SHORT COMMUNICATION

Abundance of insect seed predators and intensity of seed predation on *Shorea* (Dipterocarpaceae) in two consecutive masting events in Peninsular Malaysia

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The family Dipterocarpaceae includes 470 tree species from 13 genera in South and South-East Asian tropical forests (Ashton 1982). Many dipterocarp species in aseasonal lowland rain forests of western Malesia flower synchronously during masting (or general flowering) events, which usually occur at irregular intervals of 2–10 y (Ashton *et al.* 1988). Very few individuals flower at other times, and successful recruitment of seedlings is limited to those masting events (Ashton *et al.* 1988, Curran *et al.* 1999).

Several hypotheses have been advanced to explain the evolution of this spectacular reproductive phenology. The leading hypothesis concerns seed survival through the satiation of seed predators (Curran *et al.* 1999, Janzen 1974). The predator satiation hypothesis posits reductions in the abundance of generalist seed predators during multi-year intervals between masting events followed by satiation of the remaining seed predators by massive, synchronous seed production during these events. The effectiveness of satiation should increase with

the length of the inter-masting period and the intensity of seed production during masting.

Although many animals, both vertebrates and invertebrates, eat dipterocarp seeds (Curran & Leighton 2000, Sun *et al.* 2007), pre-dispersal seed predation by insects is a major mortality factor for dipterocarp seeds (Nakagawa *et al.* 2005, Sun *et al.* 2007). Insect seed predation lowers the total seed crop in the community, which reduces the capacity of the community to satiate post-dispersal seed predators (Sun *et al.* 2007). Therefore, insect seed predation might have a strong impact on recruitment of dipterocarps and may play an important role in promoting masting behaviour in dipterocarps.

The length of the inter-masting period is highly variable; flowering has on occasion been reported in consecutive years. Examples include 1997–1999 in Sarawak, Borneo (Sakai 2002), 2001–2002 in Sabah, Borneo (Brearley *et al.* 2007), 2001–2002 in Peninsular Malaysia (Numata *et al.* 2003) and 2004–2005 in Sarawak, Borneo (Kishimoto-Yamada & Itioka 2008). Fruiting in consecutive years would limit the potential to satiate seed predators if their populations were to build up between occurrences of masting (Sakai 2002). This possibility has never been evaluated for insect seed predators because their population dynamics have never

been documented across multiple masting events in dipterocarp forests.

We studied two masting events that occurred just 7 mo apart in the Pasoh Forest Reserve ($2°59'$N, $102°18'$E), Peninsular Malaysia, to test the following sub-hypotheses derived from the seed predator satiation hypothesis; two temporally close masting events allow the population of insect seed predators to increase, and consequently, seed predation is more severe in the second masting event than in the first.

The two masting events occurred from late August 2001 to February 2002 (M01) and from April 2002 to September 2002 (M02). Plant reproductive phenology at a 50-ha plot of the reserve was monitored since 20 August 2001 with 247 seed traps (0.5 m² each). Flowers and fruits that fell into the traps were collected, identified and counted weekly (only presence was recorded for flowers). Flowering intensity was larger in M02 than M01; 75.0% and 85.7% of dipterocarp species and 19.8% and 35.7% of dipterocarp individuals ($\geq$30 cm dbh) flowered in M01 and M02, respectively (Sun *et al.* 2007). A strong masting event occurred 65 mo before M01 in March 1996 (Numata *et al.* 2003).

We sampled 41 and 36 focal trees of five and six *Shorea* (Dipterocarpaceae) species that fruited heavily in M01 and M02, respectively (Table 1). Newly fallen fruits with green stalks were haphazardly sampled beneath the focal fruiting trees every week throughout each fruiting period. Fruiting lasted 16 wk, from November 2001 to February 2002 during M01, and 21 wk, from April 2002 to September 2002 during M02. 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 frequently, collected adult insects as they emerged and added about 1.0 ml of water every week. Four weevil species, *Nanophyes shoreae* Marshall (Nanophyidae: Coleoptera), Nanophyid sp. 1, *Alcidodes dipterocarpi* Marshall, *Alcidodes humeralis* Heller (Curculionidae: Coleoptera), and one moth species, *Andrioplecta shoreae* Komai (Tortricidae: Lepidoptera), were abundant among the *Shorea* species examined; they comprised 94.6% of the 2144 and 97.0% of the 1655 insect predators that emerged in M01 and M02, respectively (Hosaka *et al.* 2009). These predators are known to be specialists on *Shorea* and other genera in Dipterocarpaceae (Lyal & Curran 2000, Robinson *et al.* 2001, Toy 1991, cf. Nakagawa *et al.* 2003). We focused on the abundances of these five predator species.

