



Responses of pre-dispersal seed predators to sequential flowering of Dipterocarps in Malaysia

Tetsuro Hosaka^{1,6}, Takakazu Yumoto², Yu-Yun Chen³, I-Fang Sun³, S. Joseph Wright⁴, Shinya Numata¹, and Noor Md Nur Supardi⁵

¹ Department of Tourism Science, Graduate School of Urban Environmental Sciences, Tokyo Metropolitan University, 1-1 Minami-Osawa, Hachioji, Tokyo 192-0397, Japan

² Primate Research Institute, Kyoto University, Inuyama, Aichi 484-8506, Japan

³ Department of Natural Resources and Environmental Studies, National Donghwa University, Hualien 97401, Taiwan

⁴ Smithsonian Tropical Research Institute, Apartado 0843-03092, Ancón, Panamá

⁵ Forest Research Institute Malaysia, Kepong, Selangor 52109, Malaysia

ABSTRACT

Many species of Dipterocarpaceae and other plant families reproduce synchronously at irregular, multi-year intervals in Southeast Asian forests. These community-wide general flowering events are thought to facilitate seed survival through satiation of generalist seed predators. During a general flowering event, closely related *Shorea* species (Dipterocarpaceae) stagger their flowering times by several weeks, which may minimize cross pollination and interspecific competition for pollinators. Generalist, pre-dispersal seed predators might also track flowering hosts and influence predator satiation. We addressed the question of whether pre-dispersal seed predation differed between early and late flowering *Shorea* species by monitoring flowering, fruiting and seed predation intensity over two general flowering events at the Pasoh Research Forest, Malaysia. Pre-dispersal insect seed predators killed up to 63 percent of developing seeds, with *Nanophyes shoreae*, a weevil that feeds on immature seeds being the most important predator for all *Shorea* species. This weevil caused significantly greater pre-dispersal seed predation in earlier flowering species. Long larval development time precluded oviposition by adults that emerged from the earliest flowering *Shorea* on the final flowering *Shorea*. In contrast, larvae of weevils that feed on mature seeds before seed dispersal (*Alcidodes* spp.), appeared in seeds of all *Shorea* species almost simultaneously. We conclude that general flowering events have the potential to satiate post-dispersal seed predators and pre-dispersal seed predators of mature fruit, but are less effective at satiating pre-dispersal predators of immature fruit attacking early flowering species.

Abstract in Malay is available with online material.

Key words: Dipterocarpaceae; flowering phenology; general flowering; masting; plant–animal interaction; plant–herbivore interaction; predator satiation; *Shorea*.

THE TIMING OF FLOWERING AND FRUITING IS CRITICAL FOR MANY REASONS. Flowering phenology is shaped by abiotic factors including rainfall, temperature and photoperiod, and biotic factors including mutualists, for example, pollinators and seed dispersers, and antagonists, for example, floral pathogens and seed predators. Adaptations that increase pollination success are often associated with increased seed predation (this was the case for 40% of studies reviewed by Elzinga *et al.* 2007). Sequential flowering occurs among closely related species of Bignoniaceae in the Neotropics (Gentry 1974) and Madagascar (Zjhra 2008), *Shorea* in Southeast Asia (Ashton *et al.* 1988, Lafrankie & Chan 1991), *Heliconia* and *Miconia* in the Neotropics (Snow 1965, Stiles 1975) and *Acacia* in Africa (Stone *et al.* 1998). Such temporal segregation of flowering is thought to enhance pollination efficiency by preventing interspecific pollen transfer and reducing competition for pollinators (Stone *et al.* 1998, Elzinga *et al.* 2007). However,

little is known about the effect of sequential flowering on seed predation.

The Dipterocarpaceae is the dominant family in the aseasonal lowland rain forests of Southeast Asia, representing 75–80 percent of the canopy and emergent individuals in many forests (Ashton 1982). Most dipterocarp species flower and fruit in general flowering events (GFEs), which occur at irregular intervals of one to 10 yr, while few flower and fruit outside GFEs (Ashton *et al.* 1988, Curran *et al.* 1999, Sakai 2002). Seed predator satiation is the leading hypothesis to explain this interspecifically synchronous mast fruiting. The hypothesis posits reductions in the abundance of generalist seed predators during multi-year intervals between GFEs followed by satiation of the remaining seed predators by massive, synchronous seed production during GFEs (Janzen 1974, Curran *et al.* 1999).

During a GFE, flowering is staggered by several weeks among congeneric *Shorea* species (Ashton *et al.* 1988). The sequence of flowering species is consistent among events (Lafrankie & Chan 1991). This sequential flowering allows pollinator

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⁶Corresponding author; e-mail: tetsurau@yahoo.co.jp

populations to increase as flowering species are tracked one after another and reduces interspecific cross pollination and competition for pollinators (Ashton *et al.* 1988, Appanah 1993).

Sequential flowering might, however, reduce the effectiveness of satiation of pre-dispersal seed predators that attack fruit soon after anthesis and that might also track the flowering sequence (Toy 1991). Differences in the timing of flowering and predation may lead to asymmetric consequences among species depending on their position in the flowering sequence. If generalist, pre-dispersal seed predators attack in the order tree species flower, the advantage of joining GFEs might be reduced for earlier flowering species because they flower alone and are attacked before later flowering congeners can contribute to predator satiation. In contrast, if pre-dispersal seed predators have multiple generations within a GFE, later flowering species would suffer more severe seed predation due to increased populations of predators emerging from earlier flowering species. Since pre-dispersal seed predation by insects is a major cause of mortality of dipterocarp seeds (Nakagawa *et al.* 2005, Sun *et al.* 2007), the responses of these seed predators to sequential flowering must be quantified to evaluate the importance of seed predator satiation in general flowering dipterocarps.

