that the distribution of *Parkia* in the Indo-Pacific lies within that of pteropodid bats. Specifically, the distribution of the two species studied here are within the distribution of *E. spelaea* which occurs from south west India to Vietnam, to Sumatra, the Philippines and the Moluccas (Corbet and Hill 1992).

Other fruit bat species such as *Cynopterus brachyotis* and *Pteropus hypomelanus* also visit *Parkia*, but are likely to be less effective pollinators than *E. spelaea*, since they feed mainly on fruits supplemented with nectar and pollen when available (Bumrungsri and Racey, 2007). Although they are not common visitors to these plants, at least in our study site, their contribution to pollination success remains to be determined.

The role of *E. spelaea* in pollination of these *Parkia* is comparable to that of *Phyllostomus discolor* Wagner in pollinating neotropical *Parkia* in Amazonia (Hopkins, 1984), as well as to *Nanonycteris veldkampii* Matschie and *Megaloglossus woermanni* Pagenstecher in Africa (Baker and Harris, 1957; Hopkins, 1983; Grünmeier, 1990). The behaviour of landing on a capitulum of *Parkia* is significantly different between old world and new world fruit bats. Bats land head upright in the former, but head down in the latter, where they may also hover (Hopkins, 1984). It is apparent that head down is more suitable for collecting nectar which is hidden below a much larger staminodial fringe of neotropical capitula in *Parkia*, or from the nectar zone on the apex of the pendulous capitula of *Platyparkia*.

*Chiropterolophily and/or entomophily*–It is only in *P. speciosa* that insects either or both nocturnal and diurnal are responsible for fruit set although to a much lesser extent than fruit bats, with respect to both fruiting percentage and number of fruits. Generally, most insects visit nectar secreting flowers rather than fertile flowers (Baker and Harris, 1957) and they also often spend proportionally longer on the same plants. Social bees generally visit one tree and then return to the nest (Nagamitsu and Inoue, 1997). However, they may make a subsequent foraging trip and transport pollen from the nest to conspecific trees. The frequency of nocturnal insect visits is

much lower compared to bats, while diurnal insects visit in the morning when most of the pollen has gone, and the stigma is starting to wilt (S. Wongchana, personal communication) or in the early evening when nectar secretion is just beginning but the plant's reproductive organ has not ripened. The pollination success of insects in *P. speciosa* in the present study is probably over-represented, since experiments were conducted in plantations where individual trees are so close to each other that there is more chance of pollen being transferred by insects than in a more natural situation where conspecific trees are more distantly isolated. However, it shows that insects are capable of pollinating this plant. Additionally, it resembles the rural situation, since this species is commonly semi-wild planted in gardens and orchards. The pollination success by insects in African *Parkia* was previously recorded by Hopkins (1983). Insect pollination in these chiropterophilous *Parkia* could also reflect its evolutionary biology since chiropterophily in *Parkia* derives from entomophily (Luckow and Hopkins, 1995; Hopkins *et al.*, 2000). Although it is still not clear which insects are responsible for pollination success in *P. speciosa*, moths appear to be potential candidates. The co-occurrence of bat and moth pollination has been observed elsewhere and many plants that are primarily pollinated by bats are also pollinated by moths (Baker, 1960; Ramirez, 2004). Nocturnal and diurnal insects, especially moths, giant bees and stingless bees, could be more important pollinators where the fruit bat population is low, since *E. spelaea* populations are threatened by hunting, and their distribution depends on the availability of large caves with high ceilings (Start, 1974; Bumrungsri, 1997). Thus, further investigation of which insects are the most effective pollinators of this plant are required. Although other nonvolant mammals and birds were also previously reported to visit flowers of *Parkia* (Grünmeier, 1990; Hopkins, 1984, 1994), their contribution to reproductive success is still unknown. From previous observations, it is likely that they are mainly nectar thieves rather than pollinators (Grünmeier, 1990).

The fact that insects have a facultative role in pollination of *P. speciosa* implies some degree of generalisation within the specialised pollination system postulated in the genus *Parkia*. Whether this resulted from variation in spatiotemporal availability of their major pollinators remains to be investigated. Similar results have been found in *Agave* and columnar cacti, chiropterophilous plants in the arid neotropics (Fleming *et*

*al.*, 2001; Molina-Freaner and Eguiarte, 2003; Ibarra-Cerdina *et al.*, 2005). When their specialised pollinators are unreliable, plants become more generalised.

