POLLINATION SYSTEM OF *SHOREA CURTISII*, A DOMINANT SPECIES IN HILL DIPTEROCARP FORESTS

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KONDO T, OTANI T, LEE SL & TANI N. 2016. Pollination system of *Shorea curtisii*, a dominant species in hill dipterocarp forests. A crucial topic in tropical rainforest research in South-East Asia is the pollination systems of mast species, which flower abundantly at multiple-year intervals. In this study of *Shorea curtisii*, a dominant tree species in hill dipterocarp forests, we collected insects from flowering branches of a *S. curtisii* tree sampled at 6-hour intervals during peak bloom. Of the 482 collected insects, 90.7% were thrips, which are weak fliers, and 4.2% were the predatory big-eyed bug. Only one individual of these taxa was found in a sample taken during the non-flowering season. It is possible that during mass flowering of *S. curtisii*, outbreaks of thrips that use scattered floral resources attract predatory big-eyed bugs, which are strong fliers, and which move among flowering *S. curtisii* trees providing pollination services. Since the most abundant thrips species (*Haplothrips* sp., 50.0%) inhabits capsule-shaped stipules of other *Shorea* section *Mutica* species throughout the year, big-eyed bugs may be able to respond to general flowering events by preying upon stipule thrips during intervening periods. Thus, pollination of *S. curtisii* may be achieved via the ecological food chain between several types of thrips and big-eyed bugs, and such a pollination system adapted to mass flowering could be supported by diverse tree species in hill dipterocarp forests.

Keywords: Mass flowering, thrips, big-eyed bug, Dipterocarpaceae, red meranti

INTRODUCTION

Tropical rainforests of western Malaysia are among the richest in the world in terms of fauna and flora (Whitmore & Burnham 1975) and also among the most productive forest types in Asia with considerable timber value (FAO 2001). Such tropical rainforests in South-East Asia regenerate through the unique phenomenon termed 'general flowering'. During the general flowering period, which occurs at irregular intervals of 1–11 years, nearly all species of the Dipterocarpaceae and many species of other families come into flower synchronously, whereas many of these species rarely bloom during the intervening periods (Ashton et al. 1988, Appanah 1993, Sakai et al. 1999b, Numata et al. 2003).

Since the vast amount of seeds derived from synchronised mast fruiting after a general flowering satiates seed predators, mass flowering is considered to be an adaptive strategy that increases the survival rates of seeds and seedlings in tropical rainforests with diverse and numerous predators (Janzen 1971, Kelly 1994, Curran & Webb 2000). On the other hand, such intense flowering can place immense demands on pollinators for seed production as pollination of most tropical plant species is achieved by animal pollen vectors (Momose et al. 1998). However, the shortage of floral resources in the intervening periods between general flowering periods leads to population decline of pollinators that mainly feed on floral tissues as a reward for the transfer of pollen grains. Thus, it is possible that a pollinator shortage might occur during a general flowering period unless there are pollinators that can quickly respond to this phenomenon.

Studies have shown that several insect pollinators can quickly respond to this abrupt flowering phenomenon in a variety of ways (Sakai 2002). Flower thrips, which have a short generation time (< 8 days) and high reproductive rate (average fecundity of 27 eggs per female), maintain their population on understory plants during the periods between general flowering events, and they can sharply increase their population size by feeding on abundant flower resources during the general flowering period. Flower thrips are known to carry pollen of *Shorea* section *Mutica* species (Appanah & Chan 1981). The giant honey bee, *Apis dorsata*, has been documented to migrate over 100 km (Koeniger & Koeniger 1980) into lowland rainforest experiencing a general flowering period and build nests (Itioka et al. 2001). By migrating between flowering forests, giant honey bees maintain a large enough population size to provide sufficient pollination service for many mast tree species, such as *Dipterocarpus* species. In contrast, resident stingless bees can maintain their populations for 2–5 years without resupply from floral resources by using stored excess honey and pollen collected during the previous general flowering period (Inoue & Yamane 1984). They quickly respond to intense flowering and visit a wide variety of flowers (Momose et al. 1998, Sakai 2002).

