Pre-Dispersal Seed Predation of *Myrica rubra* on Yakushima Island

Mariko Fujita[1]**, Kiyoshi Matsui**[2]**, Mari Terakawa**[3]**, Furumi Komai**[4]**, Takakazu Yumoto**[5]

[1]*Kobe University*
[2]*Nara University of Education*
[3]*Hiroshima University*
[4]*Osaka University of Arts*
[5]*Research Institute for Humanity and Nature*

Introduction

Myrica rubra Sieb. et Zucc. (Myricaceae) is a common evergreen tree on Yakushima Island and produces a large amount of fleshy fruit. The fruit is an important food source for frugivores, especially for Yakushima macaques (*Macaca fuscata yakui*). However, *M. rubra* fruit production fluctuates greatly from year to year, and this annual change in crop size can affect the behavior of frugivores.

The predator satiation hypothesis was proposed by Janzen (1971) as one of ultimate causes of mast fruiting. Pre-dispersal seed predation has substantial negative effects on the relative reproductive success of individuals by limiting the number of viable seeds (Ida et al. 2004; Nakagawa et al. 2005; Sun et al. 2004). According to this hypothesis, many plants escape seed predators in mast years by controlling the number of predators in poor fruiting years via predator starvation. However, it is not known whether *M. rubra* suffers from seed predation and whether predator satiation reduces the proportion of seeds attacked.

We collected living and aborted fruit to identify major seed predators and to determine the proportion of fruit that was attacked by insects. In addition, we described the pre-dispersal survivorship patterns of fruit in 2006. We addressed the following questions. Who is the major seed predator of *M. rubra*? When does seed predation occur most heavily? Are there differences between the proportions of attacked living and attacked aborted fruit?

Materials & Methods

Study species

M. rubra is a dioecious evergreen tree that grows to approximately 15 m in height. On Yakushima Island, flowering starts from mid-March to early-April, and fleshy fruit is produced from late May to June. Each fruit has one seed. The fruit are an important food source for Japanese macaques as well as some bird species such as Japanese bulbuls.

Study site

The study site was located in a warm-temperate, evergreen, broad-leaved forest on Yakushima Island, which is located 70 km south of Kyushu, Japan. The canopy mainly consisted of Fagaceae, Hamamelidaceae, Myrsinaceae, and Lauraceae (Agetsuma 1995). The mean annual temperature was 21°C, and the annual rainfall was 2600 mm (Tagawa 1980).

In a 4-ha plot of a secondary stand (30°22' 01.26" N, 130°23' 08.23" E; 120 m above sea level), we

deployed three seed traps (each covered a 0.5 m^2 area) below each of five female trees (one was added in 2006 for six trees) during the fruiting period. The seed traps were made of nylon cloth and were placed 1 m above the ground. To observe patterns of fruiting phenology and fruit predation, we placed a ladder at three of the six female trees in 2006 to access the crown.

Patterns of seed survivorship

To describe the pre-dispersal survivorship patterns of fruit, we marked 30 branches of each of three *M. rubra* trees and counted the numbers of surviving fruit > 1 mm in diameter on 8 April, 15 May, 4 June, and 15 June in 2006. Two of the three female trees were still flowering on 8 April; therefore, we estimated the numbers of fruit by multiplying the number of infructescences by the number of fruit per infructescence determined from observations of the other individual.

Seed predators and patterns of seed predation
Aborted fruit

To monitor the patterns of seed fate and predation, all of the fruit that fell into seed traps was collected weekly from the end of April to the end of June. We extracted and counted the number of fruit > 1 mm in diameter. Some of the fruit was measured: 10 fruit from each individual in 2005; 90 fruit from each individual in 2006. We ignored dropped flowers.

For each collection, we stored a maximum of 300 fruit per tree in 2005 and 30 fruit per tree in 2006 in plastic containers (280 cm^3) and allowed any insect larvae within the fruit to emerge. We placed up to 10 fruit in each container, along with a piece of moist cotton to prevent desiccation, and observed them for 3 months. The containers were checked every two days; if insects had emerged, they were collected, killed by freezing, and mounted on pins for later identification.

After 3 months, we dissected all of the fruit stored in the containers and classified each fruit as attacked or non-attacked. Fruit that was attacked by insects had larvae, feces, and/or a hole through which the insects had escaped from inside the fruit. We considered fruit that had these marks as attacked and that without these marks as non-attacked. In 2006, we also dissected 60 fruit from each female tree soon after collection from the seed traps for comparison with the proportion of surviving fruit that was also attacked by insects.

