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**ผลงานอาจารย์**



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

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Although the specific adaptive floral traits of bat-pollinated plants are well known, this 'flower syndrome' is challenged by empirical evidence showing that other animals are also important pollinators. 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 these 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 2,422- 3,860 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 4,703:1. The stigma is receptive shortly after anthesis which occurs in early evening. Each capitulum flowers for one night. 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 4 *P. timoriana* indicated that they are essentially self incompatible. Open pollination resulted in the highest fruit set (58-62%) although this was not significantly different from hand cross pollination (43-45%). Insect pollination resulted in fruit set of 13.2% in *P. speciosa*. Nectarivorous bats are thus the most effective pollinators for these chiropterophilous plants.

Keywords: pollination, *Parkia*, *Eonycteris spelaea*, chiropterophily, flower syndrome

## ***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 (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, open at night and last for one night only. The syndrome of chiropterophily includes during which they produce a large quantity of pollen and nectar (Faegri & 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 (reviewed by Johnson & 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 (Gribel *et al.*, 1999; Grunmeier, 1990; Ibarra-Cerdina *et al.*, 2005). Some plants with the bat-flower syndrome were shown to be also pollinated by other agents. Thus diurnal visitors are as important as fruit bats in the pollination of *Agave subsimplex* Trel., a chiropterophilous plant from Mexico (Molina-Freaner & 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 (Johnson & Steiner, 2000; Ollerton, 1998).

*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 and recent studies suggest that they have medicinal properties (Aminudin & Latif, 1996; Jamaluddin *et al.*, 1995; Suvachittanon *et al.*, 1996; Woon *et al.*, 1995). Most *Parkia* are assumed to be chiropterophilous, and only a few species are thought to be pollinated by insects diurnally or nocturnally, and lemur (Birkinshaw & Colquhoun, 1998; Hopkins, 1984; Hopkins, 1998; Hopkins *et al.*, 2000; Luckow & Hopkins, 1995). 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 & Harris, 1957; Hopkins, 1983, 1984, Grunmeier 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 & Marshall, 1976). While Hopkins (1994) suggested that the distribution of *Parkia* in the Pacific overlaps with 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; Grunmeier 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), 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.

### ***Study sites***

Pollination experiments and the study of pollinator activity on *P. speciosa* was carried out mainly in Trang Horticulture Station and to a lesser extent at Prince of Songkla University (PSU), Hat Yai Campus. Nectar was collected from this species at Bala forest. The station (7° 30' N, 99° 25' E) is on the 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 occidentale* Linn., *Aquilaria*

*mallacensis* Lamk., *Elaeis guineensis* Jacq.. The station are bordered to a small hill (1\*0.5km) covered with secondary forest. Large patches of mangrove occur within 10km of the station. On average, the annual rainfall is 2,196.2 mm, and rain is heaviest in July (349.7mm). 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* covers area of 5 ha each composed of xxx selected grafting trees planted in 10 \*10 m. The study plantatations are 5-15 years old. Bala forest (05° 47' N, 101° 49' E) is in Narathiwat Province. It is characterised with 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, Songkhla Province (07° 00.4' N, 100° 30.7' E.) where ten isolated individuals of this species are found. The campus is at the outskirts of Hat Yai City, and at the base of Kor Hong Hill, which is about xx km long with the altitude 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 months (February to April), whereas rain was heaviest in October-December (for detailed site description see Bumrungsri *et al.*, 2006).

### ***Study taxa.***

*Parkia* are pantropical leguminous trees with 3 sections: *Parkia*, *Platyparkia* and *Sphaeroparkia* (Hopkins, 1998). In section *Parkia*, the capitulum or inflorescence is comprised of flowers with different forms and functions: fertile, nectar secreting and staminodial, closely packed in a globose head. In *Platyparkia* (3 species), the staminodial fringe is absent, and the nectar zone is around the apex of the capitulum, whereas in *Sphaeroparkia* (4 species), the capitulum is small, diurnal, crepuscular or nocturnal without staminodial or nectariferous flowers. Twelve 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 & Santisuk, 1985; Hopkins, 1994). For a detailed description of the inflorescences of both species see Hopkins (1994) and Nielsen & Santisuk (1985), and Wee & Rao (1980) for *P. timoriana*. Pollination in *Parkia* is related to its

taxonomic position and indicates its phylogeny. Chiropterophily occurs in *Parkia* and *Platyparkia*, while nocturnal and diurnal melittophily occurs in *Sphaeroparkia* (Hopkins *et al.*, 2000). All three sections are present in the new world tropics, whereas only *Parkia* is present in the palaeotropics. Previous studies postulated that chiropterophily in *Parkia* derives from diurnal melittophily via nocturnal melittophily (Hopkins *et al.*, 2000; Luckow & Hopkins, 1995). Mapping of pollination type onto the phylogenetic tree of *Parkia* suggests a single derivation of bat-pollination, in the neotropics. Entomophilous species appear basal in the tree (Luckow & Hopkins, 1995).