Pollination systems adapted to the phenomenon of general flowering in species-rich, heterogenous, lowland mixed dipterocarp forests have been identified (Momose et al. 1998, Sakai 2002). Little is known regarding pollination systems adapted to the phenomenon of general flowering in hill dipterocarp forests, which are characterised by extensive dominance of *Shorea curtisii* (Dipterocarpaceae, section *Mutica*). Harvesting of dipterocarp timber has now shifted from lowland to hill dipterocarp forests (Sist et al. 2003) and understanding pollinator–plant symbioses is essential for sustainable management of these forest resources (Tani et al. 2012).

In this study, we collected visitors on flowers of a *S. curtisii* tree in a hill dipterocarp forest. By analysing the flower visitation pattern of each insect taxon, we were able to identify insect taxa that contribute to the pollination of *S. curtisii*. We discuss how these pollinators maintain their populations outside of general flowering periods and respond to intense flowering. Based on our findings, we discuss the pollination system adapted to the phenomenon of general flowering in hill dipterocarp forests.

MATERIALS AND METHODS

Target tree species

Shorea curtisii dominates on ridges in Peninsular Malaysia and ranges from 300–800 m above sea level (asl) (Symington 1943). This tree species exhibits supra-annual general flowering, which is characteristic of dipterocarps (Sakai et al. 1999). Flowers are hermaphroditic and exhibit partial self-incompatibility (Tani et al. 2015). Individual pale yellow flowers open at dusk and most corollas are pushed off and drop to the forest floor the next day, when new flowers start to open. In *Shorea* section *Mutica*, anthesis is between 5.00–6.30 p.m., with flowers staying open all night and abscising their corollas in the morning (Appanah & Chan 1981). The bloom period of *S. curtisii* is nearly four weeks, and an individual tree of the close relative *Shorea leprosula* was estimated to produce more than 600,000 flowers in one day during peak bloom (Appanah & Chan 1981). The flowers release a strong sweet scent but do not secrete nectar. The pollen production of *Shorea* section *Mutica* species is generally low, varying from approximately 3000–5500 grains per flower, and the size of the pollen grains ranges from 2.5–3.0 μm (Appanah & Chan 1981). The pollen grains are sticky and are not significantly dislodged by wind, typical of insect-pollinated tree species (Appanah & Chan 1981).

Study site

Our study of *S. curtisii* pollination was conducted in an undisturbed hill dipterocarp forest plot within the Semangkok Forest Reserve (3°40 'N, 101°40 'E, 340–450 m asl), Selangor, Peninsular Malaysia. The 6-ha (200 m × 300 m) permanent plot is located on a narrow ridge and steep slope, and represents a typical hill dipterocarp forest where *S. curtisii* is the dominant tree species (Niiyama et al. 1999). A total of 320 *S. curtisii* trees with diameter at breast height (dbh) ≥ 5 cm, including 127 mature trees with dbh ≥ 20 cm, were recorded in the plot in 1992 (Niiyama et al. 1999).

Collection and enumeration of floral visitors

The study was conducted during the 2011 general flowering period where about one-fifth of the mature trees came into flower, along with many other dipterocarp species (T Otani, personal observation). Insect visitors to flowers of a large *S. curtisii* tree (identification tag number F278, dbh = 68.3 cm) were sampled for five days (20, 22, 23, 25 and 27 October) during the tree's peak bloom. The tree was chosen for its accessibility by climbing. Sampling of panicles was conducted at six-hour intervals, approximately coinciding with the start and end of anthesis (6.00 p.m. and 12.00 a.m. respectively), and the start and end of flower abscission (6.00 a.m. and 12.00 p.m. respectively). Sampling of panicles was conducted once at the 12.00 p.m. sampling, and twice at the other sampling times on two different days. In each sampling, we collected 4–10 panicles, yielding 8, 10, 16 and 10 panicles at 6.00 p.m., 12.00 a.m., 6.00 a.m. and 12.00 p.m. respectively (44 total samples). A panicle that had more than 50 flowers was quickly covered with a sealable plastic bag (270 mm × 270 mm) and cut off inside the bag. Each bag was placed on ice to slow down insect movement and brought back to the laboratory. This sampling method, while particularly effective for sampling sedentary insects, is also able to capture insects from all orders (Ozanne 2008).

