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SHORT COMMUNICATION

Chemical defences of fruits and mast-fruiting of dipterocarps

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Mast-fruiting is the intermittent and synchronous production of large fruits by a population of plants at long intervals (Herrera *et al.* 1998, Kelly 1994). Several hypotheses have been proposed concerning the adaptive advantages of mast-fruiting (Janzen 1971, 1974; Kelly 1994), and some field observations have provided evidence for these hypotheses (Norton & Kelly 1988, Shibata *et al.* 1998, Sork 1993). The predator-satiation hypothesis is one well-known explanation for reproductive synchrony in plants and animals (Janzen 1971, 1974; Kelly 1994). This hypothesis claims that mast fruiting at irregular intervals of several years is an effective means of satiating vertebrate fruit predators: low seed production can only support low densities of predators during the periods between mast-fruiting events, but more fruits are produced than predators can consume in masting years (Janzen 1971, Kelly 1994). Thus, it may be said that mast-fruiting is a defence strategy of plants against post-dispersal vertebrate fruit predators.

Many of the species of dipterocarps that dominate tropical rain forests in South East Asia synchronize flowering and fruiting at intervals of 2 to 10 y, but not all species follow this pattern (Ashton 1988, Ashton *et al.* 1988, Burgess

1972, Foxworthy 1932, Symington 1943). For example, Wood (1956) reported that approximately two-thirds of the then-known 200 dipterocarp species in Sabah (North Borneo) flowered in 1955. Similarly, Yap & Chan (1990) observed that the frequencies of fruiting events varied among mast-fruiting species.

Ashton (1988) reported that fruits of dipterocarps are chemically defended by phenolic compounds. Levels of pre-dispersal predation by small rodents were significantly negatively correlated with phenolic concentrations in fruits (M. Yasuda, *pers. comm.*). Thus, it is expected that the accumulation of phenolic compounds in fruits can work as a chemical defence against predation. If predator-satiation occurs during mast-fruiting events, the fruits of species that reproduce only during mast-fruiting years could be expected to contain lower concentrations of defensive chemicals, because the accumulation of phenolic compounds requires plants to pay a physiological cost in terms of their expenditure of carbohydrates, nitrogen and other nutrients (Chew & Rodman 1979).

For these reasons, we hypothesized that species that produce fruits only in mast-fruiting years would produce fruits with lower levels of phenolic compounds than fruits of species with higher fruiting frequencies. The present study focused on the investments in chemical defence exhibited by mast-fruiting species. We examined the relationships between the total phenol concentrations in mature fruits and fruiting frequencies among nine *Shorea* species to test our hypothesis.

The study was conducted in the Pasoh Forest Reserve (2°59′N, 102°18′E) in the state of Negeri Sembilan (Peninsular Malaysia), *c.* 70 km southeast of Kuala Lumpur. Mast-fruiting in Peninsular Malaysia occurred in September 1996. Fruiting of 20 dipterocarp species was observed in the Pasoh Forest Reserve during this mast-fruiting event (M. Yasuda, *pers. comm.*). Tremendous amounts of dipterocarp fruits were dispersed and synchronous germination was observed.

The study species were *Shorea acuminata* Dyer., *S. lepidota* Korth., *S. leprosula* Miq., *S. macroptera* Dyer, *S. maxwelliana* King., *S. multiflora* Sym., *S. ovalis* Korth., *S. pauciflora* King. and *S. parvifolia* Dyer (Dipterocarpaceae). Twenty sound, mature fruits of each species were collected from a single mother tree after the mast-fruiting that occurred from August to September 1996. The fruits were put in paper bags and immediately dried in an oven at 80 °C for 2 d. The dry weights of individual fruits (without sepals) were measured and the fruits with the sepals and pericarp removed were finely powdered for quantitative chemical analyses. The powdered samples of 3–6 fruits were mixed to a single lot to obtain appropriate amounts of samples for Folin–Denis assay. The total phenol concentrations in the mixed samples were measured by extraction with 70% acetone after removing lipids using a Soxhlet extractor. Extraction and centrifugation at 4000 rpm for 10 min were repeated four times. The total phenol concentrations in each extract, pooled for each fruit sample, were determined by the Folin–Denis assay (Waterman & Mole 1994). These procedures were repeated three times.