Living fruit

Throughout the fruiting period, 50 fruit per female tree were sampled from the canopy of three female trees using a ladder on 8 April, 15 May, 4 June, and 15 June in 2006. Upon collection, the diameter of each fruit was measured, and 10 fruit from each female tree were stored in containers in the same way as for aborted fruit. The remaining fruit was dissected and classified as attacked or non-attacked.

Data analysis

The proportion of attacked fruit was calculated by pooling the data for all female trees. For aborted fruit, the difference in the proportion of attacked fruit between 2005 and 2006 was examined using a chi-square test. To compare living and aborted fruit in 2006, we calculated the proportions of attacked fruit based on data

from the fruit that was dissected upon collection, and the difference was examined using a chi-square test.

Results

Patterns of seed survivorship

Fruit mortality was highest during the first month after flowering. In all individuals, the numbers of living fruit on branches decreased rapidly from mid-April to mid-May and moderately from late May to mid-June (Fig. 1). By late July, no fruit remained on the branches.
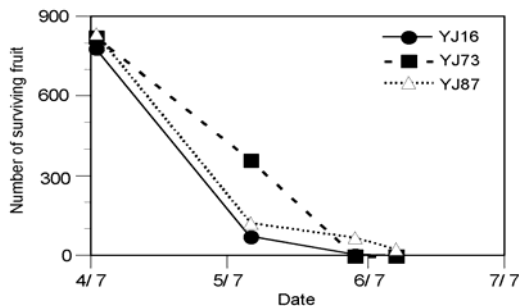

Fig. 1. Survivorship curves of fruit remaining on the branches of three female *Myrica rubra* trees. Symbols (●, ■ and △) indicate the total numbers of surviving fruit on 30 branches of each female tree.

Seed predators

In 2005, 598 individuals of *Thiotricha pancratiastis* Meyrick (Gelechiidae), two individuals of *Neoblastobasis spiniharpella* Kuznetzov & Sinev (Gelechiidae), and 109 individuals of parasitic wasp comprising seven species of Braconidae, two species of Ichneumonidae, and one species of Elasmidae emerged from 6188 stored fruit that were collected from seed traps. In 2006, 143 individuals of *T. pancratiastis* and 10 individuals of parasitic wasp emerged from 1090 stored fruit that were collected from seed traps. One individual of *T. pancratiastis* emerged from the stored fruit that was sampled directly from the branches (Fig. 2, Table 1).

Table 1. The number of insects that emerged from 6188 and 1090 aborted fruit in 2005 and 2006, respectively.

	Thiotricha pancratiastis	*Neoblastobasis spiniharpella*
2005	598	2
2006	143	0

Fate of fruit and predation

The total number of aborted fruit varied annually, at 10584 in 2005 and 6122 in 2006, and peaked at the early phase of development before fruit maturation (Fig. 3). In 2005, the peak was very clear; approximately 40% of aborted fruit fell during a single week

from 30 April to 7 May. The mean ± standard deviation fruit size during this term was 7.7 ± 2.8 mm. Ripe fruit typically reached between 15 and 20 mm in diameter. It was clear that many immature fruit were aborted during this period. In 2006, 64% of aborted fruit dropped during the first month after flowering (Fig. 3). Insects attacked fruit intensively during the primary stage of fruit development. The proportion fruit

attacked by insects reached as high as 64.9% between 7 and 14 May (Fig. 4). At other times, the attack rate was relatively low.
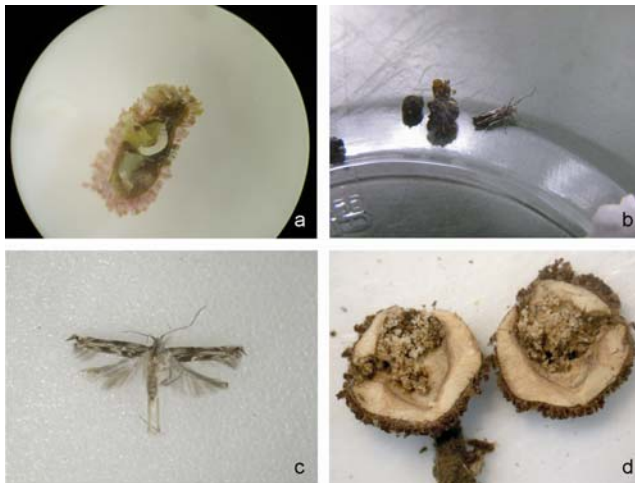

