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Fruiting phenology and the survival of insect fruit predators: a case study from the South-east Asian Dipterocarpaceae

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SUMMARY

Nanophyes shoreae is a pre-dispersal weevil fruit-predator of some species in the Dipterocarpaceae. The dipterocarps typically mass flower at supra-annual intervals, with sporadic flowering events involving a few trees of a reduced number of species in the intervening periods. The hypothesis is tested that *N. shoreae* populations are maintained between mass-fruiting events by recruitment during sporadic fruiting. A record of flowering among 143 dipterocarps of 27 species is reported in Pasoh Forest Reserve, West Malaysia from May 1985 to July 1987. A quantitative analysis of *N. shoreae* pre-imaginal survival is described in one of the five sporadic flowering events that occurred. The primary mortality factors were abscission of fruit containing eggs and consumption by vertebrates of fruit containing pupae and third instar larvae. Overall the percentage of *N. shoreae* eggs that developed to produce adult weevils varied from 0 to 1.8%. This survival is low compared with that of other fruit predators. Thus, sporadic fruiting does not greatly boost *N. shoreae* populations between mass-flowering events and the key to the survival of this weevil lies elsewhere. The implications of this low recruitment for the evolution of mass flowering are discussed.

1. INTRODUCTION

In the rain forests of South-east Asia the Dipterocarpaceae may amount to more than 50% of the large trees (Fox 1967; Walton *et al.* 1952). These trees mass flower at intervals of two to twenty-one years with sporadic flowering in the intervening periods (Barnard 1956; Wood 1956; Burgess 1972; Cockburn 1975; Tamari 1976). Soon after anthesis, dipterocarp fruit are attacked by ovipositing weevils in the genera *Alcidodes* (Curculionidae) and *Nanophyes* (Apionidae) (Toy 1988, 1991). The larvae feed on the endocarp while the fruit continues to develop. About the time of pupation the now inviable fruit fall from the tree; adult weevils emerge soon after (Daljeet-Singh 1974; Burgess 1975; Toy 1988).

The weevil predators of dipterocarp fruit have never been recovered from any other source (Toy 1988). Given the irregular and frequently lengthy periods between mass-flowering events, how do the weevils survive between these events? To understand this problem it is important to determine the significance of sporadic flowering to the maintenance of *Nanophyes shoreae* populations. This information may also indicate the forces maintaining mass flowering, for if weevil population recruitment occurs during sporadic flowering, weevils would capitalize on such flowering thus exerting a selective pressure favouring intermittent mass flowering. Contrarily, if sporadic flowering results in little predator recruitment, the weevils will avoid sporadic flowering trees inferring that mass flowering is maintained by other forces.

In this paper data on the pre-imaginal survival of *N. shoreae* during sporadic fruiting in Pasoh Forest Reserve, West Malaysia (2° 59′ N, 102° 18′ E) are presented. The frequency of fruiting is described for a 27-month period from July 1985 to May 1987, during which no mass flowering occurred, and the data are discussed in relation to the importance of sporadic flowering for the survival of this fruit predator and the evolution of its hosts' phenology.

2. METHODS

The survival of *Nanophyes shoreae* was determined by collecting fruit beneath dipterocarp trees using 1 m^2 plastic traps. The traps were placed before anthesis and left until no fruit remained on the tree. They excluded post-dispersal fruit predators and enabled the collection of very immature fruit that are hard to detect in the leaf litter on the forest floor. Six to ten traps were positioned beneath the flowering portions of each tree and emptied every three to four days. When emptying the traps, the contents of all those from one tree were combined and processed together.

The fruit in each collection were counted and a sub-

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sample of up to 50 were dissected. Pre-imaginal *N. shoreae* were extracted and stored in 75% alcohol. Subsequently, larval head-capsule widths were measured to determine the instar. Estimates of the weevil population within each collection were made by multiplying the dissection results by the inverse of the fraction of the collection that was dissected.

