

Seed predation during general flowering events of varying magnitude in a Malaysian rain forest

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Summary

1 The lowland dipterocarp forests of Southeast Asia exhibit interspecifically synchronized general flowering (GF) and mast fruiting at irregular multi-year intervals of 1 to 11 years. The predator satiation hypothesis (PSH) posits that GF events enhance seed survival by reducing the survival, reproduction and population sizes of seed predators between GF events, and then satiating the reduced seed predator populations during GF events.

2 Three GF events of different magnitudes occurred in Pasoh Forest Reserve, Peninsular Malaysia, during 2001, 2002 and 2005. We exploited this natural experiment to test two predictions of the PSH. The first prediction was that seed survival should increase with the magnitude of the GF event. The second prediction was that seed predation should decrease with time since the previous GF event.

3 A reproductive survey of all (*c.* 900) dipterocarp trees ≥ 30 cm d.b.h. in a 50 ha plot showed that flowering pervasiveness (the proportion of dipterocarp species participating) was high and similar in all three GF events. However, relative flowering magnitudes (measured by an index of individual tree participation and flowering intensity in *Shorea* species) were 2, 5 and 8 for the 2001, 2002 and 2005 GF events, respectively.

4 The percentage of *Shorea* seeds surviving pre- and post-dispersal predation increased with the magnitude of GF events, which is consistent with the first prediction.

5 Pre-dispersal insect seed predators consumed 12.9%, 11.2% and 3.4% of *Shorea* seeds in the 2001, 2002 and 2005 GF events, respectively, which is consistent with both predictions.

6 Pre-dispersal seed predation by primates (mainly leaf monkeys) increased from 11.9% to 38.6% then fell to 9.3% in the 2001, 2002 and 2005 GF events, respectively.

7 Predator satiation occurred only at population and community levels. At the individual tree level there was no relationship between the percentage of seeds surviving pre- and post-dispersal seed predation and variation in seed crop size or seed density beneath the tree. This suggests that attempts to test the PSH on the scale of individual trees may miss key community level effects.

8 Our results suggest a more significant role of pre-dispersal seed predation in the evolution of reproductive synchrony than was recognized in the original statement of the PSH.

Key-words: Dipterocarpaceae, flowering phenology, general flowering event, lowland dipterocarp forest, Pasoh, post-dispersal seed predation, predator satiation, pre-dispersal seed predation, *Shorea*

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Introduction

Trees of the family Dipterocarpaceae are among the most abundant members of the canopy and emergent layers of the hyper-diverse, aseasonal, humid lowland tropical forests of Southeast Asia (Ashton 1988). A striking feature of these forests is that many species, especially dipterocarps, flower gregariously and fruit synchronously at irregular multi-year intervals, a phenomenon known as general flowering (GF). Many tree species of other plant families also synchronize their reproduction with the dipterocarps during GF years (Medway 1972; Appanah 1985; Ashton *et al.* 1988; Sakai *et al.* 1999; Yasuda *et al.* 1999).

Hypotheses to explain the GF phenomenon have been both proximate, about the environmental cues that trigger GF events, and ultimate, about the evolution of reproductive synchrony by natural selection. The proximate triggers for GF events have not yet been established conclusively (Ashton *et al.* 1988; Yasuda *et al.* 1999; Sakai *et al.* 2006). Several ultimate hypotheses, including the resource matching hypothesis (Kelly 1994), the post El Niño-Southern Oscillation (ENSO) seedling release hypothesis (Williamson & Ickes 2002), the pollination enhancement hypothesis (Sakai 2002) and the predator satiation hypothesis (PSH) (Janzen 1974) have been proposed to explain the evolution of the GF phenomenon. The resource matching hypothesis is that plant reproduction depends on a tree's internal resource reserve and that individual trees require a certain time period to accumulate sufficient resources to support reproduction. Once a threshold is crossed, plant reproduction is triggered by environmental cues. The post-ENSO seedling release hypothesis is that GF events are coupled to ENSO events because ENSO events are usually followed by favourable (wet) conditions for seedling survival and establishment. The pollination enhancement hypothesis is that synchronized flowering attracts nomadic pollinators (giant honeybees) and allows populations of resident pollinators to increase and hence increases pollination success.

The most widely accepted ultimate explanation for GF is Janzen's predator satiation hypothesis. There are two components to this hypothesis: (i) selection for flowering at long and irregular intervals to drive down populations of seed predators, and (ii) selection for synchrony in seed fall, such that too many seeds are dropped in too short a time for all to be consumed by seed predators, allowing a greater fraction of seeds to escape by germinating and growing out of the predation-vulnerable stages. According to the PSH, selection acts against regular annual fruiting because annual reproduction supports the uninterrupted year-to-year build-up of seed predator populations (*numerical response*). Testing the PSH is complicated because generalized predators can also switch from alternative food sources to seeds during GF events in the absence of a population numerical response (*functional response*). Such functional responses can also select for greater synchrony within a

given GF event, but by themselves they cannot select for irregular, multi-year separation of GF events.

Janzen's original predator satiation hypothesis focused on seed predation after seed fall ('post-dispersal' predation). At the post-dispersal stage, the most important seed predators in lowland dipterocarp forests are relatively long-lived, ground dwelling mammals including bearded pigs (*Sus barbatus*), wild boars (*Sus scrofa*), pig-tailed macaques (*Macaca nemestrina*), and several species of squirrels and other rodents (Miura *et al.* 1997; Corlett 1998; Curran & Leighton 2000; Curran & Webb 2000; Ickes 2001; Ickes *et al.* 2001). These species all have generalized diets of fruits and seeds. However, Southeast Asian rain forest trees also often suffer heavy 'pre-dispersal' predation on flowers and immature seeds while they are still attached to the parent tree.