***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 $\pm$ SD, 6.65 $\pm$  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***. It is canopy tree, up to 50m high with 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 the study area, this species is common in lowland as well as on 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.

## METHODS

### *Floral biology*

Flowers of *P. speciosa* were accessed by an aluminum ladder and towers. In *P. timoriana*, trees are quite high, thus flowers can only be accessed by towers and mostly by climbing gears. Floral biology, including flower opening time, nectar secretion rate, time of anthesis, pollen viability and stigma receptivity were determined. Nectar was collected using a 5ml 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 was germinated for 6 hour, and fixed with formol 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 & 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 under 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 flowers randomly selected.

### *Abundance and Activity of Visitors*

#### *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 took place between 1800-1830h and 2300 h. Mistnets were checked every half an hour, and when bats were caught, nets were lowered, and bats were 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 adept 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) when bats visited flowers. Photographed bats were identified from their shape of rostrum, body size, body color and other external morphology by compared with captured specimens. Photographs which were unclear or did not show diagnostic characters were excluded.

### ***Nocturnal and diurnal insects***

Diurnal observations were made between 0630-0900h on 42 trees of *P. speciosa* at Trang for 3 days, during which diurnal insects were recorded visiting 231 capitula . Each capitulum was observed for one minute using binoculars and the part the insects visited noted. Insects were grouped into small stingless bees, medium sized stingless bees, honey bees, and moths and flies, as preliminary observations showed that these were the main types of insect visiting the flowers. 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. Nocturnal visitors were observed using a night shot video (Sony Digital 740E) with an infrared light source. Observation were made on two nights from 1930h-2330h during the peak of flowering of *P. speciosa*. Each capitulum was observed for 10 minutes, visitor taxa and duration of visit were recorded. The percentage occurrence of each taxon was calculated as:  $\text{number of capitula visited by a taxon} \times 100 / \text{total number of observed capitula}$ . Percentage frequency of visit was calculated as :  $\text{number of total visit by a particular taxon} \times 100 / \text{number of total visit by all taxa}$ . The average duration of the visit was also calculated for each visitor.

### ***Pollination Experiments***

To determine the breeding system and the pollinators of these *Parkia*, pollination experiments were conducted. 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 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, 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 between 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 those large moths with wingspan larger than 3cm.; 4) hand cross 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 bagged. Flowers were subjected to cross-pollination and self-induced pollination between 2100-2200 h when stigmas were already receptive. Large semi-permeable cloth bags (diameter 20cm, 35cm 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 trees had at least a replicate of each treatment when few capitula were available. Fruit set was checked 5-7 days after the experiments. A capitulum was scored as 'fruit set' when green pods were present, regardless of their number. From field observations, unpollinated capitula were shed within three days. 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. 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  $\pm$  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 ( $622 \pm 91$  mm in *P. speciosa* and  $188 \pm 70$  mm in *P. timoriana*). The capitulum is  $87.5 \pm 8.8$  mm long with the largest diameter of  $57.6 \pm 6.8$  mm in the former and  $68.5 \pm 8.3$  and  $46.7 \pm 6.1$  mm in the latter. *P. timoriana* has a much greater number of flowers per capitula,  $3,860 \pm 393$  (range 2997-4189,  $n = 15$ ) compared to  $2,422 \pm 314$  (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  $64.8 \pm 4.54$  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 contains 16-19 ovules (average  $\pm$  SD =  $17.14 \pm 0.91$ ,  $n=21$ ). 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. Both species are protandrous, and the stigma is receptive shortly after anthesis (0.5h). In hermaphrodite flowers, the style generally elongates to exert the stigma beyond the anther shortly (1 h) after anthesis. Two hours 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 *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 hermaphroditic capitula whereas it is 6-93% (average 41.5%,  $n = 9$ ) for *P. timoriana*. The proportion of hermaphroditic 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 hermaphroditic 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.

### ***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 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 (<0.1ml) at 0130-0200h. Total nectar volume was  $7.7 \pm 2.1$  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 (Figure 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 produce a noticeable faint smell earlier and then a musty odour later in the evening.