To evaluate variations in the fruiting frequencies of different species, the data on fruiting years of the nine *Shorea* species from Yap & Chan (1990) were used. Yap and Chan recorded the number of *Shorea* trees that flowered and fruited during the 1973–1983 period at four sites in Peninsular Malaysia (Kepong, Gombak, Ampang and Pasoh), and we counted the fruiting years when at least one tree produced fruits. The number of fruiting years from 1973 to 1983 varied from two to six among the nine *Shorea* species in our study. In 1976, 1981, and 1983, a high proportion of flowering trees produced fruits (87, 79 and 87%, respectively) (Yap & Chan 1990). *Shorea lepidota*, *S. maxwelliana* and *S. pauciflora* had lower fruiting frequencies that strictly corresponded with the species' respective mast-fruiting years. On the other hand, the other six species exhibited four to six fruiting years during the 11-year period except the mast-fruiting years (*S. acuminata*, *S. macroptera*, *S. multiflora*, *S. leprosula*, *S. ovalis* and *S. parvifolia*). Thus, fruiting patterns of each species were classified into two categories of strict and sporadic mast-fruiting species.

All statistical analyses were done using StatView J-4.5 (Abucus Concepts). Variations in the total phenol concentrations across all species and those between strict and sporadic fruiting species were tested using one-way ANOVA. Multiple comparisons of these variables among species were performed using Scheffé's post-hoc test.

Total phenol concentrations in the fruits differed significantly among species that had different fruiting frequencies ($F = 8.09$, $df = 8, 18$; $P = 0.0001$; Table 1). Figure 1 shows relationships between the total phenol concentrations in the fruits and the number of fruiting years during the 1973–1983 period for the nine *Shorea* species. Although strict mast-fruiting species (*S. lepidota*, *S. maxwelliana* and *S. pauciflora*) had significantly lower phenol concentrations in their fruits than the other species ($F = 6.00$, $df = 1, 7$; $P < 0.05$), *S. lepidota* which showed the lowest fruiting frequency had a high phenolic concentration in its fruits (Figure 1, Table 1).

Investments in chemical defences for strict mast-fruiting species (*S. lepidota*, *S. maxwelliana* and *S. pauciflora*) were expected to be low if the effects of predator-satiation at mast-fruiting were significant. In contrast, demands for such

Table 1. Fruit phenolic concentrations and size of nine *Shorea* species. Means ± SE are shown. Means that differ significantly (Scheffé's PLSD method: $P < 0.05$) between species have different superscripts.

Species	Phenolic concentration (mg g^{-1}) n = 3	Fruit size (g) n = 20
Shorea acuminata	84.3 ± 3.9^{ab}	0.37 ± 0.02^{cd}
S. lepidota	74.5 ± 8.7^{ab}	0.92 ± 0.05^{b}
S. leprosula	70.6 ± 3.1^{ab}	0.37 ± 0.02^{cd}
S. macroptera	81.5 ± 10.9^{ab}	0.49 ± 0.03^{c}
S. maxwelliana	32.0 ± 3.3^{c}	0.14 ± 0.01^{d}
S. multiflora	66.2 ± 8.7^{ab}	0.53 ± 0.02^{c}
S. ovalis	87.7 ± 6.3^{a}	0.62 ± 0.07^{c}
S. parvifolia	63.7 ± 3.6^{ab}	0.35 ± 0.02^{cd}
S. pauciflora	45.7 ± 4.1^{bc}	1.32 ± 0.08^{a}