*Economic botany and conservation–Parkia speciosa*, or petai and *Parkia timoriana* are economically important plants in south east Asia. Immature pods (petai) or germinated seeds (*P. timoriana*) are popular vegetables for various kinds of cooking, since they have a flavour similar to garlic. In Thailand, they are traditionally gathered from the wild, but are now planted in backyards and gardens for household consumption. In Malaysia, petai, a non-timber forest product, generated between 336,000-900,000 RM annually depending on the location of the domestic market (Aminudin and Latif, 1996), which was estimated to be worth 22 million US dollars in peninsular Malaysia (Woon, 1994). These nitrogen-fixers are valued as multi-purpose trees in agrofarming practice in this region (S.Bumrungsri, personal observation). Additionally, seeds and empty pods are reported to have medicinal properties including nitrite trapping (Suvachittanon *et al.*, 1996), blood glucose reduction in diabetic rats (Jamaluddin *et al.*, 1995), mitogenic effect on human lymphocytes (Suvachittanont and Jaranchavanapet, 2000) and reduction of amylase activity (Tungphothitham, 2001).

Since *E. spelaea* is the major pollinator of these self incompatible and economically important plants, the conservation status of this bat is important. *E. spelaea* has greatly declined in numbers in some areas, such as Java and the Lesser Sundas (Mickleburgh, Hutson and Racey 1992: 60). The major threats are hunting and cave destruction. Since they almost exclusively depend on caves for roosting, they are easy to exploit for food. In Thailand, some local people are still under the misapprehension that they destroy flowers of durian when they visit, so bats are killed (S.Bumrungsri, personal observation). Although they are able to reproduce twice a year (Heideman, 1987), their population in one cave has decreased seriously, from 20,000 to 8,000 individuals in two years (S.Bumrungsri *et. al.*, unpublished data). *E. spelaea* is also regarded as major pollinator of economic and ecological importance trees such as durian (*Durio zibethinus* Murr.)(Bumrungsri *et al.*, unpublised manuscript; Soepadmo and Eow, 1976), *Oroxylum indicum* Vent.( Start, 1974; Gould, 1978; Sritongchuay, 2006) and the mangrove trees, *Soneratia* spp. (Start and Marshall, 1976). The ecological and economical impact of pollinator declines is of worldwide concern,

since it effects global biodiversity loss, and crop production stability (Allen *et al.*, 1998; Kevan and Phillips, 2001). Assessment of population changes of nectarivorous bats and the ultimate consequences of these declines on plant reproduction are necessary. Thus, more protection, and increases in community-level education on the significance of bats to crop yield of a number of ecological and economic food plants are vital for their conservation. Likewise, conservation of genetic viability of these plants by preserving their natural populations is vital for longterm reproductive success in these self incompatible plants. Since *P. speciosa* is now become a crop plant, and sometimes grafted trees were commercially planted in large plantations, selection of a variety of sources trees is recommended.