Each capitulum functions for one night, and flowers start to be shed in the morning. In some areas, all pollen was removed before dawn, with some areas, although in others pollen was collected by bees in the morning. Where present, numerous white styles are clearly visible, exerted 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 germinate at the early evening just after anthesis, whereas about 50% of pollen is still viable at 24 hours. However, the germination percentage is much lower on the second morning (17%).

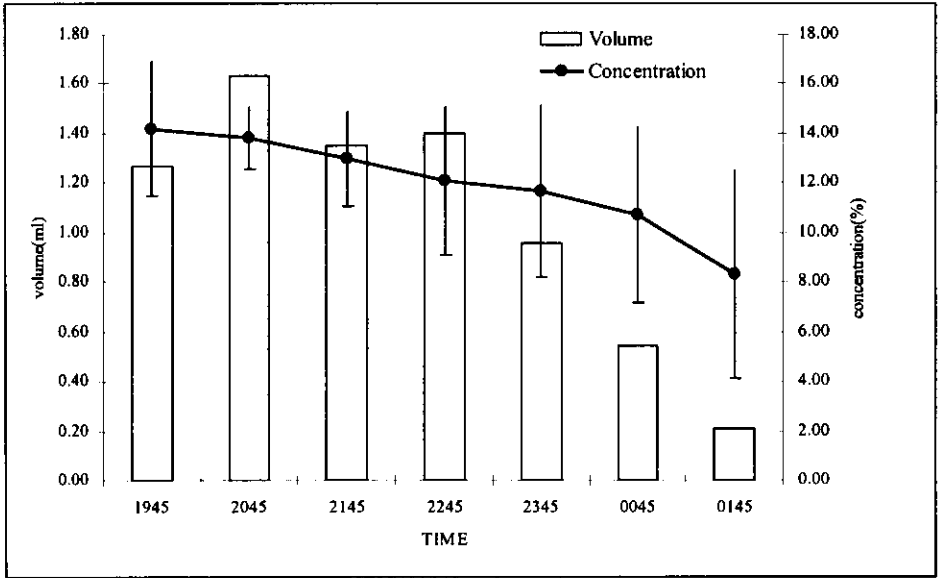


Figure 1. Average nectar volume(ml) and sucrose concentration (%) of *P. speciosa* (n=30) from Bala Forest. Standard deviation of concentration is shown. FIGS 1 & 2 SHOULD BE IN SAME FORMAT – THIS IS BAR CHART PLUS GRAPH. FIG 2 IS TWO GRAPHS

### *Parkia timoriana*

Flowers opened completely at about 1700h. Anthesis occur 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 <0.2ml 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 (Figure 2.). 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.

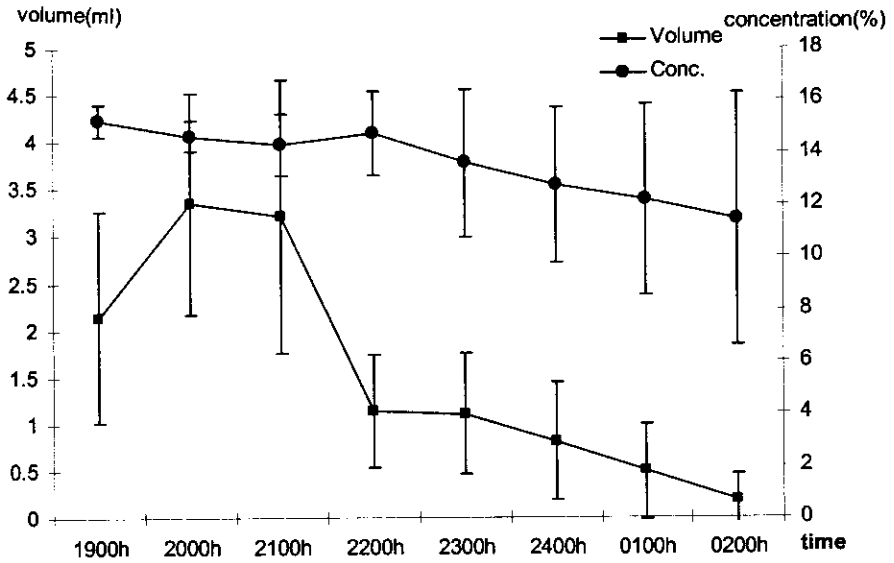


Figure 2. Average nectar volume(ml) and sucrose concentration (%) (+ standard deviation)of *P. timoriana* (n=30) from PSU.