In addition to intact fruit, collections contained fragments of fruit 'nut' (pericarp) and loose calyx wings left over from pre-dispersal, vertebrate predation. Cotyledon adhering to nut fragments distinguished fruit that had not contained insect predators from those that had. Often this cotyledon was scored by tooth marks. Only nut apex fragments were counted, thereby avoiding duplicate counting of the same fruit. The number of extraneous wings exceeded the number of nuts in the collections. These excess wings were assumed to be from fruit in which vertebrates had completely consumed the nut or had removed it from the tree. It was also assumed that the probability of a nut being removed from the tree was independent of whether or not that fruit was previously attacked by an insect predator. The number of larvae destroyed by predators was then estimated by the equation

$$L = V + (A \times B),$$

where L is the number of weevil larvae destroyed by vertebrates, V is the number of fruit collected that had been attacked by both vertebrates and insects, A is the number of fruit nuts removed from the tree as deduced by the excess number of wings, and B is the proportion of collected nuts attacked by insects.

Fruit remaining in each collection after the subsample had been taken for dissection were stored to rear out the fruit predators. Stored fruit were kept in ventilated containers and examined weekly. Emerged predators and parasitoids were killed, set and stored.

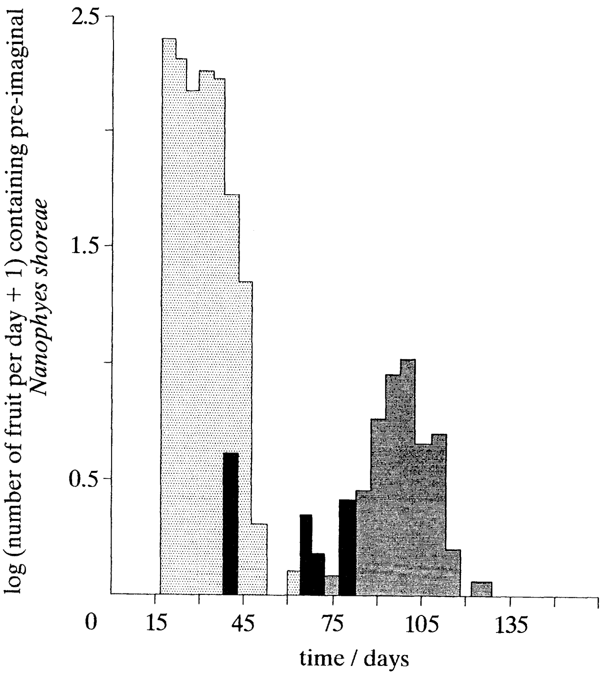

Figure 1. Abscission of fruit containing pre-imaginal *Nanophyes shoreae* from *Shorea macroptera*, tree 177. Day 5 is 24 August 1986, the date of peak anthesis. ▭, Fruit containing eggs; ■, fruit containing I or II instar larva; ▨, fruit containing III instar larva or pupa.

Usually *N. shoreae* adults emerged from fruit after they fell to the ground. The fruit traps intercepted falling fruit, thus preventing post-dispersal predation. To determine the effect of post-dispersal predation on pre-dispersal, pre-imaginal predators, freshly fallen fruit were removed from 20 traps, individually labelled and placed in 1 m^2 quadrats on the forest floor. To aid relocation of the labelled fruit all other litter was removed from the quadrats. Every five to seven days the labelled fruit were sought, searching around and within the quadrats. The fate of each fruit was recorded including whether those relocated showed signs of vertebrate attack; the fruit were then returned to the positions in which they had been found.

The abundance of fruiting trees was determined in a phenological survey among 143 trees of 27 dipterocarp species. All the trees were large for their species. The survey was conducted over a two-day period, initially at two-week intervals and subsequently at monthly intervals. The visible crown was examined using binoculars and the ground beneath was inspected for fallen flower buds, spent corollas or fruit.

3. RESULTS

(*a*) *Qualitative description of pre-imaginal sources of mortality*

Many fruit containing eggs were aborted early in their development (figure 1). Dissection of such fruit stored for periods of 3, 5, 10, 15 and 20 days showed that none of the eggs in these fruit produced larvae. Fruit abortion was the apparent source of mortality; no egg parasites were found.