In this study, we monitored flowering and fruiting of seven sympatric *Shorea* species to address the following questions: (1) do the same generalist, pre-dispersal seed predators track *Shorea* species in the order of their flowering?; (2) do the seed predators have multiple generations within a GFE?; and (3) do earlier or later flowering species suffer more severe pre-dispersal seed predation?

METHODS

STUDY SITE—We conducted our survey in the 50-ha forest dynamics plot in the Pasoh Forest Reserve (2°58'N, 102°18'E) in Peninsular Malaysia. Here, all free-standing trees and shrubs ≥ 1 cm in diameter at breast height (dbh) are mapped, measured for dbh, and identified to species following Condit (1998). The initial census

included more than 320,000 individuals belonging to 814 species, 294 genera, and 78 families (Kochummen *et al.* 1990).

FRUITING EVENTS AND TREE SPECIES EXAMINED—We examined two GFEs which occurred from August 2001 to February 2002 (GF2001) and from March 2002 to September 2002 (GF2002). Flowering intensity was greater in GF2002 than GF2001, with 85.7 percent versus 75.0 percent of dipterocarp species and 35.7 percent versus 19.8 percent of dipterocarp individuals (≥ 30 cm dbh) flowering, respectively (Sun *et al.* 2007).

We examined the timing of flowering for five and six *Shorea* species (seven total species) that fruited in GF2001 and GF2002, respectively (Table 1). These species are common in the 50-ha plot (Kochummen 1997). Five are closely related in *Shorea* section *Mutica*, *S. maxwelliana* King is in section *Shorea*, and *S. pauciflora* King is in section *Brachypterae* (Ashton 1982). We included the last two species because they share pre-dispersal seed predators with the *Mutica* species.

FLOWERING AND FRUITING PHENOLOGY—We monitored the reproductive phenology of dipterocarps weekly starting on 20 August 2001 with 247 seed traps (0.5 m² each) located at 13.5-m intervals on alternating sides of pre-existing trails in the 50-ha plot. Flowers and immature and mature fruits were collected from the traps, identified and counted weekly (only presence was recorded for flowers). We used the number of traps which caught flowers or fruits as an index of flower- or fruit-fall intensity for each week. Since the corollas of dipterocarp flowers open and drop within a day (Appanah 1993), the flower-fall intensity reflected the flowering intensity at the time. We used modal dates of flowering and mature fruit dispersal to define peak flowering and fruiting dates, respectively (Fig. 1). When two or more weeks had the same number of flower records, we used the median date to represent the peak.

SAMPLING OF INSECT SEED PREDATORS—The seven *Shorea* species share one smaller weevil (small weevil, hereafter), *Nanophyes shoreae*

TABLE 1. Flowering order, number of seeds captured by traps, number of trees and seeds examined, and the fruit mass of *Shorea* species in GF2001 and GF2002. Fruit mass is represented by the largest mean of fresh fruit masses (wings removed) in weekly samples. Numbers in parentheses are the number of trees used to compare intensity of seed predation.

GFE	Flowering order	Tree species	Code	N seeds trapped (/m ²)	N trees examined	N seeds examined	Fruit mass (mg)
GF2001	1	<i>Shorea macroptera</i>	MC	2.4 ± 0.9	8 (5)	1365	1400
	2	<i>Shorea pauciflora</i>	PU	0.3 ± 0.2	3 (2)	695	2500
	3	<i>Shorea parvifolia</i>	PR	7.8 ± 2.8	12 (12)	4862	490
	4	<i>Shorea acuminata</i>	AC	10.5 ± 4.7	9 (7)	3896	380
	5	<i>Shorea leprosula</i>	LR	3.9 ± 1.6	7 (5)	2633	610
GF2002	1	<i>Shorea macroptera</i>	MC	1.9 ± 0.7	9 (6)	3123	1310
	2	<i>Shorea pauciflora</i>	PU	1.1 ± 0.6	5 (0)	1397	1760
	3	<i>Shorea lepidota</i>	LI	3.0 ± 1.6	6 (5)	2234	1500
	4	<i>Shorea acuminata</i>	AC	12.7 ± 4.0	6 (4)	1906	380
	5	<i>Shorea maxwelliana</i>	MX	38.3 ± 12.4	6 (5)	2077	340
	6	<i>Shorea leprosula</i>	LR	15.0 ± 5.4	6 (5)	1477	690

Marshall (Coleoptera: Nanophytidae); two larger weevils (large weevil), *Alicododes dipterocarpi* Marshall, and *A. humeralis* Heller (Coleoptera: Curculionidae); and several moths including *Andrioplecta shoreae* Komai (Tortricidae) and *Assara albicostalis* Walker (Pyralidae) as pre-dispersal seed predators (Hosaka *et al.* 2009). The three weevils are primarily specific to *Shorea* seeds (Toy 1991, Lyal & Curran 2000, Hosaka *et al.* 2009). Since the two large weevils have similar ecological traits (*e.g.*, the timing of abortion of fruits containing larvae and adult emergence), we combined their data in the present study. The moths have hosts in other genera of dipterocarps and non-dipterocarps (Robinson *et al.* 2001) and were less abundant than the weevils (Table S1). For this reason, we focused on the three weevils in the present study.