Pre-dispersal seed predation, although not emphasized in Janzen's original PSH, may also be important. If losses to pre-dispersal seed predation are heavy, such losses could lower the capacity of the GF event to satiate post-dispersal seed predators, whether or not pre-dispersal seed predators are satiated. In contrast to post-dispersal predators, most pre-dispersal seed predators are insects, such as weevils, bark beetles and moths (Toy 1991; Toy & Toy 1992; Ghazoul *et al.* 1998; Lyal & Curran 2000; Lyal & Curran 2003; Nakagawa *et al.* 2005). These pre-dispersal insect seed predators lay their eggs in the flowers or in immature fruits of early stage and the larvae develop inside the seed ovary as fruit mature. They are relatively host-specific, attacking at most a few closely related species in the same genus (Toy 1991; Toy & Toy 1992). Many have short generation times and can exhibit numerical responses to seed availability by increasing their population sizes several fold within a single year (Toy 1991; Toy & Toy 1992). However, not all pre-dispersal predators are insects (Curran & Leighton 2000). Vertebrate pre-dispersal seed predators recorded in Southeast Asian dipterocarp forests include several species of squirrels, long-tailed parakeets (*Psittacula longicauda*), red leaf monkeys (*Presbytis rubicunda*), dusky leaf monkeys (*Presbytis obscurus*), orang-utans (*Pongo pygmaeus*) and hornbills (*Buceros rhinoceros*) (Gould & Andau 1989; Corlett 1998; Curran & Leighton 2000; Curran & Webb 2000).

Our test of the PSH was conducted in the 50-ha Forest Dynamics Plot (Kochummen *et al.* 1990) in Pasoh Forest Reserve, Negri Sembilan, Malaysia. Two relatively weak, back-to-back GF events occurred only 9 months apart in this forest in August 2001 (2001 GF) and April 2002 (2002 GF). A third larger GF event occurred in April 2005 (2005 GF). In this paper, we focus only on the GF behaviour of dipterocarp species because of the central role hypothesized for dipterocarps in the GF phenomenon, and because not all of the seeds of non-dipterocarp species in the Pasoh forest can yet be identified.

We took advantage of this natural experiment (variably sized GF events with different temporal spacing) to address several key questions. (i) How variable are GF events in the proportion of dipterocarp species that

participate in the GF event, in the proportion of individuals of a given species that participate and, at the tree level, in the proportion of each tree crown that participates in flowering and fruiting? (ii) Does the rate of pre-dispersal and post-dispersal predation vary among species and among the three GF events? (iii) If so, is there evidence for numerical and/or functional responses among the pre- and post-dispersal seed predators, as predicted?

Methods

STUDY SITE

The Pasoh Forest Reserve (2°58'47"N, 102°18'29"E) includes 2450 ha of lowland dipterocarp forest. There are oil palm plantations on three sides of the Reserve, but the forest is connected to continuous hill dipterocarp forest along the fourth side. The present study took place within a 50-ha forest dynamics plot, which was established in the centre of a core area of 600 ha of primary lowland dipterocarp forest in 1989. All stems ≥ 1 cm in trunk diameter at breast height (d.b.h.) were mapped to the nearest 0.5 m, measured to the nearest mm, and identified to species in 1987, 1990, 1995, 2000 and 2005. The initial census included more than 320 000 individuals belonging to 814 species, 294 genera and 78 families (Kochummen *et al.* 1990).

FLOWERING PHENOLOGY OF DIPTEROCARPACEAE

We conducted a whole-plot survey of the reproductive status of all dipterocarp trees ≥ 30 cm d.b.h., which included 28 species, and 936, 936 and 876 individuals in the 2001, 2002 and 2005 GF events, respectively. Two other dipterocarp species present in the plot were excluded. *Hopea mengerawan* was excluded because its adults mature at smaller sizes than the 30 cm d.b.h. cut-off. *Neobalanocarpus hemii* was excluded because it flowered frequently but did not drop its seeds during the GF events when this study was conducted. We used binoculars to score the flowering commitment of each tree to reproduction on a five-point scale. Sterile trees that lacked flowers were scored zero. Trees bearing flowers over 1–25%, 26–50%, 51–75%, or 76–100% of their crown were scored 1, 2, 3 and 4, respectively. We used these data to evaluate pervasiveness, intensity and commitment of flowering and fruiting for all dipterocarp trees in the three GF events. Flowering pervasiveness is the proportion of dipterocarp species that participate in the GF event (at least one individual scoring ≥ 1). Flowering intensity is the proportion of individuals of a given species that participate (score ≥ 1). Species-level flowering commitment is the proportion of species in which more than 50% of individuals flowered (score ≥ 1). Individual-level flowering commitment is the percentage of individuals in which more than 50% of the crown flowered (score ≥ 3).

We estimated the relative flowering magnitudes of the three GF events as the sum of flowering commitments of all trees surveyed, divided by the magnitude of the smallest GF event in 2001. There were 60 fewer large dipterocarp trees in the 2005 GF event. For this reason, we used the sum of flowering commitment over trees instead of the mean to represent relative levels of community-wide seed production. A strong correlation was found between flowering commitment and seed production in *Shorea* species based on unpublished seed trap data ($n = 12$ species; $r^2 = 0.90, 0.72$ and 0.98 for 2001, 2002 and 2005 GF, respectively). Thus, flowering commitment is a good surrogate of seed production and provides a legitimate basis for comparing rates of seed predation.