At the laboratory, flowers were examined under a binocular microscope for insects, which were then identified up to genus level. Corollas and stipules were carefully examined for insects such as flower thrips (*Thrips* spp., Thripidae), which are common visitors to flowers of *Shorea* section *Mutica* species in lowland mixed dipterocarp forests (Appanah & Chan 1981, Sakai et al. 1999a, Kondo et al. 2011), and stipule thrips (Phloeothripidae, *Haplothrips* spp.), which are frequently found in the capsule-shaped stipules of *S. acuminata* section *Mutica* (Kondo et al. 2011). Flower thrips feed on floral tissues and oviposit on unopened flower buds while stipule thrips shelter in, feed and oviposit on stipules (T Kondo, personal observation). The insects were preserved in vials filled with 70% alcohol and voucher specimens deposited at the Biotechnology Division, Forest Research Institute Malaysia and Graduate School for International Development and Cooperation, Hiroshima University. For comparison, we also collected four leafy twigs during the non-flowering season (6 July 2012) using the same method.

The mean number of insects collected from each panicle was calculated for the four sampling times. Statistical analysis of the differences in mean insect numbers among sampling times were conducted using one-way ANOVA followed by Scheffé's multiple-comparison test.

RESULTS

Flower visitors on the *Shorea curtisii* tree

Thrips (Thysanoptera) accounted for 90.7% of the 482 insects collected during the flowering season, while hemipteran bugs and small beetles comprised 6.4 and 1.4% of the total catch respectively (Table 1). Only one insect,

Table 1 Insect taxa sampled from a *Shorea curtisii* tree during the flowering and non-flowering season

Order	Flowering season			Non-flowering season		
Family	n	Average	%	n	Average	%
Hemiptera						
Geocoridae (*Geocoris* sp.)	20	0.45	4.2	0	0.00	0.0
Anthocoridae	5	0.11	1.0	0	0.00	0.0
Miridae	2	0.05	0.4	0	0.00	0.0
Homoptera						
Cicadellidae	4	0.09	0.8	0	0.00	0.0
Thysanoptera						
Thripidae (*Thrips* spp.)	196	4.45	40.7	0	0.00	0.0
Phloeothripidae (*Haplothrips* sp.)	241	5.48	50.0	1	0.25	100.0
Coleoptera						
Chrysomelidae	2	0.05	0.4	0	0.00	0.0
Curculionidae	5	0.11	1.0	0	0.00	0.0
Hymenoptera	4	0.09	0.8	0	0.00	0.0
Unknown	3	0.07	0.7	0	0.00	0.0
Total	482	10.95	100.0	1	0.25	100.0

n = number of insects, Average = average number sampled per branch, % = percentage of column total a *Haplothrips* sp. (Thripidae), was collected during the non-flowering season. Flower thrips were collected from corollas and accounted for 40.7% of the collected insects while stipule thrips accounted for 50.0% of the collected insects. Stipule thrips always occurred in the small space between the thin stipules overlaying immature flowers and not within the stipule proper. Of note was the number of big-eyed bugs, *Geocoris* sp. (Geocoridae), which comprised 4.2% of the insects collected. Combined, these three families accounted for 94.9% of the insects collected, and only these families yielded percentages of insect counts greater than 1% (Table 1). Adherent pollen grains were observed on both flower thrips and big-eyed bugs, but rarely on stipule thrips. Common pollinators, i.e. giant honey bees, stingless bees and flies of some species of Dipterocarpaceae with larger flowers than *S. curtisii* (Momose et al. 1998) were not incidentally observed during sampling.

Temporal flower visitation patterns of insect species on the *Shorea curtisii* tree

The number of flower thrips per collected branch differed significantly among collection times (F = 5.55, df = 3, $p < 0.01$; Figure 1a) and was synchronous with flowering stage. Significantly more flower thrips were counted per branch at 12.00 a.m. (mean ± SD; 7.70 ± 3.93) than at 6.00 p.m. (2.38 ± 2.23) and 12.00 p.m. (3.00 ± 2.53). The number of flower thrips counted per branch at 6.00 a.m. (4.31 ± 2.84) was not significantly different from that at 6.00 and 12.00 p.m., which were also not significantly different. On the other hand, the numbers of stipule thrips counted from the same branches were not significantly different with regard to collection time (F = 0.97, df = 3, p = 0.418; Figure 1b), and likewise for the big-eyed bug (F = 1.49, df = 3, p = 0.233; Figure 1c).