The weevils use their snouts to dig through endocarps and lay their eggs on cotyledons (Daljeet-Singh 1974, Toy 1988). Larvae feed on cotyledon and embryo, complete development in the seed, and emerge from the fruit as adults. Usually, a single larva develops in a single seed and kills the seed. Our previous study revealed that the small weevil feeds on immature seeds while the two larger weevils feed on mature or nearly mature seeds (Hosaka *et al.* 2009).

To quantify levels of seed predation and identify seed predators, we sampled fruits from the forest and reared all larvae in the seeds until adult emergence. We selected 32 and 38 focal trees of the seven *Shorea* (Dipterocarpaceae) species located near the traps and that fruited prolifically in GF2001 or GF2002 (Table 1). Fifty newly fallen (pedicels still green) fruits were randomly sampled beneath each focal tree each week throughout the period of seed fall in GF2001 and GF2002. We cut wings from fruits and recorded fresh masses without wings before rearing. All fruits were incubated in plastic boxes with moist paper towels for 4 mo. We checked the boxes and added about 1.0 mL of water every week. When adult insects emerged, we identified the species and recorded the date of adult emergence. All adults of small and large weevils emerged within 2 mo after fruit sampling, and we are confident that no living larvae of these weevils remained after 4 mo.

QUESTION 1: DO SEED PREDATORS TRACK *SHOREA* SPECIES IN THE ORDER OF THEIR FLOWERING?—We reasoned that fruit with larvae would be aborted in the order in which eggs were laid since infested fruits fell sooner than intact fruits (T. Hosaka, unpubl. data). We examined correlations between the mean date of abortion of fruits containing larvae and mean flowering dates for *Shorea* species using Spearman rank correlation tests.

QUESTION 2: DO SEED PREDATORS HAVE MULTIPLE GENERATIONS WITHIN A GFE?—In order to assess whether the offspring of small weevils that oviposit on earlier flowering species might oviposit on later flowering species, we defined oviposition windows as the time when developing seeds are vulnerable to attack by small weevils. Oviposition windows for the small weevil extends 0–4 wk, 2–6 wk, and 1–4 wk after the modal date of flowering of *S. macroptera* Dyer, *S. parvifolia* Dyer and *S. leprosula* Miq., respectively (Toy 1991). We estimated oviposition windows for

the remaining *Shorea* species to be from 1 to 5 wk after peak flowering, where the estimated starting time (1 wk after peak flowering) is the mean of the starting times for the three species studied by Toy (1991) and the length of the oviposition window (4 wk) is the same for all species studied by Toy (1991). We then checked whether small weevils emerged from earlier flowering species before the end of the oviposition window for later flowering species. Additionally, newly emerged small weevils are known to be sexually immature and would not mate or oviposit immediately after emergence (Daljeet-Singh 1974, Toy 1988). We did not observe mating among our reared adult small weevils during the first 2 wk or more after emergence (T. Hosaka, pers. obs.).

Oviposition windows are unknown for the large weevils. Therefore, we compared the timing of adult emergence from earlier flowering species to the timing of abortion of fruits containing their larvae in later flowering species. The timing of adult emergence from earlier flowering species would have to precede the abortion of fruits containing larvae by later flowering species if seed predators emerging from earlier flowering species lay their eggs on later flowering species within a single GFE.

QUESTION 3: DO EARLIER OR LATER FLOWERING SPECIES SUFFER MORE SEVERE PRE-DISPERSAL SEED PREDATION?—Each fruit used for insect rearing was dissected after 4 mo to assess the cause of seed death. If any trace of predation was observed in a seed without germination (*e.g.*, frass of predators, oviposition/emergence holes), we regarded the seed as ‘killed by insects’. To estimate the intensity of seed predation, we calculated the proportion of seeds killed by pre-dispersal predators for each *Shorea* species for each GFE. Specifically, we multiplied week values of the proportion of seeds killed by insects by the number of conspecific seeds encountered in traps in the same week, summed over weeks, and standardized by the total number of conspecific seeds in traps (Hosaka *et al.* 2011).

Similarly, the proportion of seeds killed by each weevil species was calculated using the number of weevils per seed and the number of seeds in traps for each week. The number of weevils per seed can be regarded as the number of seeds destroyed by weevils (*i.e.*, weevil infestation rate) since one individual weevil consumes one individual seed. Focal trees with >100 seeds sampled in total and with >5 sampling wk were included in this analysis. Fruits aborted before the weekly mean mass reached 15 percent of the maximum fruit mass of the species were excluded (Table 1) in order to standardize the stage of seed development among species. The percentage of seeds killed by insects was always low (<10%) before seeds reached 15 percent of their maximum mass. Seed predation intensity was not calculated for *S. pauciflora* in GF2002 since seed fall intensity was too low to monitor with traps. We evaluated the effect of flowering time on the intensity of seed predation with generalized linear models (GLMs) using proportions of seeds killed by small weevils, large weevils, or all insects as response variables, the modal date of flowering for each species and year of sampling (*i.e.*, GF2001 or GF2002) as explanatory variables and Gaussian error structure. Seed predation intensity (%) was logit-transformed prior to the