PRE-DISPERSAL SEED PREDATION

We quantified pre-dispersal seed predation for focal trees for all species of the genus *Shorea* section *mutica* having five or more qualifying individuals in February 2002, September 2002 and August 2005 (for the 2001, 2002 and 2005 GF events, respectively). Focal trees for this study bore flowers over $> 75\%$ of their crowns (commitment category 4) and were located at least 30 m from the nearest flowering conspecific to minimize overlap in seed shadows. Several species lacked five qualifying individuals for the smaller 2001 (*S. lepidota* and *S. maxwelliana*) and 2002 (*S. macroptera* and *S. parvifolia*) GF events and were excluded for these GF events.

We established eleven 1-m² quadrats within 3 days of peak seed fall for each focal tree. One, one, two, three and four quadrats were located at randomly chosen angles and at distance intervals of 0–2, 2–4, 4–6, 6–8 and 8–10 m from the focal tree, respectively. Fruiting phenologies of focal trees were monitored daily to ensure that all quadrats were established within three days of peak seed fall. To estimate pre-dispersal seed predation, we collected all seeds and diaspore remains present in these quadrats once. We sorted this material into six categories based on germination status and mortality agent: germinated seedlings, intact seeds, and seeds killed by primates, rodents, beetles or fungi. We found no evidence of pre-dispersal seed predation by insects other than beetles. We were able to distinguish mortality agents as follows. Primate seed predators consume seeds on trees and drop the outer shells, these empty shells with clear primate teeth marks often littered the ground. Rodents gnaw on seeds and leave distinctive teeth marks on any remaining endosperm. Beetles either left an exit hole or the larva was present inside the seed. We classified seeds that were black and mouldy outside and/or inside as killed by fungi.

We dissected all intact seeds and seeds believed to be dead to verify assignment to these six categories. Additional reasons for confidence in the assignments follow. Beetles oviposit on immature, developing fruits and the developing larvae usually consume the seeds entirely and leave distinct exit holes when emerging. This is easily distinguished from the post-dispersal damage caused

by chewing insects that attack dispersed seeds from the outside. We can discount oviposition and emergence on dispersed seeds because germination occurs within 3 days of dispersal, which is too short a time for larval development. Moreover, the damage types assigned to pre-dispersal predators were routinely encountered in weekly censuses of seeds in 336 seed traps suspended 80 cm above the ground on a PVC frame, whereas the damage types assigned to post-dispersal predators were not. For these reasons, we are confident in the assignment of damage types to pre-dispersal vs. post-dispersal seed predators.

Pre-dispersal predation by primates was problematic to assign definitively. Although direct observation lead us to believe the great majority of empty shells with teeth marks were opened by leaf monkeys (and hence these seeds were assigned to pre-dispersal predation by primates), it remains possible that other arboreal mammals might have caused similar damage.

POST-DISPERSAL SEED FATE

To study the fate of seeds after dispersal, we placed one 1-m² quadrat within each 2-m wide annular ring around each focal tree, out to a distance of 10 m (five quadrats per tree). The same focal trees used to quantify pre-dispersal seed predation were again used for the post-dispersal seed predation study. Every third day, each newly fallen seed in these quadrats was marked with a coloured wooden stick labelled with a numbered bird-band. The status of all previously marked seeds was also checked. We classified the fate of each marked seed as follows: (i) germinated, (ii) disappeared, (iii) killed by rodents (iv) killed by ants (v) killed by other insects, or (vi) killed by fungi. Seeds that disappeared were assumed to have been removed and eaten by ground foraging mammals. The seeds of *Shorea* section *mutica* are not cached by mammals because they usually germinate 1 or 2 days after falling. Seeds that disappeared were pooled with the seeds killed by rodents to estimate post-dispersal seed predation by mammals. Seeds killed by ants were covered by soil, while seeds killed by other insects had distinct holes burrowed into the outer surface of the seed. Seed fall for *Shorea* section *mutica* was limited to 5 weeks in the 2001 and 2002 GF and 9 weeks in the 2005 GF. We monitored seed fate every 3 days or until all seeds died or germinated for the 2002 and 2005 GF and for the first 4 weeks of the 2001 GF. We divide the *Shorea* section *mutica* seed fall period into four, five and nine 7-day periods for several analyses for the 2001, 2002 and 2005 GF events, respectively.

ANALYSES OF SEED PREDATION AND SURVIVAL

We performed a two-way analysis of variance to investigate the effect of GF year and tree species on the percentage of seeds lost to pre-dispersal predation by beetles, primates, rodents and fungi. The proportion of seeds lost was calculated for each quadrat and averaged within trees.

We also performed a two-way analysis of variance to investigate the effect of GF year and tree species on the proportion of seeds lost to post-dispersal predation by mammals, ants, other insects and fungi. Proportions were arcsine square root transformed to meet the assumptions of the analysis.

We performed a multiple linear regression analysis to evaluate the effect of distance from focal trees (0–2 m, 2–4 m, 4–6 m, 6–8 m and 8–10 m), seed density, and the seasonal timing of seed fall (the 7-day periods described under *Methods: post-dispersal seed fate*) for post-dispersal seed predation. The multiple linear regression analysis used seed predation rate as the dependent variable and distance from focal trees, seed density and timing of seed fall as independent variables. All statistical analyses were carried out in SAS (SAS Institute 2003).