Each fruit used for insect rearing was dissected after 4-mo rearing in order to assess the cause of seed death. The length of the rearing period was sufficient since all of the adult weevils and moths emerged within 2 mo after fruit sampling. If any trace of predation in a seed without germination was observed (e.g. frass of predators,

oviposition/emergence holes), we regarded the seed as 'killed by insects'.

In estimation of seed production, let S_{wtp} equal the number of seeds of plant species p encountered in trap t in week w. Then the number of seeds of species p encountered in trap t in a masting event is as follows:

$$S_{pt} = \sum_w S_{ptw} \qquad (1)$$

We used a Wilcoxon signed-rank test and the 247 values of S_{pt} to evaluate the null hypothesis that seed production was equal in M01 and M02 for each plant species. In estimation of predator abundance, we used the weekly data on the number of insect individuals per seed, which has been published in Hosaka *et al.* (2009), with that on the number of fallen seeds. Let E_{ipw} equal the average number of individuals of insect species i that emerged as adults per seed of plant species p collected in week w. To estimate numbers of insect species i for each trap t (N_{it}), we multiplied E_{ipw} by values of S_{ptw} for the same week and finally summed over plant species and weeks. Thus,

$$N_{it} = \sum_w \sum_p (S_{ptw} \times E_{ipw}) \qquad (2)$$

We used a Wilcoxon signed-rank test and the 247 values of N_{it} to evaluate the null hypothesis that abundances were equal in M01 and M02 for each insect species. In estimation of the intensity of seed predation, let P_{fpw} equal the proportion of seeds collected beneath focal tree f of plant species p that were killed by any insect species in week w. To estimate the proportion of seeds killed by insects for each focal tree and plant species (M_{fp}), we multiplied weekly values of P_{fpw} by the number of seeds of plant species p encountered in traps in the same week ($\sum_t S_{ptw}$), summed over weeks, and standardized by the total number of seeds of species p. Thus,

$$M_{fp} = \sum_w \left(P_{fpw} \times \sum_t S_{ptw} \right) \Big/ \sum_w \sum_t S_{ptw} \qquad (3)$$

We used a standard t-test and values of M_{fp} for focal trees to evaluate the null hypothesis that the M_{fp} values were equal in M01 and M02 for *S. acuminata*, *S. leprosula* and *S. macroptera*. These three species fruited strongly in both events (Table 2). Focal trees with >100 seeds sampled in total and with >5 sampling weeks were included in this analysis. Fruits aborted before the weekly mean mass reached 15% of the maximum fruit mass of the species (Table 1) were excluded in order to standardize the stage of seed development between masting events. The percentage of seeds killed by insects was low (<10%) in most samples at this stage.

Data were arcsine-transformed and checked for normality and equality of variances by a

Table 1. Focal tree species, numbers of trees and seeds sampled, and size of fruits in two fruiting events (M01 and M02). Fruit mass is represented by the largest mean of fresh fruit masses (wings removed) in weekly samples. Numbers in parentheses are the numbers of trees used for the comparison in the intensity of seed predation. Dashes indicate species that did not produce seeds.

| Tree species | Section | M01 | | | M02 | | |
		N trees	N seeds	Fruit mass (mg)	N trees	N seeds	Fruit mass (mg)
Shorea acuminata Dyer	*Mutica*	9 (7)	4046	379	6 (4)	1914	381
S. lepidota (Korth.) Bl.	*Mutica*	–	–	–	5	1480	1500
S. leprosula Miq.	*Mutica*	7 (5)	2644	610	5 (5)	2187	687
S. macroptera Dyer	*Mutica*	9 (5)	1393	1400	9 (6)	3130	1310
S. maxwelliana King	*Shorea*	–	–	–	6	2039	343
S. parvifolia Dyer	*Mutica*	12	5001	491	–	–	–
S. pauciflora King	*Brachypterae*	4	928	2500	5	1397	1760

Kolmogorov–Smirnov test and a Levene test, respectively, prior to the t-test.