Four sources of larval mortality were identified. (i) Abortion of fruit containing I and II instar larvae. Adult *N. shoreae* did not emerge from fruit collections in which III instar larvae (or pupae) were absent at collection, even when I and II instars were present. Adult *N. shoreae* did emerge from subsequent fruit collections containing both II and III instars indicating that for successful development, larvae must enter at least the II, and probably the III, instar before their host fruit are aborted. (ii) Cannibalism. Some fruit contained more than one egg but none contained more than one larva, indicating cannibalism. (iii) Parasitism. Hymenoptera, primarily of the families Braconidae, Ichneumonidae and Chalcidae, were reared from collections of fruit, and ecto-parasitic larvae were found attached to III instar *N. shoreae* larvae. (iv) Vertebrate predation of fruit containing pre-dispersal insect predators. Vertebrate predation began shortly before the abscission of fruit containing III instar *N. shoreae* larvae. The tooth marks scored in cotyledon fragments showed rodents to be among the predators, and Prevost's Squirrel (*Callosciurus prevostii* Desmarest) and Plantain Squirrel (*C. notatus* Boddaert) were occasionally seen handling dipterocarp fruit. Fruit containing larvae or pupae were also attacked by vertebrates on the ground.

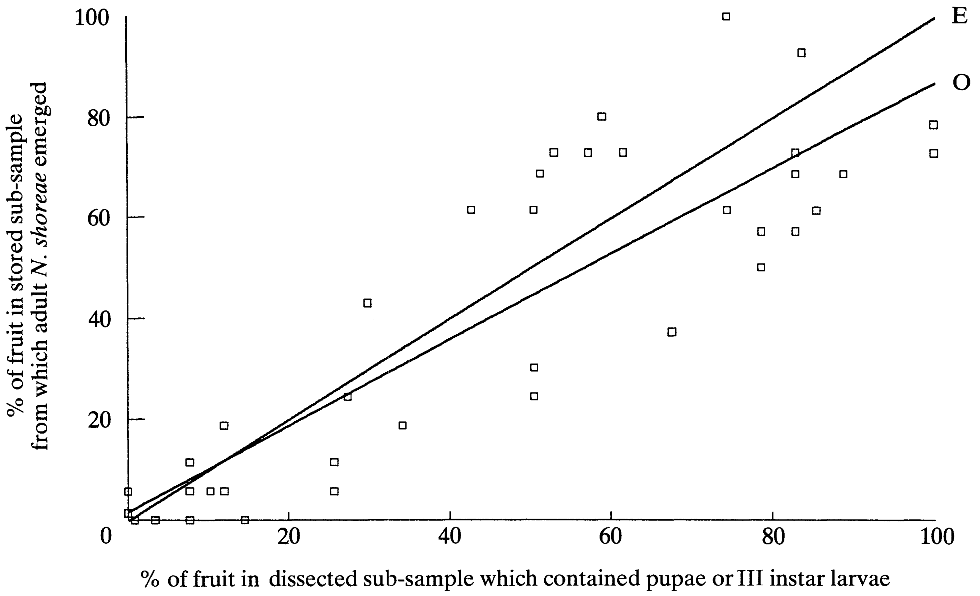

Figure 2. The relationship between the percentage of fruit containing III instar larvae or pupae of *Nanophyes shoreae* and the percentage from which adults emerged. O = observed regression, $y = 1.25 + 0.903x$; E = expected relationship, $y = x$.

Table 1. *Nanophyes shoreae mortality and survival in Shorea macroptera, tree 177*

(Data from dissections of fruit collected in traps.)

	number of fruit containing:							
		larval instar						
collection days[a]	egg	I	II	III	pupa	exit hole[b]	parasitoid	number of larvae destroyed by vertebrates[c]
0–17	0	0	0	0	0	0	0	0
17–21	979	0	0	0	0	0	0	0
21–25	803	0	0	0	0	0	0	0
25–29	582	0	0	0	0	0	0	0
29–34	903[d]	0	0	0	0	0	0	0
34–38	683	0	0	0	0	0	0	0
38–43	263[d]	6	10	0	0	0	0	0
43–47	86[d]	0	0	0	0	0	0	0
47–53	6	0	0	0	0	0	0	0
53–60	0	0	0	0	0	0	0	0
60–64	1	0	0	0	0	0	0	0
64–68	5	2	3	0	0	0	0	0
68–72	0	0	2	0	0	0	0	0
72–77	0	0	0	1	0	0	0	0
77–83	0	4	4	0	0	0	0	0
83–88	0	0	3	9	0	0	0	11
88–93	0	0	4	24	0	0	0	35
93–98	0	2	0	32	9	6	1	16
98–103	0	0	1	31	16	4	1	16
103–108	0	0	0	15	3	4	3	67
108–113	0	0	0	17	3	3	1	53
113–118	0	0	0	3	0	4	2	45
118–122	0	0	0	0	0	2	0	14
122–129	0	0	0	1	0	1	1	11
129–136	0	0	0	0	0	2	0	3
136–143	0	0	0	0	0	2	2	6
143–155	0	0	0	0	0	1	0	0
155–166	0	0	0	0	0	2	0	2
166–174	0	0	0	0	0	1	1	1
174–183	0	0	0	0	0	1	0	1
Total	4311	14	27	131	31	33	12	281

[a] Collection day: day 0 is 19 Aug 1986, date of peak anthesis is day 5.