To calculate overall seed survival or the proportion of seeds that survived both pre- and post-dispersal predation, we multiplied the proportion of seeds surviving pre-dispersal predation by the proportion of seeds surviving post-dispersal predation for each species using means over individuals. We defined a survival ratio as the ratio of overall seed survival in 2005 to overall seed survival in 2001. For species that did not reproduce in 2001, the survival ratio was calculated as the ratio of overall seed survival in 2005 to overall seed survival in 2002.

Results

PERVASIVENESS AND INTENSITY

All three GF events were characterized by relatively high pervasiveness. At the species level, 75.0%, 85.7% and 85.2% of the species with individuals larger than 30 cm d.b.h. flowered in the 2001, 2002 and 2005 GF events, respectively (Fig. 1a). However, there was a large difference in the intensity of flowering among GF events. Over all species, 19.8%, 35.7% and 65.1% of dipterocarp individuals flowered during the 2001, 2002 and 2005 events, respectively (Fig. 1b). Furthermore, species flowering commitment, which was measured as the percentage of species having more than 50% of individuals flowering, increased from 23.1% in 2001 GF to 63.6% in 2005 GF (Fig. 1c).

The levels of individual tree commitment to reproduction also varied among GF events. The percentage of reproductive trees that flowered over more than 50% of their crowns was 56.1%, 75.4% and 86.1% for the 2001, 2002 and 2005 GF events, respectively (Fig. 1d). Relative flowering magnitude was 2, 5 and 8 for the 2001, 2002 and 2005 GF events, respectively.

PRE-DISPERSAL SEED PREDATION

We measured pre-dispersal seed predation rates with sample sizes of 7760, 10 217 and 22 835 freshly fallen seeds in the 2001, 2002, and 2005 GF events, respectively. Significant heterogeneity existed in the percentage of

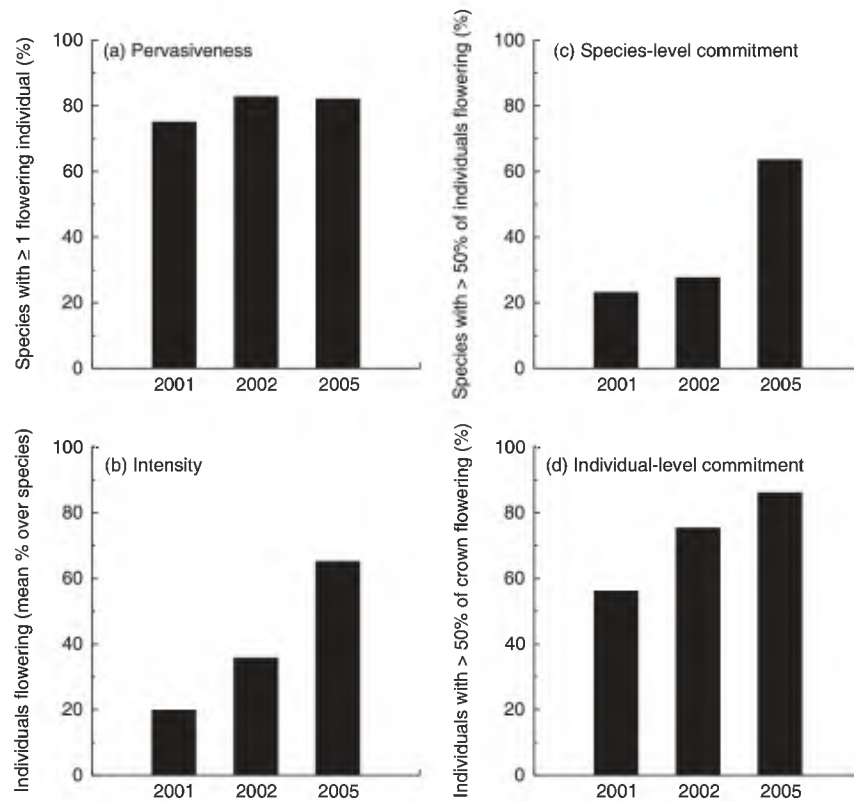


Fig. 1 Community-wide comparison of dipterocarp flowering in three general flowering events for the Pasoh Forest Reserve, Malaysia. (a) Pervasiveness is the percentage of dipterocarp species that flowered in the general flowering event. (b) Intensity is the percentage of individuals that flowered averaged over species. (c) Species-level commitment is the percentage of species for which more than 50% of the individuals flowered. (d) Individual-level commitment is the percentage of reproductive individuals for which more than 50% of their crown flowered during the general flowering event.