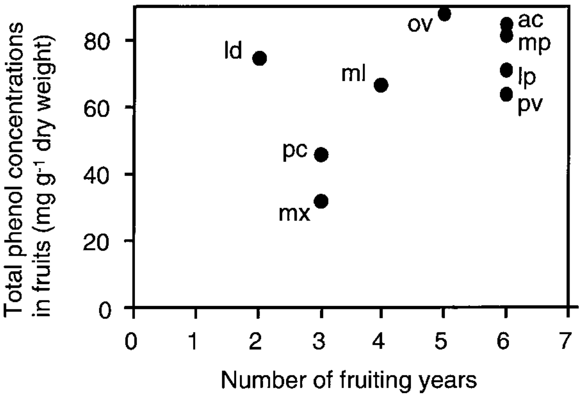

Figure 1. Relationships between the total phenol concentrations in the fruits and the number of fruiting years during the 1973–1983 period for the nine *Shorea* species in the study. Data points indicate individual species, and data for the number of fruiting years were taken from Yap & Chan (1990). Abbreviations for the species name are as follows: ac (*S. acuminata*), ld (*S. lepidota*), lp (*S. leprosula*), mp (*S. macroptera*), mx (*S. maxwelliana*), ml (*S. multiflora*), ov (*S. ovalis*), pv (*S. parvifolia*) and pc (*S. pauciflora*).

defences should increase with increasing fruiting frequency among sporadic mast-fruiting species (the other six species in the study). Indeed, investments in chemical defences tended to increase with the fruiting frequencies, except for the species with the lowest frequency of fruiting, *S. lepidota*. This result would suggest the effects of predator-satiation at mast-fruiting. However, the data for *S. lepidota* apparently contradict the hypothesis since the species with the lowest fruiting frequency invested relatively high levels of resources in the chemical defences of its fruits. This may imply that additional factors beyond predator-satiation determine the defence investment among mast-fruiting species.

There are needs to consider protein contents as well as mass or energy contents to understand the ecological meaning of mast-fruiting (Grubb & Burslem 1998, Grubb *et al.* 1998). One explanation for this assertion is that large fruits may have stronger chemical defences than small fruits. It is widely believed that the optimal foraging strategy for a vertebrate predator to maximize intake of energy per unit of handling time would be to consume larger fruits (Martin 1985). If so, it would be logical to assume that larger fruits would require larger investments in chemical defences than smaller fruits. The mean dry weights of fruits differed among the species in this study, and ranged from 0.137 g (*S. maxwelliana*) to 1.318 g (*S. pauciflora*) ($F = 63.0$, $df = 8, 171$; $P < 0.0001$; Table 1). The dry weight of fruits with the lowest fruiting frequency were significantly heavier than those of the species with more sporadic fruiting (Figure 2, Scheffé's post-hoc test; Table 1). If larger fruits are more susceptible to damage by predators, species that produce larger fruits at lower fruiting frequencies should invest more resources in chemical defence than species that produce smaller fruits. Therefore, if predation depends on fruit size among mast-fruiting species, the species that produce larger fruits should invest their resources in creating higher levels of phenolics in their fruits.

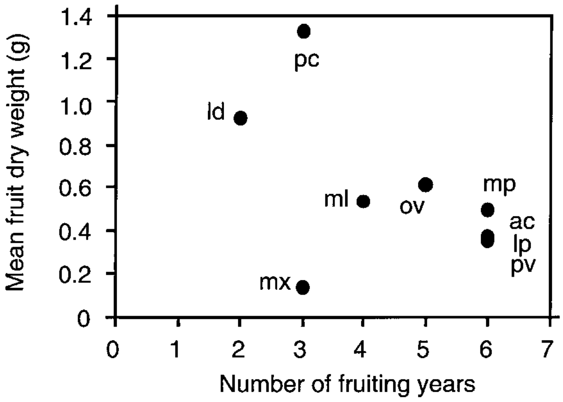

Figure 2. Relationships between the mean dry weights of the fruits and the number of fruiting years during the 1973–1983 period for the nine *Shorea* species in the present study. Data points indicate individual species, and data for the number of fruiting years were taken from Yap & Chan (1990). Species name abbreviations are shown in the legend for Figure 1.

The present study showed that investments by mast-fruiting species in defensive compounds could be explained by a combination of the effects of predator-satiation and the size dependence of fruit predation. Our results suggest that defence investment may not be solely explained by the effects of predator-satiation, but that other factors related to the foraging strategies of fruit predators should also be considered. The accumulation of additional information on the fruiting phenology and seed characteristics of other species would be needed to verify our assertions.

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