[b] Exit hole: adult *Nanophyes shoreae* emerged before the fruit fell from the tree.

[c] Number of larvae destroyed by vertebrates: numbers calculated by the equation in the Methods section.

[d] Some fruit within these collections contained more than one egg; total number of eggs in all collections was 4467.

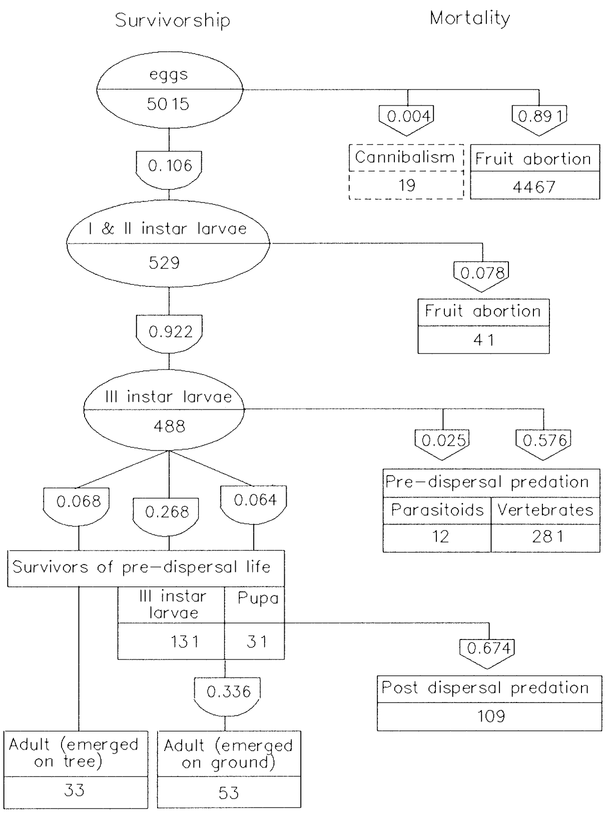

Figure 3. *Nanophyes shoreae* mortality in *Shorea macroptera*, tree 177. ▽, proportional mortality; ⬭, proportional survival.

Larval and pupal developmental failures were examined using fruit collections from which at least 30 fruit were dissected and a further 30 stored. The percentage of dissected fruit containing *N. shoreae* pupae and III instar larvae was compared with the percentage of stored fruit from which *N. shoreae* adults emerged (figure 2). The regression equation:

$$\%\ \text{emergents} = 1.25 + 0.903\ (\%\ \text{pupae} + \text{III instar larvae})$$

is not significantly different from the line (% emergents = % pupae + III instar larvae) that would indicate no pupal or III instar larval developmental failure ($t = -1.33$, d.f. $= 42$, $p \gg 0.05$).

(*b*) *Quantitative analysis of pre-imaginal mortality factors*

Detailed survival analyses were made on pre-imaginal populations in five *Shorea macroptera* Dryer trees during a fruiting event in 1986. An example of the data obtained is given in table 1 and illustrated in figure 3. The numbers in solid rectangles (figure 3) were taken directly from the dissection or ground experiment results; all other numbers have been back-calculated from these results. The figure for cannibalism (dashed rectangle) is an approximation made from the proportion of multiply oviposited fruit in the fruit rain. Cannibalism has to be approximated because there are no remains after cannibalism and yet it must exist because fruit containing more than one egg occur but fruit containing more than one larva do not. A summary of weevil mortality occurring before fruit are dispersed is shown in table 2. Pre-dispersal survival varied from 0 to 4.2%. The primary cause of mortality was abortion of fruit too immature to sustain pre-imaginal development; in one tree (tree 180) this factor alone accounted for the complete failure of *N. shoreae* reproductive effort.