Table 1 Two-way analyses of variance for the effect of general flowering year and *Shorea* species on the proportion of seeds killed by different pre- and post-dispersal seed predators. Sample sizes are 96 and 76 trees for pre-dispersal and post-dispersal predation, respectively

Pre-dispersal seed predation				Post-dispersal seed predation			
Cause of mortality	Source	F-Ratio	Probability $\geq F$	Cause of Mortality	Source	F-Ratio	Probability $\geq F$
Beetles	Year	15.71	<0.0001	Mammal	Year	81.9	<0.0001
	Species	8.47	<0.0001		Species	1.62	0.1674
Primates	Year	38.13	<0.0001	Ants	Year	3.62	0.03
	Species	19.0	<0.0001		Species	0.76	0.5789
Rodents	Year	67.84	<0.0001	Other insects	Year	72.94	<0.0001
	Species	1.71	0.1409		Species	0.56	0.7265
Fungi	Year	9.38	0.0002	Fungi	Year	235.71	<0.0001
	Species	1.87	0.1068		Species	2.46	0.0414

pre-dispersal seed predation among species and among GF events (Table 1). Across all species, the percentage of pre-dispersal seed survival was always highest in the third and largest 2005 GF event (Table 2). For *S. acuminata* and *S. leprosula*, which flowered in all three GF events, the percentage of pre-dispersal seed survival increased monotonically with the pervasiveness and intensity of the GF event (Table 2).

At the community level, pre-dispersal insect seed predators consumed 12.9%, 11.2% but only 3.4% of *Shorea* seeds in the 2001, 2002 and 2005 GF events, respectively (Table 3). However, pre-dispersal seed predation by primates, mainly leaf monkeys, increased

from 11.9% to 38.6% then fell to 9.3% in the 2001, 2002 and 2005 GF events, respectively (Fig. 2). Other pre-dispersal predators such as squirrels and other rodents consumed 17.1%, 6.3% and c. 0% in the 2001, 2002 and 2005 GF events, respectively (Fig. 2). Pre-dispersal fungal attack killed 14.2% and 8.9% of all seeds in 2001 and 2002 GF events, respectively, and then increased to 17.5% in the 2005 event (Fig. 2), compensating in part for the reduced mortality from rodents. Of all freshly fallen seeds examined, 43.8%, 34.9% and nearly 70% were still alive and had not been attacked by pre-dispersal seed predators in the 2001, 2002 and 2005 GF events, respectively.

Table 2 Variation among species and general flowering events in pre- and post-dispersal seed survival and their product or overall seed survival. Entries are mean percentages (± 1 SE) calculated over trees. n is the number of trees. The survival ratio is the ratio of total percentage survival in 2005 divided by total percentage survival in 2001. For species that did not reproduce in 2001, the survival ratio denominator was total percentage survival in 2002

<i>Shorea</i> species	Year	n	Means percentage survival rate			
			Pre-dispersal survival (%)	Post-dispersal survival (%)	Total survival (%)	Survival ratio
<i>S. acuminata</i>	2001	8	52.3 \pm 5.6	15.9 \pm 6.8	7.4 \pm 2.3	1.0
<i>S. acuminata</i>	2002	6	60.1 \pm 4.6	36.1 \pm 4.2	22.3 \pm 2.9	3.0
<i>S. acuminata</i>	2005	5	81.5 \pm 2.3	75.2 \pm 8.1	61.9 \pm 8.0	8.4
<i>S. leprosula</i>	2001	7	34.3 \pm 3.3	41.9 \pm 7.6	14.7 \pm 2.6	1.0
<i>S. leprosula</i>	2002	6	43.2 \pm 6.5	24.4 \pm 4.5	10.2 \pm 1.6	0.7
<i>S. leprosula</i>	2005	5	77.8 \pm 2.4	71.4 \pm 5.7	56.0 \pm 5.8	3.8
<i>S. lepidota</i>	2002	4	10.5 \pm 4.7	40.3 \pm 11.0	5.4 \pm 3.4	1.0
<i>S. lepidota</i>	2005	5	76.9 \pm 7.3	64.8 \pm 6.4	51.6 \pm 8.4	9.6
<i>S. macroptera</i>	2001	4	28.5 \pm 7.5	16.6 \pm 2.9	4.5 \pm 1.0	1.0
<i>S. macroptera</i>	2005	5	80.5 \pm 1.6	62.1 \pm 4.8	49.9 \pm 3.6	11.1
<i>S. maxwelliana</i>	2002	5	16.4 \pm 2.9	34.4 \pm 7.3	5.9 \pm 1.3	1.0
<i>S. maxwelliana</i>	2005	5	35.6 \pm 4.4	56.6 \pm 10.0	21.7 \pm 5.6	3.7
<i>S. parvifolia</i>	2001	4	49.5 \pm 6.5	32.3 \pm 10.6	15.5 \pm 2.8	1.0
<i>S. parvifolia</i>	2005	5	66.7 \pm 2.6	72.1 \pm 4.1	47.8 \pm 2.6	3.1

Table 3 Percentages of seeds killed by pre- and post-dispersal predators and overall seed survival for three general flowering events. Overall seed survival is estimated as the product of pre- and post-dispersal survival. Entries in the table are mean percentages calculated over trees (± 1 SE for total seed survival only)

	Pre-dispersal predation (%)			Total post-dispersal predation (%)	Total seed survival (%)
	Beetles	Primates	Total		
2001 GF	12.9	11.9	56.2	73.3	11.3 \pm 1.5
2002 GF	11.2	38.6	65.1	68.3	11.6 \pm 1.6
2005 GF	3.4	9.3	30.2	32.9	48.2 \pm 3.3

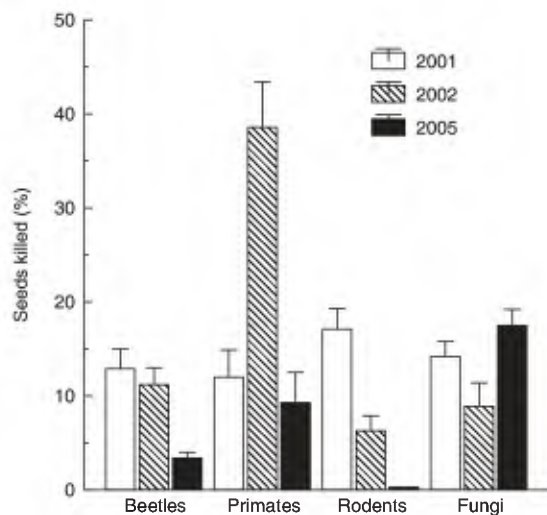


Fig. 2 Pre-dispersal predation by beetles, primates, rodents and fungi of *Shorea* seeds produced during the 2001, 2002 and 2005 general flowering events in Pasoh Forest Reserve, Malaysia. Values are means (± 1 SE) across species.