DISCUSSION

The extremely large combined percentage (94.9%, n = 482) of thrips and their predator, the big-eyed bug, collected from *S. curtisii* panicles bagged during peak bloom is similar to the 85.8% (n = 500) previously reported for *S. acuminata* (section *Mutica*) from Pasoh Forest Reserve, a lowland dipterocarp forest in Peninsular Malaysia (Kondo et al. 2011). The thrips genera, *Thrips* and *Megalurothrips*, have similarly been reported to comprise over 95% of insects visiting flowers of six *Shorea* species in Pasoh Forest Reserve (Appanah & Chan 1981). Insect counts on flowers bagged from *S. parvifolia* likewise yielded a large percentage of thrips (74%, n = 273)– nearly three times more than beetles (Sakai et

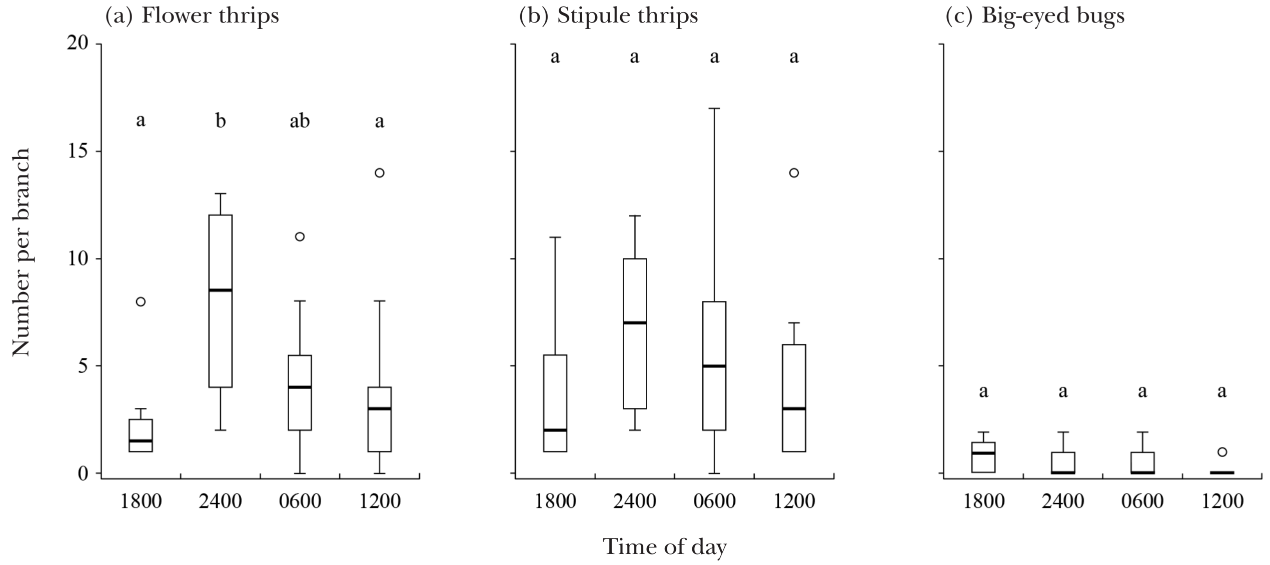

Figure 1 Daily changes in the number of each flower visitor per branch, for (a) flower thrips, (b) stipule thrips and (c) big-eyed bugs; maximum and minimum in each sample (except for the outliers represented by circles) are shown by the upper and lower ends of the vertical bar, 75th and 25th percentiles are given by the upper and lower ends of the box and the thick line represents the median value, values labeled, with the same letters are not significantly different from each other at $p \leq 0.05$

al. 1999). Interestingly, net-sweeping of flowers from the same tree yielded a lower percentage of thrips (32.4%, n = 148) than beetles (66.2%). The increase in thrips counts from bagged flowers versus net-sweeping was attributed to the ability of the former method to collect thrips sheltering in corollas (Sakai et al. 1999). The sampling method used in the present study, while effectively collecting cryptic thrips, likely under-sampled insects that are larger, sensitive to disturbance and/or highly mobile (Ozanne 2008), such as the fast-moving big-eyed bugs.