Data from the experiment to determine predation of pre-imaginal *N. shoreae* on the ground have been analysed only for the period over which the pre-imagines were vulnerable. This period was calculated as the time between the mean date of abortion of fruit containing III instar larvae or pupae, and the mean date of adult emergence from stored fruit; it was 21 days. In the ground predation experiment, 531 fruit fell during the critical period; 136 of these were attacked within 21 days and a further 222 ‘disappeared’. The ground around the experimental quadrats was carefully searched indicating that the ‘disappeared’ fruit had been actively removed rather than rolling out of the quadrats. Thus, predators attacked or removed 136 + 222 = 358 fruit (67%). Of the 136 fruit attacked by post-dispersal predators, but not removed from the quadrats, only one subsequently produced an adult *N. shoreae*. The fate of the 222 fruit removed from the quadrats is not known; they may have been consumed. However, Ashton (1982) reported caches of dipterocarp fruit and subsequent clumps of seedlings where these hoardes were forgotten, so some larvae in the removed fruit may have survived. Thus, 67% may overestimate post-dispersal mortality.

Survival of *N. shoreae* before fruit abscission was greatest in tree 179 in which 0.6% of eggs produced adult *N. shoreae* that emerged on the tree and a further 3.6% of eggs produced viable pre-imagines that would have been subject to 67% post-dispersal vertebrate predation. Thus, overall *N. shoreae* pre-imaginal sur-

Table 2. *Mortality of pre-imaginal Nanophyes shoreae in Shorea macroptera trees during a flowering event in 1986*

vulnerable stage:	egg		larva		larva/pupa	overall
mortality factor:	fruit abortion	cannibalism	fruit abortion	parasitoids	pre-dispersal vertebrate predation	pre-dispersal survival
tree number						
177	89.1	3.5	7.8	2.5	59.0	3.9
178	94.8	0	3.9	2.4	13.2	3.7
179	92.6	0	11.0	3.1	42.0	4.2
180	99.8	0	100.0	0	0	0
74	98.6	0	2.9	3.1	15.9	1.1

Table 3. *Record of flowering phenology among the dipterocarps surveyed*

(Flowering events: A, 7 Aug.–30 Oct. 1985; B, 13 Feb.–2 Oct. 1986; C, 8 Jly 1986; D, 13 Sep.–5 Dec. 1986; E, 13 Mar.–21 May 1987.)

		number of trees flowering					
		flowering event					
species	number of trees surveyed	'A'	'B'	'C'	'D'	'E'	Total
Anisoptera curtisii	4	0	0	0	0	0	0
A. laevis	3	0	0	0	0	0	0
A. megistocarpa	1	0	0	0	0	0	0
Dipterocarpus cornutus	13	2	0	0	5	9	16
D. costulatus	2	0	0	0	2	2	4
D. crinitus	4	3	0	0	4	4	11
D. kunstleri	4	4	0	0	3	4	11
D. sublamellatus	12	0	0	0	4	4	8
Hopea dryobalanoides	—	—	—	—	a	—	—
H. mengerawan	7	5	0	0	0[a]	0	5
H. pubescens	1	0	0	0	0	0	1
Neobalanocarpus heimii	8	2	0	0	3	0	5
Parashorea densiflora	4	0	2	0	0	0	2
Shorea acuminata	6	6	0	0	0	2	8
S. bracteolata	3	2	0	0	0[a]	1	3
S. dasyphylla	2	0	0	0	0	0	0
S. hopeifolia	—	—	—	—	a	—	—
S. lepidota	7	3	0	0	0	1	4
S. leprosula	8	4	0	0	1	1	6
S. macroptera	15	7	0	0	4	9	20
S. maxima	1	0	0	0	0	0	0
S. maxwelliana	9	0	0	0	2	0[a]	2
S. multiflora	3	0	0	0	0[a]	2	2
S. ochrophloia	5	1	0	0	0	0	1
S. ovalis	3	2	0	0	0	0[a]	2
S. parvifolia	7	4	0	0	3	0	7
S. pauciflora	7	3	0	0	0	0[a]	3
Vatica bella	3	2	0	0	0	2	4
V. odorata	1	0	0	1	0	0	1

[a] Trees discovered flowering during the course of the study but not included in the survey.

vival will have varied between *S. macroptera* trees from 0 (table 2) to $0.6+(3.6(1-0.67))=1.8\%$.