POST-DISPERSAL SEED PREDATION

We recorded post-dispersal seed predation rates using sample sizes of 1841, 1810 and 5484 fallen seeds in all

plots that escaped pre-dispersal seed predation in the 2001, 2002 and 2005 GF events, respectively. Natural seed densities on the ground varied from < 1 seed m^{-2} to > 50 seeds m^{-2} among the eleven 1-m^2 plots under each tree crown. As with pre-dispersal seed predation, we analysed post-dispersal predation at the level of individual trees, species and the entire *Shorea* community.

Multiple linear regression analyses indicated that post-dispersal seed predation was not related to seed density beneath individual trees (Fig. 3) nor to distance to focal trees (data not shown) in any of the three GF events. However, a temporal trend in post-dispersal predation beneath individual trees was detected (significant partial regression coefficients at $P < 0.001$ for the 2001 GF event and at $P < 0.05$ for both the 2002 and 2005 GF events). In the 2001 and 2002 GF events, the percentage of post-dispersal seed predation increased as the season of seed fall progressed (Fig. 4). In the 2005 GF, this pattern was reversed and the percentage of post-dispersal seed predation decreased later during the period of seed fall (Fig. 4).

Post-dispersal seed predation differed significantly among the three GF events for each type of seed predator (Table 1). Post-dispersal seed predation also differed significantly among species for seed lost to fungi (Table 1).

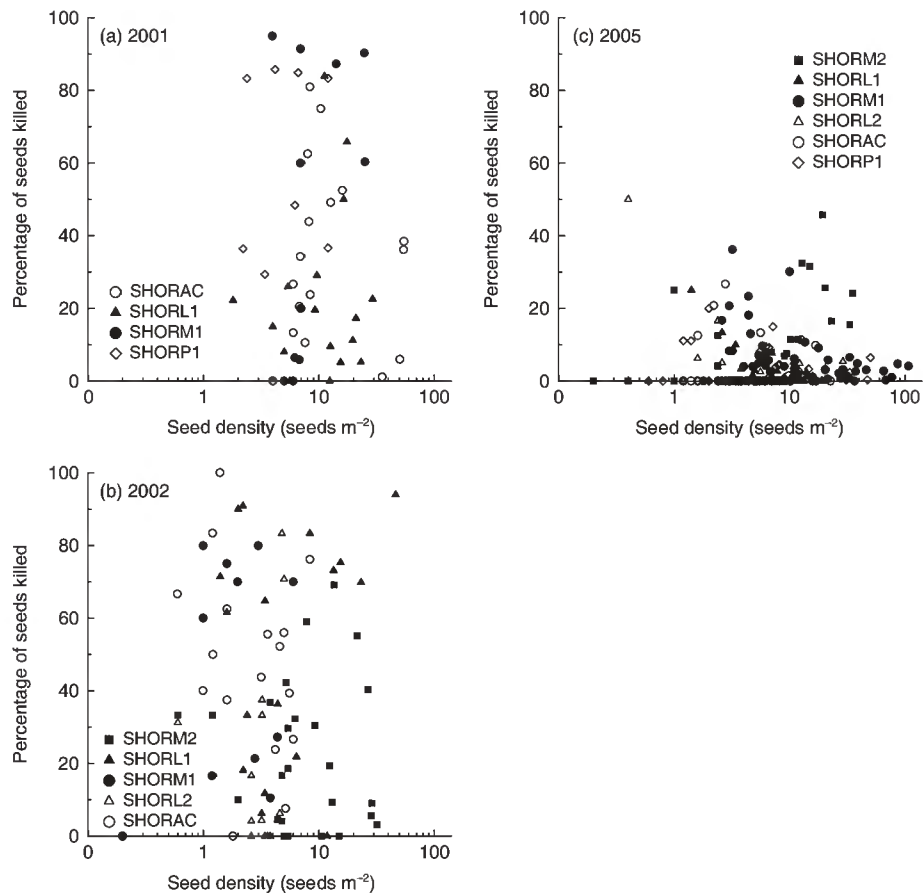


Fig. 3 Relationships between levels of post-dispersal predation of *Shorea* seeds and seed density for the (a) 2001, (b) 2002 and (c) 2005 general flowering events. Each symbol represents one focal tree at one weekly census. Species mnemonics are SHORAC for *S. acuminata*, SHORL1 for *S. leprosula*, SHORL2 for *S. lepidota*, SHORM1 for *S. macroptera*, SHORM2 for *S. maxwelliana*, and SHORP1 for *S. parvifolia*.