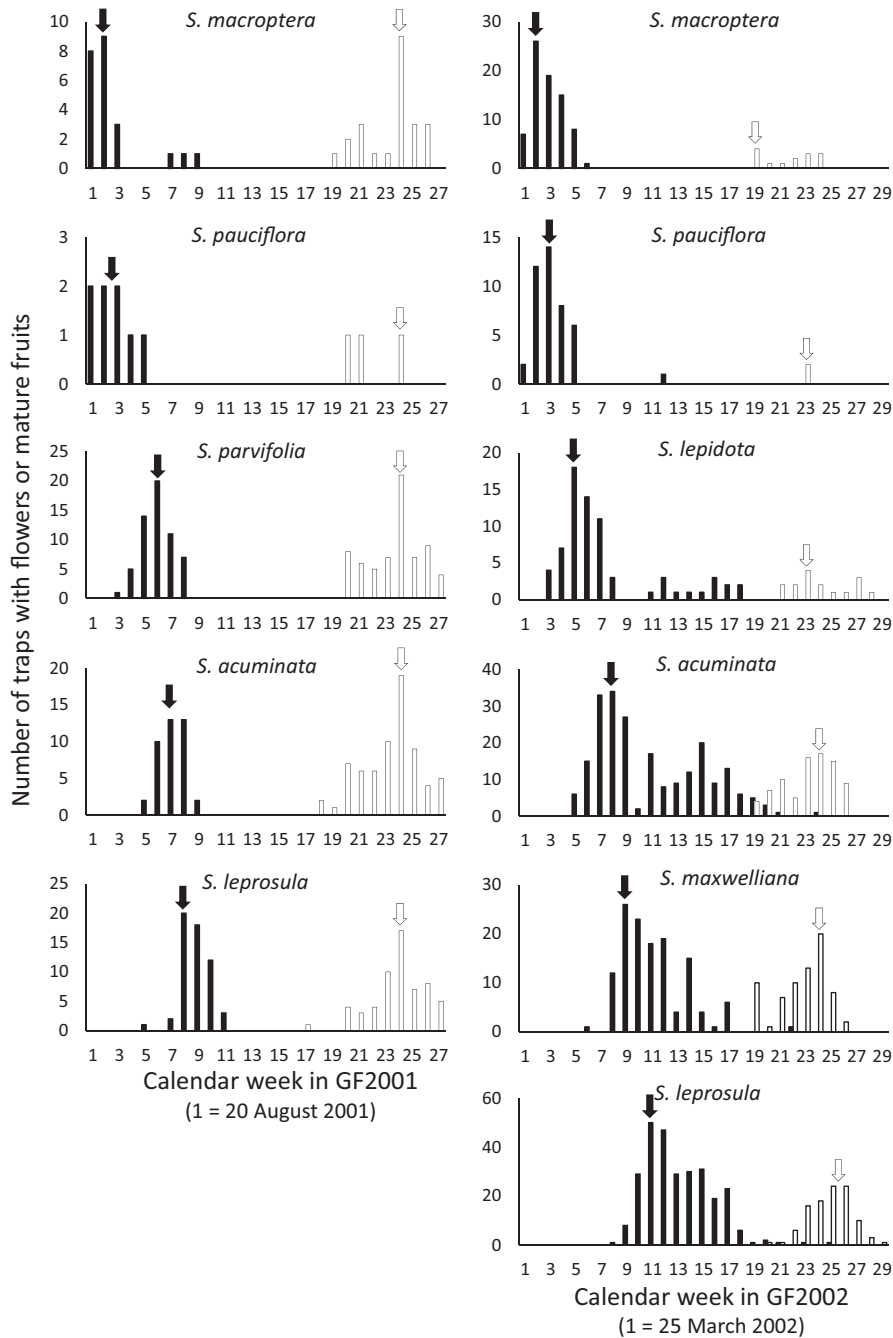


FIGURE 1. The weekly number of traps with flowers (solid bars) and mature fruits (blank bars) in GF2001 (left column) and GF2002 (right column). Arrows indicate the modal dates used to define peak timing for flowering (solid arrow) and mature fruit dispersal (blank arrow).

analysis (Warton & Hui 2011). All analyses were performed with R v. 3.0.1 (R Core Team 2013).

RESULTS

FLOWERING AND FRUITING PHENOLOGY—Flowering peaks occurred over 6 wk in GF2001 and 9 wk in GF2002 (Fig. 1). Flowering order was consistent between events; *S. macroptera* flowered earliest, followed

by *S. pauciflora*, *S. lepidota*, *S. parvifolia*, *S. acuminata*, *S. maxwelliana*, and *S. leprosula*, although *S. lepidota* and *S. maxwelliana* did not flower in GF2001 and *S. parvifolia* did not flower in GF2002.

In contrast to flowering, all *Shorea* species that fruited in GF2001 shared the same week of peak mature fruit dispersal (Fig. 1). The peak of mature fruit dispersal varied by 7 wk among *Shorea* species in GF2002; however, this fell to 3 wk when *S. macroptera* was excluded.

QUESTION 1: DO SEED PREDATORS TRACK *SHOREA* SPECIES IN THE ORDER OF THEIR FLOWERING?—In total, 2312 and 697 individuals of small and large weevils were collected, respectively, from 25,929 seeds of seven *Shorea* species in two GFEs (Table S1). Figure S1 presents the number of the small weevils found in fallen fruits and emerging as adults in relation to the flowering and fruiting phenology of each *Shorea* species.

The estimated oviposition windows of small weevils for each *Shorea* species indicate that small weevils tracked *Shorea* species

one after another in the order of flowering (Fig. 2). This is also supported by strong correlations between the flowering order of *Shorea* species and the mean date of abscission of fruits containing larvae of small weevils in both GF2001 (Spearman $\rho = 0.76$, $P < 0.001$; Fig. 2A) and GF2002 ($\rho = 0.82$, $P < 0.001$; Fig. 2B). The date of abortion of fruits containing larvae of large weevils was less strongly correlated with flowering order in GF2001 ($\rho = 0.14$, $P < 0.001$; Fig. 3A) and not significantly correlated in GF2002 ($\rho = -0.07$, $P = 0.52$; Fig. 3B).