Big-eyed bugs are generalist predators known to prey on thrips (Crocker & Whitcomb 1980, Sweet 2000), and although not directly observed in the present study, the possibility that a predator-prey relationship exists between *Geocoris* spp. and thrips cannot be discounted. The pollen grains found on *Geocori*s spp. and flower thrips in the present study, lends weight to the supposition that both are pollinators of *S. curtisii*, with flower thrips attracting and eaten by *Geocoris* spp.. The absence of pollen grains on the stipule thrips and the enumeration of those thrips exclusively from *S. curtisii* stipules, suggest that these cryptic stipule thrips may not be pollinators of *S. curtisii*. Recent microsatellite DNA analyses of adherent pollen grains on flower thrips and big-eyed bugs visiting *S. acuminata* flowers in Pasoh Forest Reserve indicated that big-eyed bugs were the principal pollinator contributing to the regeneration of *S. acuminata* via cross-pollination while flower thrips played a supporting role as prey drawing the bugs to flowers (Kondo et al. 2011). *Shorea acuminata* in that study and *S. curtisii* in the present study report the same major flower visitors and thus may have similar pollination systems.

For *S. acuminata,* big-eyed bugs are thought to maintain their populations during non-flowering periods by preying upon stipule thrips that inhabit the stipules present on *S. acuminata* throughout the year (Kondo et al. 2011). For *S. curtisii* in the present study however, the enumeration of only one stipule thrips during the non-flowering season may exclude the possibility of stipule thrips as alternative prey for big-eyed bugs during that period. For *S. curtisii*, stipule thrips appear limited to the space between the stipules overlaying flower buds that are available only during the flowering season, instead of the stipule chambers that are present year-round. It is unlikely that big-eyed bugs are able to respond quickly as pollinators during general flowering events by increasing population size because they have a long generation time (> 21 days) and a low reproductive rate (average fecundity of 11 eggs per female; Naranjo & Stimac 1985). In the same manner as giant honey bees (Itioka et al. 2001) and stingless bees (Inoue & Yamane 1984), it seems more likely that big-eyed bugs respond quickly to the abrupt flowering phenomenon by maintaining a sufficient population size during the periods between general flowering events. Several *Shorea* section *Mutica* species that can provide shelter and feeding sites for stipule thrips (Kondo et al. 2011) grow in hill and lowland dipterocarp forests. For example, in the present research plot, there were 1.67 trees ha^{-1} for *S. acuminata*, 2.50 trees ha^{-1} for *S. parvifolia* and 8.16 trees ha^{-1} for *S. leprosula* (Niiyama et al. 1999). Thus, big-eyed bugs could settle down and forage in such *Shorea* section *Mutica* species in hill dipterocarp forests throughout the year, allowing populations to be maintained during the periods between general flowering events.

The present study is the first to investigate the pollinators of a *Shorea* section *Mutica* species in a hill dipterocarp forest in Peninsular Malaysia; a finding previously only recorded for the lowland dipterocarp forests: Pasoh Forest Reserve in Peninsular Malaysia (see Appanah & Chan 1981, Kondo et al. 2011) and Lambir Hills National Park in Borneo (Sakai et al. 1999). While our study revealed that major visitors to flowers of *S. curtisii* in the hill dipterocarp forest plot were thrips and the predatory big-eyed bugs, further DNA analyses of pollen grains adhering to these flower visitors are needed to substantiate the supposition that big-eyed bugs and flower thrips are major and indirect pollinators respectively. Sampling and studying these insects outside of general flowering events could also elucidate where and how they persist in hill dipterocarp forests during non-flowering periods. The results of these studies could contribute to sustainable management of *S. curtisii* populations in hill dipterocarp forests in Peninsular Malaysia.

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