### ***Abundance and activity of visitors***

#### ***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 group foraging - a few bats continuously moved around the trees whilst a group of many bats intermittently visited flowers for ten minutes, and then disappeared. 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* (5; 2 mature males, a non-reproductive female, a lactating female, and 2 juvenile female) 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 major visitor to this tree (xx%, n= ). *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. When clinging on capitula, the length from head to feet is almost equal to the length of the capitulum.

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 were the most common (58% frequency) followed by moths (33.3%) and rock bees (8.7%). Likewise, most of sampled capitula were visited, by moths (77.4%) and bats (67.7% occurrence) whereas about half of them were visited by rock 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.

### *Insects*

From field observation, moths are also the major nocturnal insect visitors to flowers at night especially on dark nights. During light nights, giant honey bees (*Apis dorsata*) frequently visited capitula especially the nectar-secreting flowers of *P. speciosa*. Several different species of bees, including giant honey bees, also visited nectar secreting flowers of *P. timoriana*, since nectar is produced in late afternoon in this species. Beetles were occasionally observed at flowers of both *Parkia* species. Diurnal observations made on 289 capitula in 62 trees of *P. speciosa*, indicated that,

in about half of observed capitula , the majority of insect visitors were small stingless bees (*Trigona* spp.) (74.4%), followed by larger stingless bees ( ) (13.5%), while rock bees , flies, unknown insects and moths were minor visitors (1.5-4%). Most small bees (75.6%) visited nectar-secreting flowers, while all other insects observed (except moths) did so, Other small bees and half of the moths visit 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.), but they are nectar thieves rather than pollinators.

### Pollination experiments

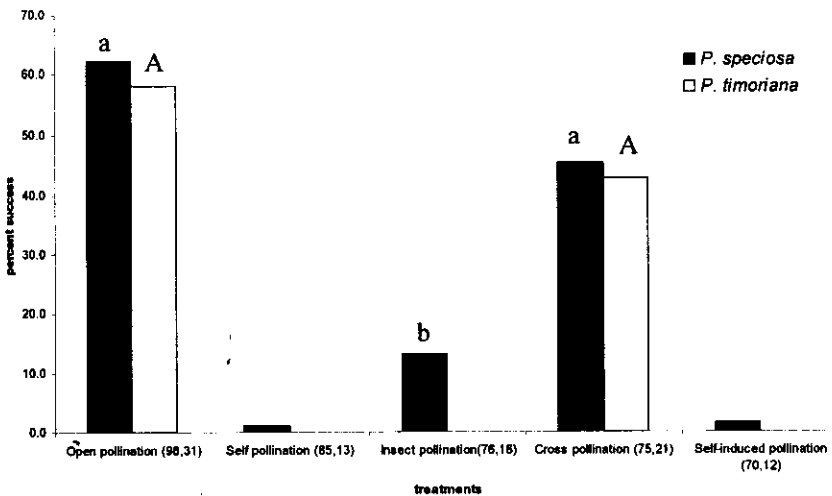


Fig. 3 Pollination success in experiments carried out in 28 *P. speciosa* and four *P. timoriana* trees during September 2002-January 2004 (no. of capitula in parenthesis). Different letters represent statistically significant differences ( $P < 0.05$ ).

There were significantly different pollination successes among treatments ( $p < 0.001$ ) (Fig.3) 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 days. 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  $9.0 \pm 6.5$ , range 1-27 pods,  $n=30$ ) compared to open pollination (mean  $6.1 \pm 4.4$ , range 1-19,  $n=62$ ) and insect pollination (mean  $4.2 \pm 3.2$ , range 1-11,  $n=11$ ). The observed mature pods per synflorescence in natural conditions is 1-15 pods ( $5.6 \pm 3.0$ ,  $n=81$ )

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: ( $\% \text{ of insect pollination} / \% \text{ of open pollination}$ )  $\times 100 = (13.2/62.2) \times 100 = 21.22 \%$ . 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 & 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 (Hopkins, 1998; Luckow & Hopkins, 1995). In addition, the pendant inflorescence, the nectar ring, the staminoidal fringes over the nectariferous flowers and the production of polyads probably represent specialization 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 & Knudsen, 2001), characteristic of many