The total number of *Shorea* seeds trapped was 2.7 times larger in M02 than in M01 (Table 2). The seven focal *Shorea* species comprised 100% and 97.2% of total seed fall of *Shorea*, and 89.9% and 88.8% of total seed fall of dipterocarps in M01 and M02, respectively. As for the three *Shorea* species examined for the intensity of seed predation, *Shorea acuminata* and *S. leprosula* produced significantly more seeds in M02 than in M01 and *S. macroptera* seeded at similar level in both events.

The estimated abundances (mean individuals per trap ± 1 SE) of *Nanophyes shoreae* and nanophyid sp. 1 were significantly higher in M02 than in M01 (*N. shoreae*: 0.20 ± 0.05 (M01) vs. 1.11 ± 0.18 (M02), $z = 6.31$, $P < 0.001$; nanophyid sp. 1: 0.05 ± 0.02 vs. 0.23 ± 0.07, $z = 2.29$, $P = 0.022$). In contrast, the estimated abundances of *Alcidodes dipterocarpi*, *Alcidodes humeralis* and *Andrioplecta shoreae* did not change significantly between the two events (*A. dipterocarpi*: 0.11 ± 0.03 vs. 0.05 ± 0.01, $z = 0.177$, $P = 0.860$; *A. humeralis*: 0.12 ± 0.03 vs. 0.04 ± 0.01, $z = 1.06$, $P = 0.289$; *A. shoreae*: 0.08 ± 0.02 vs. 0.05 ± 0.01, $z = 0.372$, $P = 0.710$). The total abundance of the five predators was 2.6 times higher in M02 than in M01 (0.56 ± 0.13 vs. 1.48 ± 0.24, $z = 4.78$, $P < 0.001$). *Nanophyes shoreae* was the dominant predator species in terms of abundance during both masting events.

The proportion of seeds killed by insects (mean ± 1 SE) was higher for all three species in M02 than M01 (significant for *S. acuminata*: 27.9% ± 2.7% (M01) vs. 43.0% ± 3.9% (M02), $t = 3.12$, df = 9, $P = 0.012$ and *S. leprosula*: 26.7% ± 1.6% vs. 34.8% ± 2.3%, $t = 2.89$, df = 8, $P = 0.020$; but not significant for *S. macroptera*: 34.3% ± 3.9% vs. 48.5% ± 5.0%, $t = 2.14$, df = 9, $P = 0.061$).

This is the first study to document abundances of insect seed predators in dipterocarp masting. However, our study covers only two masting events, which is far from sufficient to generalize our interpretation of observed population dynamics. Population size in insects fluctuates not only by resource limitation but also because of seasonality (Kato *et al.* 2000), stochastic environmental changes (e.g. drought; Kishimoto-Yamada *et al.* 2009), the abundance of natural enemies (Nakamura *et al.* 1988) and other unknown factors (Wolda 1992), even in aseasonal tropical habitats. Therefore, we need to interpret our results carefully and consider the biological and environmental information available.

The total abundance of insect seed predators was 2.6 times greater in M02 than in M01. This is consistent with the possibility that populations of insect seed predators built up between the two masting events, which occurred just 7 mo apart; however, population fluctuations were not consistent among insect species.

The abundances of two nanophyid weevils, *N. shoreae* and nanophyid sp. 1, were 5.4 and 4.2 times greater in M02 than in M01, respectively. Larvae of nanophyid weevils fed on immature seeds and developed rapidly. Most nanophyid adults from M01 emerged in November

Table 2. Seed fall density (mean ± SE) of *Shorea* species in two fruiting events (M01 and M02) and its ratio (M01/M02). Seed densities were estimated from 247 seed traps. The density ratios were very high (represented with '≫1') for two species due to low densities in M01. Comparisons of seed densities among events were made by a Wilcoxon signed-rank test.