(*c*) *The phenology survey*

There were five flowering events during the study. Species of dipterocarps flower sequentially and a flowering event has been defined as the period from the first flowering to the start of a four-week period during which no new trees come into flower. The events were: 'A', 7 Aug–30 Oct. 1985; 'B', 13 Feb–10 Mar. 1986; 'C', 8 Jly 1986; 'D', 13 Sep.–15Dec. 1986; 'E', 13 Mar.–21 May 1987. The number of flowering trees is shown in table 3. No additional flowering events were observed among trees not included in the survey but some additional species were observed flowering during events 'D' and 'E' (table 3).

4. DISCUSSION

To evaluate the importance of sporadic flowering to the maintenance of *N. shoreae* populations, it is necessary to determine the extent to which the results of this study can be extrapolated.

There were five dipterocarp fruiting events during the study, three of which involved species that are hosts of *N. shoreae*. However, a 27-month study is short compared with dipterocarp flowering patterns and the results of the phenology survey may therefore be atypical. Low rainfall, or some factor associated with it, may trigger dipterocarp flowering (Burgess 1972; Ng 1977; Whitmore 1984; Ashton *et al.* 1988). By examining the rainfall during the study period with respect to the variance in rainfall during an extended period, the typicality of rainfall during the study (and by supposition of dipterocarp flowering) can be assessed (figure 4). The probabilities of total monthly rainfall as high or low as that observed (figure 4) were calculated from the differences between mean monthly rainfall (1951–1980) and observed monthly rainfall (1985 and 1986) in terms of each month's standard deviation from the mean monthly rainfall in the 1951–1980 period. In both 1985 and 1986, three months were dry to an extent that would not be

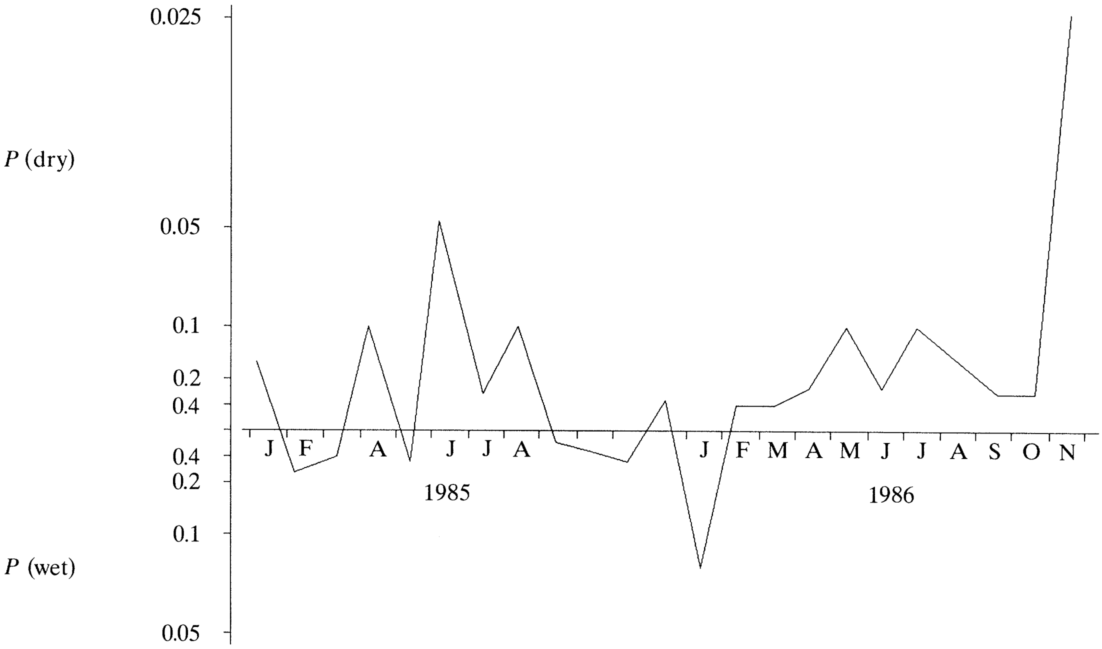

Figure 4. The probability of the rainfall record observed during the study (see text for explantation). *P* (dry) = probability of a result as dry (or dryer) than that observed; *P* (wet) = probability of a result as wet (or wetter) than that observed.

expected more than one year in ten. Thus, 1985 and 1986 were particularly dry years and flowering may therefore have occurred unusually frequently.