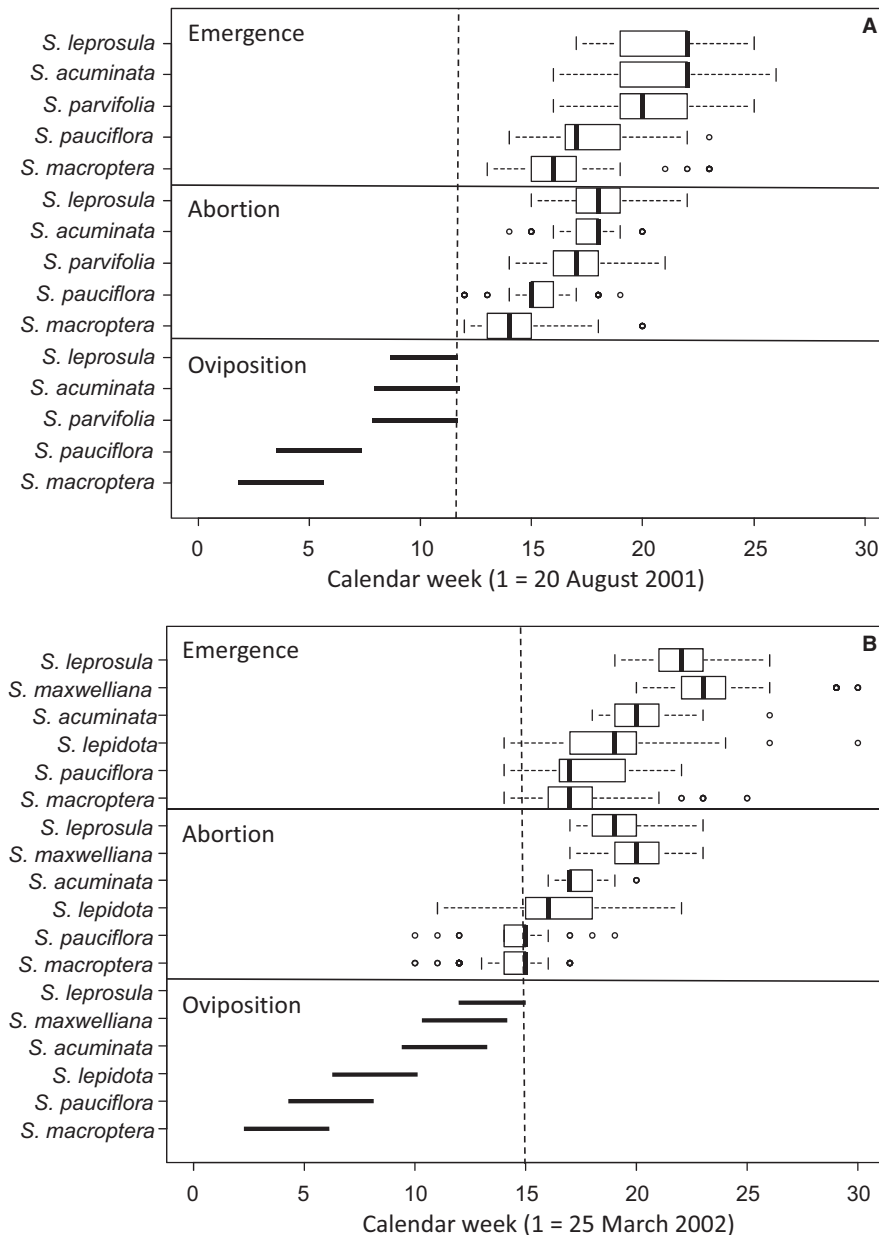


FIGURE 2. Oviposition window for small weevils (*Nanophyes shoreae*) and box-and-whisker plots for the timing of abortion of fruits containing larvae and of adult emergence in GF2001 (A) and GF2002 (B). The oviposition window extends 0–4 wk, 2–6 wk, 1–4 wk, and 1–5 wk after the modal date of flowering of *S. macroptera*, *S. parvifolia*, *S. leprosula*, and other *Shorea* species, respectively, based on Toy (1991). The vertical broken lines show the end of the oviposition window for the *Shorea* community. In the box-and-whisker plots, the bottom, bolded band, and top of the box represent the first, second (the median), and third quartiles, respectively; the whiskers represent the first and last dates within the 1.5 interquartile range; and points represent outliers beyond the 1.5 interquartile range.