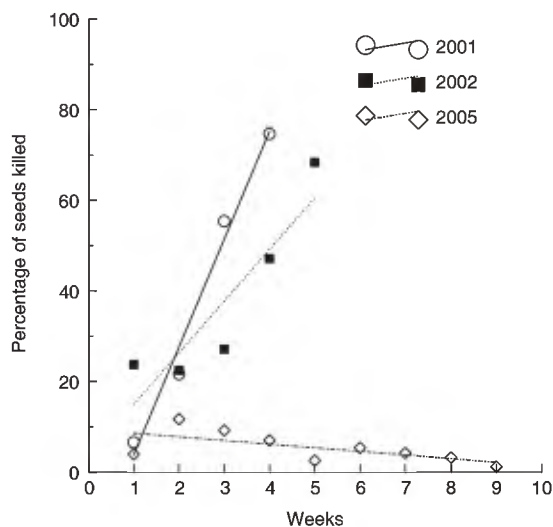


Fig. 4 Relationships between post-dispersal predation of *Shorea* seeds and the timing of seed fall for three general flowering events in Pasoh Forest Reserve, Malaysia. The horizontal axis divides the entire period of *Shorea* seed fall into consecutive 7-day intervals. *Shorea* seeds fell for five (we have data for the first four only), five and nine 7-day periods during the 2001, 2002 and 2005 general flowering events, respectively. The percentage of seeds killed was averaged over all species. Fitted lines are ordinary least squares regression lines.

At the level of the genus *Shorea*, there were no significant differences in the weekly or total percentage of post-dispersal seed predation between the first two GF events: the mean percentage loss per week was $35.2\% \pm 13.3\%$ (mean ± 1 SE) during the 5 weeks of peak seed fall in the 2001 GF event, and $36.1\% \pm 8.9\%$ in the 2002 GF event. However, the mean percentage loss per week was $4.6\% \pm 1.1\%$ in the 2005 GF event, which is significantly lower than in the previous two GF events. If we include seed predation from all categories of post-dispersal seed predators, the total seed loss was 73.3%, 68.3% and 32.9% in the 2001, 2002 and 2005 GF events, respectively (Table 3).

OVERALL SEED SURVIVAL

We multiplied the percentages of pre- and post-dispersal seed survival to estimate overall seed survival (Table 2). Overall seed survival was greatest in the 2005 GF event for every species. However, there was considerable variation among species in the degree to which overall seed survival was elevated, as revealed by the ratio of the mean percentage seed survival in 2005 to mean percentage seed survival in 2001 (or 2002 for species that reproduced in 2002 but not in 2001) (Table 2). At the

low end, three species (*S. leprosula*, *S. maxwelliana* and *S. parvifolia*) exhibited 3- to 4-fold increases in percentage seed survival. However, the other three species (*S. acuminata*, *S. lepidota* and *S. macroptera*) all exhibited more than an 8-fold increase in percentage seed survival, with the greatest increase in the large-seeded *S. macroptera* (11.1-fold increase). Thus, the latter three species gained proportionally more in the 2005 event relative to the former three species.

Discussion

We can now return to our initial questions. (i) How variable are GF events in pervasiveness (fraction of species flowering), intensity (fraction of individuals flowering) and commitment (proportion of individual crowns flowering)? The GF events at Pasoh varied greatly in intensity and commitment to reproduction, but varied little in pervasiveness at the species and community level. Several previous studies of dipterocarp flowering phenology have documented that the intensity (fraction of trees participating) in GF events can be highly variable (Yap & Chan 1990; Sakai *et al.* 1999; Curran & Leighton 2000; Numata *et al.* 2003; Maycock *et al.* 2005; Nakagawa *et al.* 2005). These studies did not report pervasiveness (fraction of species participating) because in many cases the sample sizes of individuals was quite small for most species. Based on the levels of commitment of more than 900 individuals of 28 dipterocarp species, the magnitude of the 2005 GF event was 4.0 times stronger than the 2001 GF event, and 2.5 times stronger than the 2002 GF event. A second, more inclusive measure, based on seed rain of both dipterocarp and non-dipterocarp species, indicates that the magnitude of the 2005 GF event was 8.7 and 2.1 times larger than the 2001 and 2002 GF events, respectively (Y.Y.C. and colleagues, unpubl. data).

(ii) Does the rate of pre-dispersal and post-dispersal predation vary among species and among the three GF events? Our findings indicate that it does. Although all species exhibited higher per capita rates of escape from seed predators in the largest of the three GF events (2005) than in the previous two weaker events (2001 and 2002), some species benefited much more than others.

(iii) Is there evidence for either numerical and/or functional responses among the pre- and post-dispersal seed predators as predicted? The original statement of the predator satiation hypothesis (PSH) posited an interaction between numerical responses of seed predators and the spacing of GF events. Numerical responses require actual changes in population density due to mortality, recruitment and migration. We lack such data for any pre- or post-dispersal seed predator. Nevertheless, differences in pre-dispersal seed predation between the 2001 GF and the 2002 GF are suggestive of a numerical response among beetles and a functional response among leaf monkeys. Pre-dispersal insect seed predators consumed more than twice as many seeds in the 2002 GF than in the 2001 GF (Table 4). The short generation

Table 4 The relative number of *Shorea* seeds consumed by three types of seed predators during three general flowering events at the Pasoh Forest Reserve, Malaysia. Entries are the total number of *Shorea* seeds consumed by each predator divided by the number consumed in the smallest general flowering event in 2001