Given the diversity and spatial variability of tropical forest, to what extent can results from five trees in one species during one sporadic fruiting event be extrapolated to overall weevil population recruitment during sporadic fruiting events? *N. shoreae* feeds on several dipterocarp species (Toy 1991), but during the events studied, flowering *S. macroptera* were more abundant and *S. macroptera* fruit development was greater than in any other host species. *N. shoreae* pre-imaginal survival in other host species was not studied quantitatively, but very few fruit containing larvae were collected and, as in *S. macroptera*, adults did not emerge from fruit collections containing eggs. Thus, in the three fruiting events in which *N. shoreae* population recruitment occurred (events 'A', 'D' and 'E'), it was greatest through development of *S. macroptera* fruit crops. Different dipterocarp species flower with varying frequencies and *S. macroptera* is among the species that flower most frequently (S. K. Yap, personal communication); thus these observations may be generally applicable.

Given that fruiting of host dipterocarps may have been unusually frequent during this study, and given that fruit development in *S. macroptera* trees was more extensive than in other host species, the 0–1.8% pre-imaginal survival in *S. macroptera* is notably low. Reported figures for the survival of other fruit-predators under field conditions include: *Bruchus brachialis* (Bruchidae), 10.7% survival (Dickason 1960); *Bruchidus ater* (Bruchidae), 4–17.7% (Parnell 1966); *Mimosestes amicus* (Bruchidae), 8% (Mitchell 1977); *Apion fuscirostre* (Apionidae), 'very low' to 6.3% (Parnell 1966); and *Pseudanthonomus hamamelidis* (Curculionidae) 20% survival (De Steven 1981). The studies of Dickason (1960), Parnell (1966) and Mitchell (1977) were conducted on annually fruiting plant species; the study of De Steven (1981) was also conducted on an annually fruiting species, *Hammamelis virginiana*, but this species shows great inter-annual variability in the number of fruit initiated, a situation more akin to the dipterocarps. Thus, the key to *N. shoreae* survival between mass-fruiting events is unlikely to be sporadic fruiting, inferring the existence of an alternative (undiscovered) host plant, quiescence or diapause of adult weevils.

To further understand *N. shoreae* survival between mass-flowering events a comparison of the significance of mortality factors in sporadic and mass-flowering events is required. In sporadic flowering events the primary source of pre-imaginal mortality is abortion of fruit soon after anthesis. During a mass-flowering event a greater number of fruit mature and thus a greater number of insects must survive early stages of development. Thus, because *N. shoreae* oviposit within the fruit least likely to abort (Toy & Toy 1992), pre-imaginal mortality due to fruit abortion would be expected to be lower during a mass-flowering event. The second most important source of pre-imaginal mortality, predation by pre-dispersal vertebrates, might also be expected to be lower during a mass-flowering event as vertebrate foraging effort will be dissipated among a greater number of fruit.

Pre-dispersal fruit predation has been shown to promote flowering synchrony in other species (Augspurger 1981; Pettersson 1991) and it has been suggested that fruit predation may have led to the evolution of mass flowering in the Dipterocarpaceae but that the predators responsible may no longer exist (Janzen 1974). Evolution aside, fruit predation might currently maintain mass flowering, but to show this it would be necessary to determine the stability of the predator on host interaction and to quantify fruit losses to predators during mass and sporadic fruiting. Neither requirement is logistically possible: the size of the trees prohibits the exclusion experiments that are required to interpret the ecological importance of predation vis-à-vis other sources of crop failure (Stephenson 1984; Auld & Myerscough 1986), and the mass flowering phenology necessitates impractically long-term studies (Chan 1977). However, one inference of low weevil recruitment during sporadic flowering is that weevils that discern which events are sporadic will be at a selective advantage and hence over prolonged periods weevil predation will be expected to decrease during sporadic fruiting events and so will not maintain mass flowering. Other features of dipterocarp phenology lead to the same conclusion; for example, interspecific asynchrony in flowering times is such that *N. shoreae* is able to 'track' the sequence of flowering species (Toy 1991). Thus, even if mass flowering has evolved as a predator satiation strategy it is probably not being maintained in response to pre-dispersal weevil predators.

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REFERENCES

Ashton, P.S. 1982 Dipterocarpaceae. *Flora Malesiana* series 1 (Spermatophyta) **9**(2), 237–552.