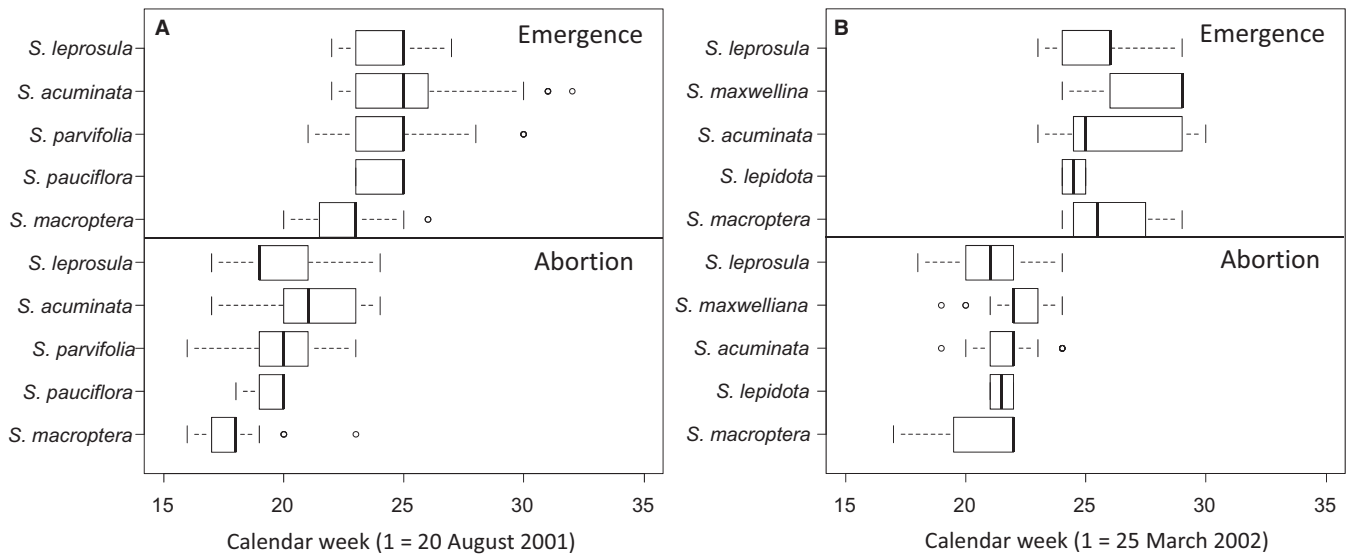


FIGURE 3. Box-and-whisker plots for the timing of abortion of fruits containing larvae of large weevils (*Alcidodes dipterocarpi* and *A. humeralis*) and of adult emergence in GF2001 (A) and GF2002 (B). The caption to Figure 2 explains the box-and-whisker plots.

QUESTION 2: DO SEED PREDATORS HAVE MULTIPLE GENERATIONS WITHIN A GFE?—In GF2001, just 1.4 percent of the small weevils that emerged from *S. macroptera* fruit emerged before the end of the oviposition window of the last flowering *Shorea*. In GF2002, 16, 10 and 6.4 percent of the small weevils that emerged from *S. macroptera*, *S. pauciflora* and *S. lepidota* fruit emerged before the end of the oviposition window of the last flowering *Shorea*, respectively (Fig. 2). The majority (84–99%) of small weevils emerging from earlier flowering species are unlikely to have a chance to lay their eggs on later flowering species during the same GFE.

Adult emergence of large weevils from earlier flowering species occurred after the abortion of fruits containing larvae of large weevils in later flowering species (Fig. 3). Only 13 and 0 percent of the larvae in seeds of the final flowering species (*S. leprosula*) were found after the first adult emergence of large weevil from the first flowering *Shorea* (*S. macroptera*) in GF2001 and GF2002, respectively. Thus, large weevils found in seeds of later flowering species were not offspring of those from earlier flowering species.

QUESTION 3: DO EARLIER OR LATER FLOWERING SPECIES SUFFER MORE SEVERE PRE-DISPERSAL SEED PREDATION?—The proportion of seeds killed by small weevils was negatively correlated with modal date of flowering ($\beta = -0.16 \pm 0.06$, $t = -2.59$, $P < 0.05$), suggesting that seed predation by small weevils was more frequent for the earliest flowering species (Fig. 4A). The proportion of seeds killed by small weevils was significantly higher in GF2002 than GF2001 ($\beta = 1.66 \pm 0.33$, $t = 5.02$, $P < 0.001$). In contrast, the proportion of seeds killed by large weevils was positively correlated with modal date of flowering ($\beta = 0.16 \pm 0.06$, $t = -2.77$, $P < 0.01$; Fig. 4B) and was lower in GF2002 than GF2001 ($\beta = -2.41 \pm 0.31$, $t = -7.90$, $P < 0.001$). The

proportion of seeds killed by all insects was negatively correlated with modal date of flowering ($\beta = -0.14 \pm 0.03$, $t = -4.08$, $P < 0.001$) and higher in GF2002 than GF2001 ($\beta = 0.68 \pm 0.18$, $t = 3.76$, $P < 0.001$) (Fig. 4C).

DISCUSSION

Generalist pre-dispersal insect seed predators kill a variable and often surprisingly high percentage of seeds of general flowering Dipterocarps. The percentage killed ranged from just 3.4 to 78 percent in studies restricted to pre-dispersal predation of mature fruit (Maycock *et al.* 2005, Nakagawa *et al.* 2005, Sun *et al.* 2007, Baguchi *et al.* 2011). Insect seed predation can also be severe at immature stages of seed development (Nakagawa *et al.* 2005, Hosaka *et al.* 2009). In this study, the percentage of developing fruit killed by generalist pre-dispersal insect seed predators ranged from 14 (*S. maxwelliana* in GF2002) to 63 percent (*S. lepidota* in GF2002) (Fig. 4C). Other studies that included immature seeds (and excluded abortion immediately after flowering) reported that insects destroyed 28 and 33–53 percent of seeds of *Shorea laxa* (Takeuchi *et al.* 2010) and *S. pilosa* (Tokumoto *et al.* 2009) before dispersal, respectively. Seed predation on both immature and mature stages must be included in any evaluation of the costs and benefits associated with general flowering.