chiropterophilous plants (Bestmann *et al.*, 1997; Knudsen & Tollsten, 1995) and Gmelin *et al.* (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 (Grunmeier, 1990; Hopkins, 1984). 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 \* 10 anther \* 1747 flowers); there are 1083 ovaries, since 62% of 1747 flowers are hermaphrodite (0.62 \* 1,747), and since there are 4.5 male capitula to one hermaphrodite capitulum, the polyad:ovary ratio is 4,703 :1. This ratio is about twice that reported in *Parkia nitida* Miq. in the neotropics (Hopkins, 1984). Increasing pollen:ovule ratio 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, up to five species of plants were found in the faeces of *E. spelaea* in a night (Bumrungsri *et al.*, unpubl. Data; 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 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; Grunmeier, 1990). Both Grunmeier (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 Grunmeier (1990) reported that visits to *P. bicolor* A. Chev. continued until dawn). When the style is exerted 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 it 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 Grunmeier (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, 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. Grunmeier (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 completely self incompatible. A further investigation to examine how self incompatibility is achieved in these plants is required. High pollen:ovule ratio in these plants suggests obligate outcrossing (Cruden, 2000), which is common among tropical forest plants (Bawa, 1974; Heithaus *et al.*, 1974; Kress & Breach, 1994). This breeding system provides a higher quantity and quality of fruit set (Bawa, 1990; Gribel *et al.*, 1999; Lim & Eow, 1998). 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; Grunmeier, 1990; Hopkins, 1984). 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. 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 when they are flowering 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.*, unpubl. data). Likewise, *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 & Marshall, 1976). With its capacity for long distance foraging, up to 38km (Start & 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 & 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 & Racey, 2006). 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 *Phyllostomus discolor* in neotropical *Parkia* in Amazonia (Hopkins, 1984), as well as to *Nanonycteris veldkampii* Matschie and *Megaloglossus woermanni* Pagenstecher in Africa (Baker & Harris, 1957; Grunmeier, 1990; Hopkins, 1983). 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, which 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*.

### ***Chiropterophilily 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 & Harris, 1957) and they also often spend proportionally longer on the same plants (S. Bumrungsri, pers. obs.). Social bees generally visit one tree and then return to the nest (Nagamitsu & Inoue, 1997). However, they may make a subsequent foraging trip and transport pollen from the nest to conspecific trees. The abundance and 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, pers. com.) 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 and 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 (Hopkins *et al.*, 2000; Luckow & Hopkins, 1995). Although it is still not clear which

insects are responsible for pollination success in *P. speciosa*, moths appear to be the most potential candidate. The co-occurrence of bat and moth pollination has been observed. Many plants that are primarily pollinated by bats are also pollinated by moths (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 fruit bats populations are threatened by hunting, and their distribution depends on the availability of large caves with high ceilings (Bumrungsri, 1997; Start, 1974). Thus, further investigation of which insects are the most effective pollinators of this plant are highly recommended. Although other nonvolant mammals and birds were also previously reported to visit flowers of *Parkia* (Grunmeier, 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 (Grunmeier, 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 in response to differences in flowering duration remain to be investigated. Similar results have been found in *Agave* and columnar cacti, chiropterophilous plants in the arid neotropics (Fleming *et al.*, 2001; Ibarra-Cerdina *et al.*, 2005; Molina-Freaner & Eguiarte, 2003). 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 vegetable 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 depend on the locality in domestic market (Aminudin & Latif, 1996), and it 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, pers. obs.). Additionally, seeds and empty pods are reported to have

the medicinal properties including anticancer (Susilo & Gmelin, 1982), nitrite trapping (Suvachittanon *et al.*, 1996), blood glucose reduction in diabetic rats (Jamaluddin *et al.*, 1995), mitogenic effect on human lymphocytes (Suvachittanon & Jaranchavanapet, 2000) and amylase activity reduction (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 *et al.*, 1992). 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, pers. obs.). 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.*, unpubl. data). *E. spelaea* is also regarded as major pollinator of economic and ecological importance trees such as durian (*Durio zibethinus*) (Bumrungsri *et al.*, unpubl. data; Soepadmo & Eow, 1976), *Oroxylum indicum* Vent. (Gould, 1978; Sritongchuay, 2006; Start, 1974) and *Soneratia* spp. (Start & 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 & 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.

#### ACKNOWLEDGEMENTS

This research was supported by the Thailand Research Fund, The Carnegie Trust for the Universities of Scotland and The British Council. We are also grateful to S. Wongchana, B. Wongchana and staff of The Trang Horticulture Station for permitting to carry out field work there, and their hospitality and support. Thanks are also due to S. Thong-Aree and staff of Bala-Hala Wildlife Research Station for generous support to A. Harbit and C. Benzies, to S. Sotthibundhu and C. Satasuk for logical support, P. Poonsawad and ... for training in tree climbing techniques, E.

Sripaoraya, T. Sritongchuay and S. Karnphun for assistance in the field, and S. Wonchana and C. Wilcock for valuable discussion.

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