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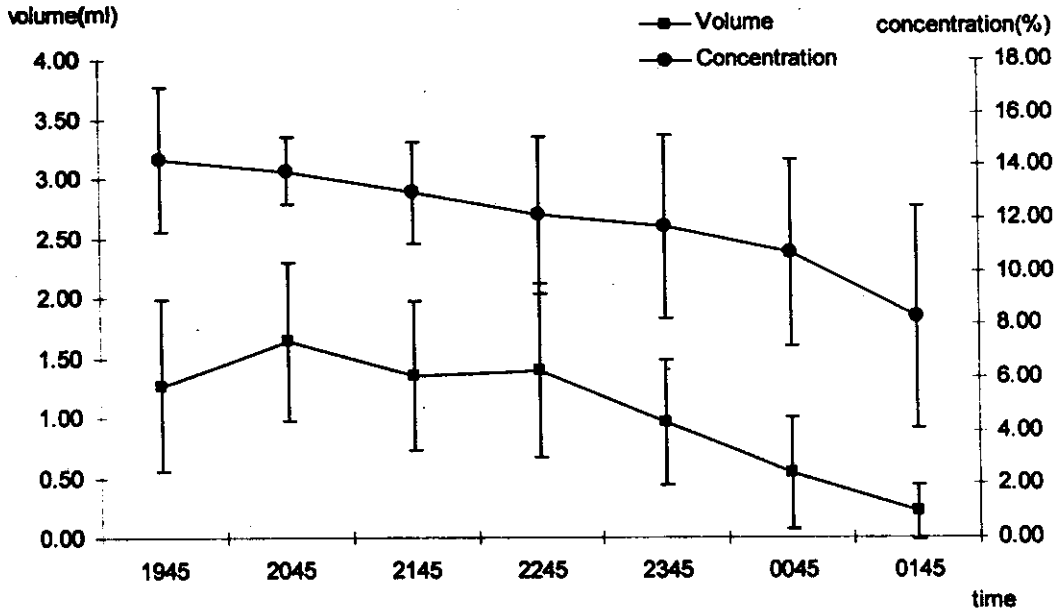
Figure 1. Average (± standard deviation) of nectar volume(ml) and sucrose concentration (%) of *P. speciosa* (n=30) from Bala Forest.
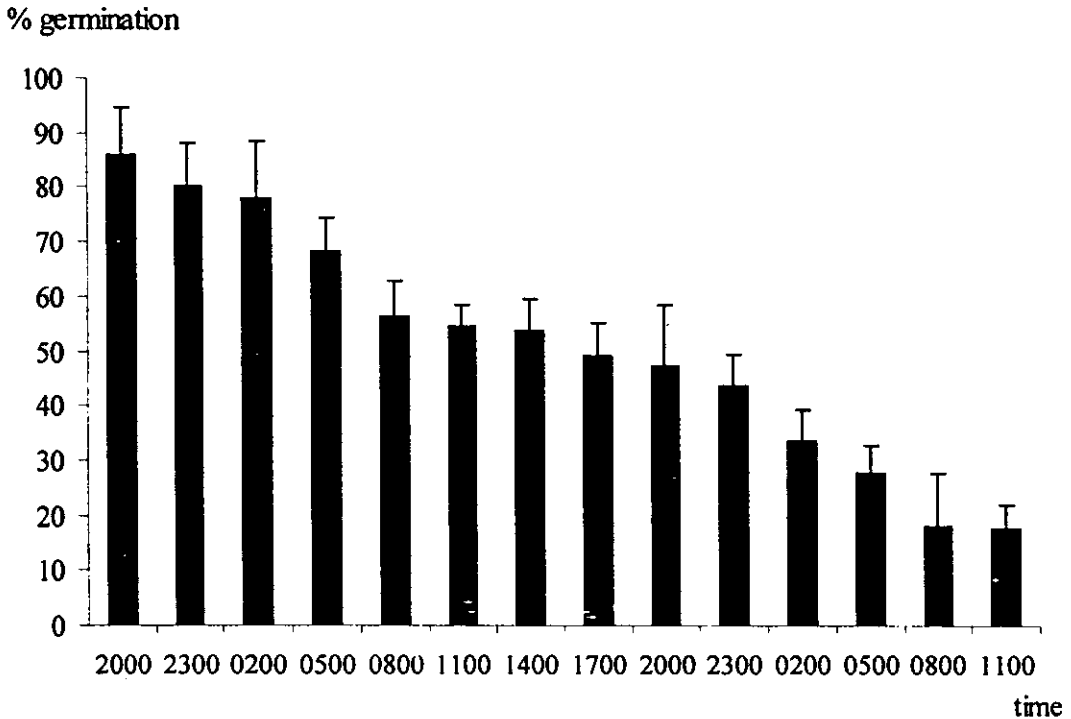
Figure 2 Average germination percentage of pollen of *P. speciosa* (n = 3 capitulum) in a 15% sucrose solution. In each time interval, 68-664 pollen grains were germinated (average 364.95 ±183.28). Standard deviation is shown.