FLOWERING AND FRUITING PHENOLOGY OF SHOREA—*Shorea* species flowered sequentially over 3–4 mo as reported previously (Ashton *et al.* 1988, Appanah 1993). Interspecific synchrony was greater for mature fruit dispersal, with all *Shorea* species having peak seed dispersal in the same week in GF2001 and, with the exception of *S. macroptera*, over 3 wk in GF2002 (Fig. 1). Synchronous mature fruit dispersal was also observed in other GFEs at Pasoh (*e.g.*, Chan 1977, Toy 1991) and in Borneo (*e.g.*, Wood

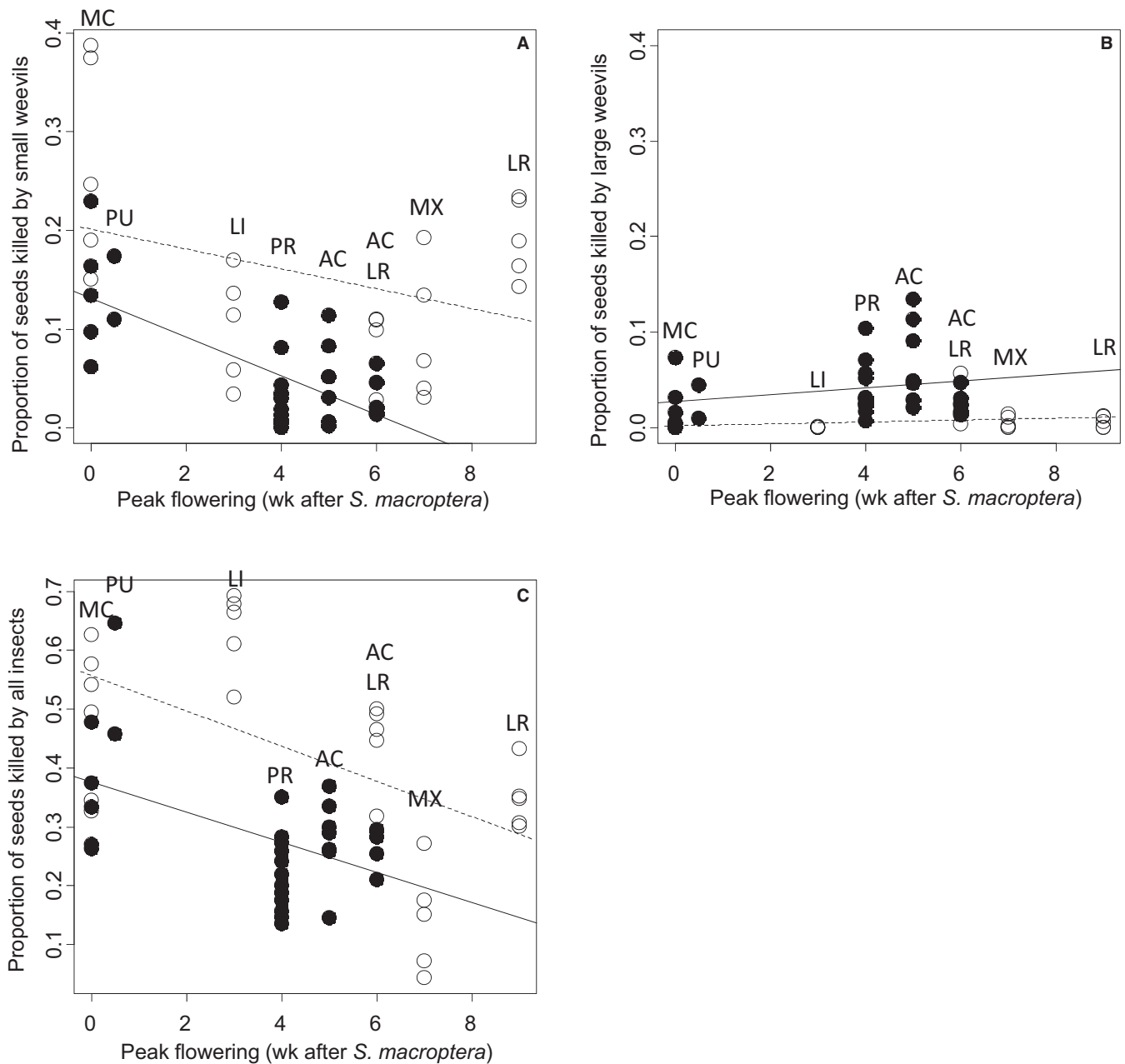


FIGURE 4. The relationship between the week of peak flowering for *Shorea* species and the proportion of seeds killed by small weevils (A: *Nanophyes shorea*), large weevils (B: *Alcidodes dipterocarpi* and *A. humeralis*), or all insects (C: the proportion of seeds with any trace of predation by any insects including those that failed to emerge). Each symbol represents the proportion of seeds killed for an individual tree. Black symbols and solid regression lines represent GF2001. Open symbols and broken regression lines represent GF2002. Codes for *Shorea* species are shown in Table 1.

1956, Curran *et al.* 1999, Brearley *et al.* 2007). Sequential, staggered flowering and synchronous seed dispersal are a common phenomenon among many dipterocarp species in this region (Wood 1956, Brearley *et al.* 2007).

A possible advantage of synchronized fruit dispersal is satiation of post-dispersal seed predators (Janzen 1974). Curran and Webb (2000) reported that *Shorea* species which fruited later than other species suffered greater seed losses to post-dispersal seed

predators. In order to synchronize mature seed dispersal among species, later flowering species develop seeds quickly compared to earlier flowering species (Fig. S2). This provides evidence consistent with the importance of satiation of post-dispersal seed predators.