Ashton, P.S., Givnish, T.J. & Appanah, S. 1988 Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *Am. Nat.* **132**, 44–66.

Augspurger, C.K. 1981 Reproductive synchrony of a tropical shrub: experimental studies on effects of pollinators and seed predators on *Hybanthus prunifolius* (Violaceae). *Ecology* **62**, 775–788.

Auld, T.D. & Myerscough, P.J. 1986 Population dynamics of the shrub *Acacia suaveolens* (SM) Willd: seed production and predispersal seed predation. *Aust. J. Ecol.* **11**, 219–234.

Barnard, R.C. 1956 Recruitment, survival and growth of timber-tree seedlings in natural tropical rain forest. *Malay. For.* **19**, 156–161.

Burgess, P.F. 1972 Studies on the regeneration of the hill forest of the Malay Peninsula: the phenology of the dipterocarps. *Malay. For.* **35**, 103–123.

Burgess, P.F. 1975 Silviculture in the Hill Forest of the Malay Peninsula. Kuala Lumpur, Malaysian Forestry Department Research Pamphlet **66**.

Chan, H.T. 1977 Reproductive biology of some Malaysian dipterocarps. Ph.D. thesis, University of Aberdeen.

Cockburn, P.F. 1975 Phenology of dipterocarps in Sabah. *Malay. For.* **38**, 160–170.

Daljeet-Singh, K. 1974 Seed pests of some dipterocarps. *Malay. For.* **37**, 24–36.

De Steven, D. 1981 Abundance and survival of a seed-infesting weevil *Pseudanthonomus hamamelidis* (Coleoptera, Curculionidae) on its variable-fruiting host plant, witch-hazel (*Hammamelis virginiana*). *Ecol. Entom.* **6**, 387–396.

Dickason, E.A. 1960 Mortality factors for the vetch bruchid, *Bruchus brachialis*. *J. econ. Entomol.* **53**, 555–558.

Fox, J.E.D. 1967 An enumeration of lowland dipterocarp forest in Sabah. *Malay. For.* **30**, 263–279.

Janzen, D.H. 1974 Tropical blackwater rivers, animals and mast fruiting by Dipterocarpaceae. *Biotropica* **6**, 69–103.

Mitchell, R. 1977 Bruchid beetles and seed packaging by Palo Verde. *Ecology* **58**, 644–651.

Ng, F.S.P. 1977 Gregarious flowering of dipterocarps in Kepong, 1976. *Malay. For.* **40**, 126–137.

Parnell, J.R. 1966 Observations on the population fluctuations and life histories of the beetles *Bruchidus ater* (Bruchidae) and *Apion fuscirostre* (Curculionidae) on broom (*Sarcothemna scoparius*). *J. Anim. Ecol.* **35**, 157–188.

Pettersson, M.W. 1991 Flower herbivory and seed predation in *Silene vulgaris* Caryophyllaceae, effects of pollination and phenology. *Holarc. Ecol.* **14**, 45–50.

Stephenson, A.G. 1984 The cost of over-initiating fruit. *Am. Midl. Nat.* **112**, 379–386.

Tamari, C. 1976 Phenology and seed storage trials of dipterocarps. Kuala Lumpur, Forest Research Institute Malaysia Research Pamphlet, no. 69.

Toy, R.J. 1988 The pre-dispersal insect fruit-predators of Dipterocarpaceae in Malaysian rain forest. Ph.D. thesis, University of Aberdeen.

Toy, R.J. 1991 Interspecific flowering patterns in the Dipterocarpaceae in West Malaysia: implications for predator satiation. *J. trop. Ecol.* **7**, 49–57.

Toy, R.J. & Toy, S.J. 1992 Oviposition preferences and egg survival in *Nanophyes shoreae* (Coleoptera, Apionidae), a weevil fruit-predator in South-east Asian rain forest. *J. trop. Ecol.* **8**. (In the press.)

Walton, A.B., Barnard, R.C. & Wyatt-Smith, J. 1952 The silviculture of lowland dipterocarp forest in Malaysia. *Malay. For.* **15**, 181–197.

Whitmore, T.C. 1984 *Tropical rain forest of the Far East* 2nd edn. Oxford University Press.

Wood, G.H.S. 1956 The dipterocarp flowering season in North Borneo, 1955. *Malay. For.* **19**, 193–201.