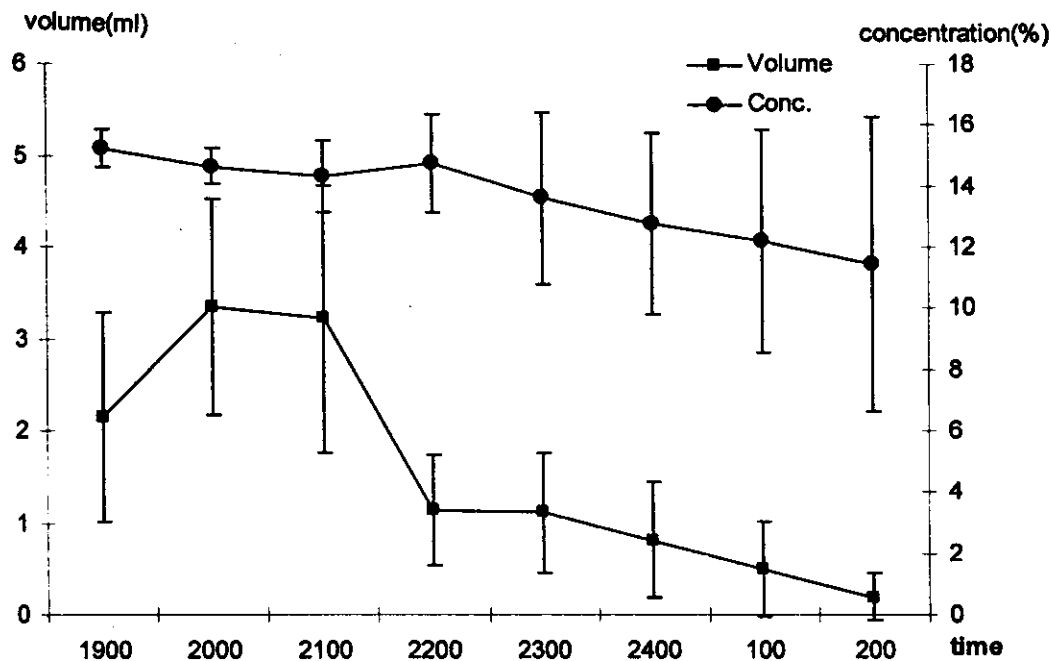
Figure 3. Average (± standard deviation) of nectar volume(ml) and sucrose concentration (%) (+ standard deviation) of *P. timoriana* (n=30) from PSU.
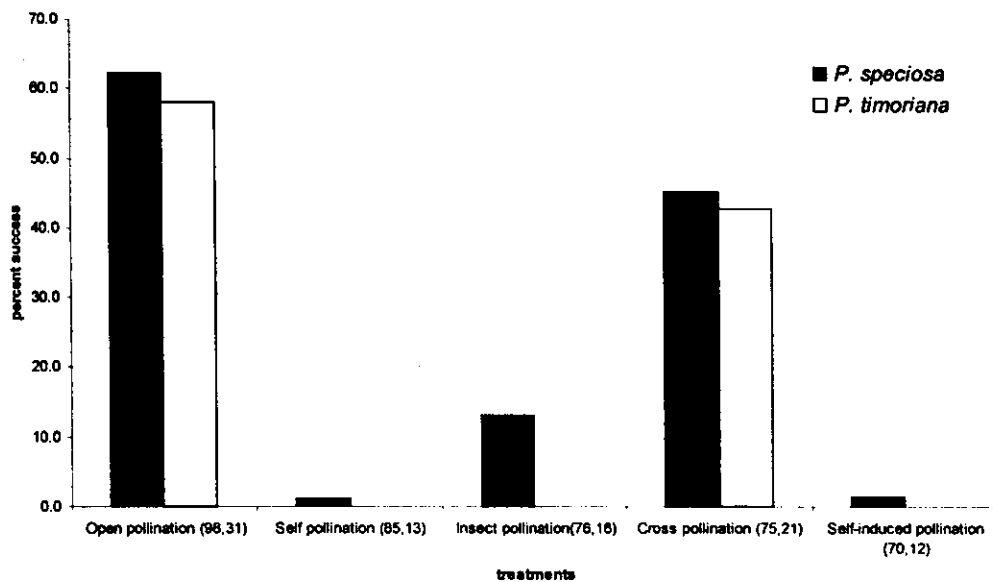
Fig. 4 Pollination success in experiments carried out in 28 *P. speciosa* and four *P. timoriana* trees during September 2002-January 2004 (no. of capitula in parenthesis).