BEHAVIOR OF PRE-DISPERSAL SEED PREDATORS AND PREDATION INTENSITY—We showed that small weevils attacked *Shorea* species

in the order of flowering, but temporal overlap between emergence of the first adults of the small weevil and the end of the oviposition window of the last flowering *Shorea* species was only 1 wk in GF2001 and 2 wk in GF2002. The small weevil is unlikely to build up its population during a GFE because very few adults emerged before the end of the oviposition window of the last flowering species.

There are two caveats. First, our oviposition windows do not consider intraspecific variation in the timing of flowering. Late flowering individuals of late flowering species might still be vulnerable to oviposition after the end of our oviposition window, which is based on peak population-level flowering times. Intraspecific variation in flowering times is much smaller than interspecific variation in flowering times among the Dipterocarps (Lafrankie & Chan 1991), however. In addition, newly emerged weevils are sexually immature making it doubtful whether eggs could be laid within a GFE unless *Shorea* flowering extended over an unusually long period since.

The second caveat concerns differences between GFEs. The lag between the peak flowering times of the first and last flowering species (*S. macroptera* and *S. leprosula*, respectively) was 6 wk in GF2001 and 9 wk in GF2002. As a consequence, just 1.4 and 16.0 percent of the small weevils from *S. macroptera* emerged before the end of the oviposition window of *S. leprosula* in GF2001 and GF2002, respectively (Fig. S1). A second generation of small weevils might have contributed to an increase in seed predation observed for the later flowering species, *S. maxwelliana* and *S. leprosula*, in GF2002 relative to GF2001 and relative to intermediate flowering species in GF2002 (Fig. 4A). The time lag between flowering times of *S. macroptera* and *S. leprosula* was approximately 7 wk for general flowering events in 1976, 1986, and 1989 at Pasoh (48, 50, and 50 d, respectively) (Lafrankie & Chan 1991, Toy 1991). The variation in the time lags between flowering of the first and last *Shorea* species and the uptick in seed predation observed in GF2002 when that lag was exceptionally long is consistent with selection against late flowering.

Differences in seed predation by small weevils among *Shorea* species also suggests that participation in GFEs is not equally advantageous to all species. Earlier flowering species are vulnerable to pre-dispersal seed predators before their eggs are depleted and before alternative hosts flower and become vulnerable. In contrast, later flowering species will have a relative advantage because the small weevils deplete their egg supplies through oviposition on earlier flowering species and alternative hosts are also flowering and vulnerable. Indeed, seed predation intensity was higher for earlier flowering species than later flowering species mainly due to more severe predation by small weevils on earlier flowering species in both GFEs (Fig. 4). Wright (1990) also reported that later fruiting individuals of a palm escaped seed predation by a host specialist bruchid beetle in Panama because the bruchid depleted its egg supply early in the season and long larval development times precluded a second generation within the fruiting season.

Two large weevils that oviposit on mature seeds were likely to attack all *Shorea* species simultaneously because seeds mature

simultaneously across species (Fig. S2). Interspecific synchrony in fruit maturation times is likely to facilitate satiation of pre-dispersal predators of mature seeds as well as post-dispersal predators.

Seed predation by small weevils and by all insects and was more severe in GF2002 than GF2001 (Fig. 4). This is probably due to increases in the population of small weevils during back-to-back GFEs (Hosaka *et al.* 2011).

CONSEQUENCES OF SEQUENTIAL FLOWERING—Earlier flowering species tend to suffer more severe pre-dispersal seed predation than later flowering species, particularly by small weevils (Fig. 4). This should lead to selection to synchronize flowering as well as seed maturation and dispersal. This potential disadvantage of early flowering might be compensated by advantages that accrue from staggered flowering such as decreased pollen contamination and competition for pollinators with other species.

Longer seed development times may also allow earlier flowering species to produce larger seeds. Since later flowering species develop their seeds more rapidly than earlier flowering species (Fig. S2), later flowering species may not have time to produce equally large seeds before interspecifically synchronous seed dispersal. The three earlier flowering species *S. macroptera*, *S. pauciflora*, and *S. lepidota*, produce much larger seeds than do the remaining later flowering species (Table 1). A positive relationship between seed mass and development time across species was also demonstrated in dry sclerophyll woodland in Australia (Moles & Westoby 2003). Earlier flowering species may have an advantage since seedling survival generally increases with seed size (Moles & Westoby 2006). The effects of sequential flowering on other ecological processes such as plant–pollinator interactions and seedling establishment need to be considered together with seed predation to understand the importance of sequential flowering for plant fitness.

In conclusion, synchronized fruit maturation may facilitate satiation of both pre-dispersal and post-dispersal predators of mature seeds. Pre-dispersal predators of immature seeds oviposit on *Shorea* species as they flower, however, with the result that earlier flowering species suffer greater pre-dispersal predation of immature seeds. Pre-dispersal seed predators killed up to 63 percent of developing seeds (Fig. 4C) and cannot be ignored when the costs and benefits of general flowering are evaluated.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

TABLE S1. *The number of seed predators collected, seeds dissected, and seeds infested by insects in GF2001 and GF2002 for each Shorea species.*

FIGURE S1. The weekly number of traps with flowers, immature and mature fruits, and the weekly number of the small weevils found in the fallen fruits and emerging as adults in GF2001 and GF2002.

FIGURE S2. Weekly changes in fruit weight of *Shorea* species during GF2001 and GF2002 expressed as a percentage of the largest weekly mean value observed for each species.

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