	General flowering event		
	2001	2002	2005
Pre-dispersal insect predation	1	2.2	1.1
Pre-dispersal primate predation	1	8.0	3.1
Post-dispersal mammal predation	1	1.7	1.1

times of many insects suggests a numerical response is possible with adults emerging from seed during the 2001 GF laying eggs just 9 months later during the 2002 GF. In contrast, leaf monkeys, which consumed eight times more seeds in the 2002 GF than in the 2001 GF, are unlikely to have undergone a numerical response because generation times are much longer and immigration is unlikely because these monkeys are territorial and Pasoh is isolated on three sides. T. Yasuda (pers. comm.) recorded a switch in the diet in leaf monkeys at Pasoh between the 2001 GF and the 2002 GF, from leaves to seeds, with a strong preference for *S. maxwelliana* seeds. There was no further sign of a numerical or functional response in the leaf monkeys in 2005 because they consumed the same absolute number of seeds in both the 2002 and 2005 GF events. Because we lack data on the population densities of seed predators, our results fall short of a definitive test of the PSH.

At the individual tree level, we found no correlation between variation in seed density beneath individual tree crowns and the proportion of seeds removed by post-dispersal seed predators (Fig. 3). This result is consistent with Curran & Webb (2000), but contrasts with the finding of Maycock *et al.* (2005). Maycock *et al.* (2005) found a positive short-term relationship between post-dispersal seed survival and seed density manipulated experimentally beneath individual tree crowns in a lowland dipterocarp forest in Sepilok Forest Reserve, Sabah. We found no such relationship in our natural experiments in which seed density actually varied more among individual trees than in the experiment of Maycock *et al.* (2005). The lack of correlation between seed survival and seed density in our study occurred because ground-foraging predators removed virtually all seeds beneath a fruiting tree once they found them. Thus, our study provides no support for predator satiation at the level of individual trees, but only at the population and community levels.

Janzen (1974) argued that the dominance of the dipterocarps in these forests was due to the differential escape of seeds of dipterocarps from seed predation due to general flowering accompanied by masting. Based on long-term seed trap records from Pasoh (Y.Y.C. and colleagues, unpubl. data), seeds produced by the

dipterocarps represented 55.6%, 30.4% and 47.8% of the total number of seeds plus fruits captured in the 2001, 2002 and 2005 GF events, respectively. However, even in the large 2005 GF event, more than half of all seeds were produced by non-dipterocarp species. Exactly how these species affected pre- and post-dispersal predation on dipterocarp seeds remains unclear. Curran & Leighton (2000) reported that arboreal, vertebrate pre-dispersal seed predators, such as leaf monkeys, preferred seeds of non-dipterocarp species over dipterocarps in Gunung Palung National Park, West Kalimantan (Indonesian Borneo). Because so many species of non-dipterocarps reproduce in synchrony with dipterocarps during general flowering events, it seems unlikely that general flowering alone will explain the dominance of the dipterocarps.

Forest vertebrate faunas are changing rapidly throughout Southeast Asia in response to unsustainable levels of hunting and forest fragmentation (Corlett 1998, 2007), and the Pasoh Forest Reserve is no exception. The native pig (*Sus scrofa*) has been hyper abundant at Pasoh in the recent past (Ickes 2001). Ickes (2001) hypothesized that the loss of tigers and possibly leopards and/or provisioning by adjacent oil palm plantations contributed to this hyper abundance. The adjacent oil palm plantation was cut down in November 2001, and the numbers of native pigs declined by an order of magnitude between July 2001 and February 2002 (S.J.W. unpubl. data). Emigration was responsible for the decline as corpses were not evident. By 2005, the number of native pigs declined even further due to the combined effects of food shortage and poaching. We only encountered one native pig nest in the whole 50-ha plot during the flowering phenology survey in the 2005 GF. By contrast, we encountered 10 or more active pig nests during flowering phenology surveys in the 2001 and 2002 GF events (Y.Y.C. pers. observ.). Oil palm was replanted in May 2004 and should begin to fruit within 5 years; however, plantation workers also constructed a ditch and fence around the Pasoh Forest Reserve in 2004 to prevent native pigs from raiding future oil palm crops. Hopefully, the extreme hyper-abundance of native pigs documented by Ickes (2001) will not recur. The crash in pig numbers occurred before seed fall associated with the 2001 GF. Thus, this study is not compromised by the hyper-abundance of native pigs reported by Ickes (2001). Nevertheless, pig numbers might have been higher than in undisturbed forests. A long-term monitoring program of the pig population is needed to fully understand the impact of native pigs on seed predation in this forest.

This study supports two predictions of the predator satiation hypothesis advanced by Janzen (1974) to explain the evolution of general flowering events. First, the proportion of *Shorea* seeds killed by pre-dispersal insect seed predators was greatest during the weakest GF event in 2001 and when a stronger GF event occurred just 9 months later in 2002. Second, the proportion of *Shorea* seeds killed by all pre- and post-dispersal seed

predators was least when a GF event occurred 3 years after the previous GF event and also involved the greatest levels of seed production. Our study also suggests that pre-dispersal predation may be a more important selective force for reproductive synchrony in GF events than was realized when the predator satiation hypothesis was originally proposed (Janzen 1974). Between 30% and 65% of all seeds were consumed by pre-dispersal seed predators in three GF events. Pre-dispersal seed predation reduces the total seed rain in the community, which reduces the capacity of the community to satiate post-dispersal seed predators. This in turn should increase selection for greater synchrony in seed rain to increase the level of satiation of the post-dispersal seed predators, and thereby increase rates of seed survival.

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