Tree species	M01 (seeds m^{-2})	M02 (seeds m^{-2})	M02/M01	Z	P
Shorea acuminata	10.5 ± 4.7	12.7 ± 4.0	1.2	2.08	0.037
S. lepidota	0.0 ± 0.0	3.0 ± 1.6	≫1	4.23	>0.001
S. leprosula	3.9 ± 1.6	15.0 ± 5.4	3.8	5.51	>0.001
S. macroptera	2.4 ± 0.9	1.9 ± 0.7	0.8	0.64	0.522
S. maxwelliana	0.0 ± 0.0	38.3 ± 12.4	≫1	5.58	>0.001
S. parvifolia	7.8 ± 2.8	0.0 ± 0.0	0.0	5.33	>0.001
S. pauciflora	0.3 ± 0.2	1.1 ± 0.6	3.6	1.28	0.202
All *Shorea*	24.9 ± 6.1	73.5 ± 14.0	2.7	5.20	>0.001

and December 2001, well before the fruits from M02 began to develop in April 2002. Thus, nanophyid adults were likely to experience M02 and build up their population.

In contrast, the abundances of two *Alcidodes* weevils, *A. dipterocarpi* and *A. humeralis*, were not significantly different between M02 and M01. This might be related to the timing of a drought and of adult emergence. A drought occurred from mid-January to late February, with only 5.8 mm of rainfall in February 2002 (Chen 2007). Only 26.0% of *A. dipterocarpi* and 33.1% of *A. humeralis*, compared with 98.7% of *N. shoreae* and 96.4% of nanophyid sp. 1, had emerged by mid-January in the laboratory. *Alcidodes* pre-emergence could not survive without watering for 1 mo in the laboratory (Hosaka pers. obs.). Thus, the January–February drought could explain why populations of nanophyid weevils built up between the two masting events and *Alcidodes* weevils did not.

Similarly, the population of *Andrioplecta shoreae* was not significantly different between the flowering events. This species has an alternative host, *Neobalanocarpus heimii* (Dipterocarpaceae), which flowers every year and fruits at almost any time of year at Pasoh (Hosaka *et al.* 2009). *Andrioplecta shoreae* frequently emerged from *N. heimii* during inter-masting periods (Hosaka unpubl. data). The population size of *A. shoreae* may be maintained by *N. heimii*, the second most abundant dipterocarp species at Pasoh (Kochummen 1997), and may be little affected by mast fruiting by other dipterocarps.

Finally, many living weevil larvae, comprising 19.9% and 2.6% of all insect seed predators in M01 and M02, respectively, remained in seeds after 4 mo of rearing although all of the adult insects that emerged did so within 2 mo after the fruits were collected. Some larvae survived more than 1 y in small vials of soil without feeding. Thus, they were presumably in dormancy. Prolonged dormancy is frequent in insect seed predators as a counter-adaptation to hosts with masting behaviour (Hanski 1988). These larvae might skip a long inter-masting period and emerge in response to the same proximate cues that trigger general flowering.

The percentage of seeds killed by insects was greater in M02 than in M01 for all three *Shorea* species, although they fruited at greater or similar levels in M02. The increased total abundance of predators would be one of the reasons for the more severe seed predation experienced by the three *Shorea* species in M02. Another important factor would be host preference of seed predators. A 2.7-fold greater seed production at the community level could have compensated for a 2.6-fold greater predator population if predators had attacked their hosts equally in M02. In fact, *S. maxwelliana*, which produced more than half of all *Shorea* seeds in M02, suffered much lower intensity of seed predation (9.8% on average) than other species (35–49%). This suggests that the increased

seed predator populations in M02 selectively attacked the other *Shorea* species, including the three we examined. Therefore, the species composition of synchronously fruiting trees and the host preferences of the predators would also influence the intensity of seed predation for a particular plant species.

Finally, further research on the population dynamics of insect seed predators across sufficient number of masting events is needed to verify the pattern we observed. Information on life history and host range, especially that concerning how insect seed predators sustain their populations during years in inter-masting periods, remains limited. Such information could hold the key to reveal dipterocarp–seed predator interactions and the net direction of selective forces on the reproductive phenology of dipterocarps.

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