Fig. 2. Photographs of *Thiotricha pancratiastis* Meyrick (Gelechiidae) and attacked fruit. (a) Fruit infested by a larva. (b) *T. pancratiastis* adult just after emergence. (c) *T. pancratiastis* adult. (d) Attacked fruit containing insect feces.
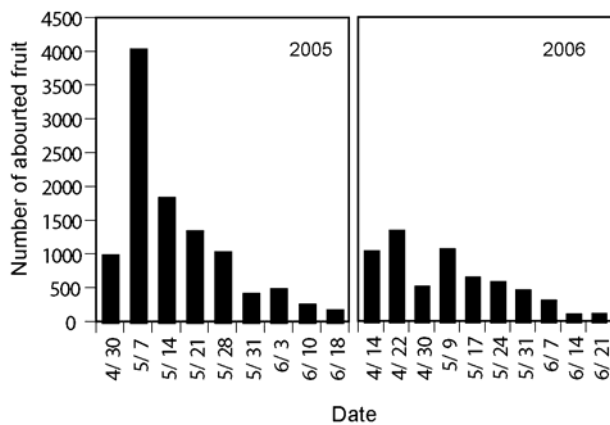

Fig. 3. Patterns of seed abortion throughout the fruiting period in 2005 and 2006.Data from all individuals were
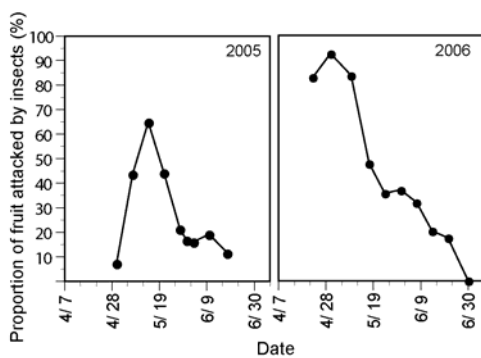

Fig. 4. Proportions of fruit that suffered predation by insects in 2005 and 2006.

Thus, predation by insects occurred only during the early phase of fruit development in 2005. In contrast, in 2006, insects attacked fruit continuously and at a higher intensity than in 2005 from just after flowering onward. From mid-April to mid-May, most of the aborted fruit was infested by insects, with the highest percentage of 92.6% occurring during the week of 23–30 April (Fig. 4). The overall proportion of fruit attacked throughout the fruiting period of 2006 was 50.5%, which was approximately 20% higher than in the previous year. A greater proportion of fruit was attacked in 2006 than in 2005 ($\chi^2 = 175.51$, p < 0.001; Table 2).

Table 2. Comparison of the annual percentage of attacked fruits between 2005 and 2006. *** p<0.001.

| | Number of fruits | | χ^2 |
	Attacked	Non-attacked	
2005	2121	4067	175.51***
2006	540	415	

For the surviving fruit, the proportion of fruit attacked was consistently low throughout the fruiting period, with the highest proportion of 19.6% measured on 8 April. The proportion of attacked fruit differed significantly between surviving and aborted fruit; from early April to early June, the insect predation rate was significantly lower in surviving than in aborted fruit (8–14 April, $\chi^2 = 64.4$, p < 0.001; 14–17 May, $\chi^2 = 83.19$, p < 0.001; 4–7 June, $\chi^2 = 11.6$, p < 0.001; Fig. 5). However, there was no difference after mid-June (15–21 June; $\chi^2 = 0.58$, p = 0.448; Fig. 5).
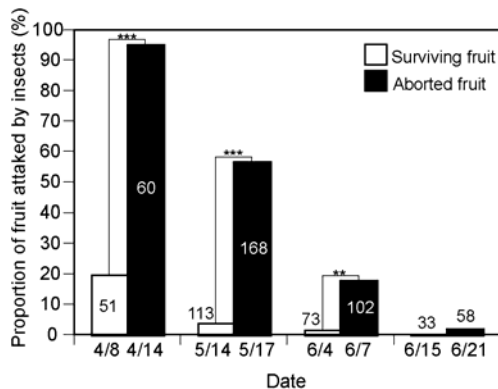

Fig. 5. Comparison of insect attack between living and aborted fruit in 2006. Bars indicate the proportions of aborted attacked (■) and surviving attacked (□) fruit pooled for all six female trees sampled. The numbers in the bars indicate the numbers of dissected fruit. The numbers under the bars indicate the dates on which fruit was collected; living fruit was collected that day and aborted fruit was collected 1 week from that day. *p < 0.05, **p < 0.01, ***p < 0.001.

Discussion

Throughout the 2 years of the study, we identified two lepidopteran species that may be major seed predators of *M. rubra*. The emergence of large numbers of *T. pancratiastis* individuals in both years

indicates that it is a major seed predator and may play an important role in the pre-dispersal seed predation of *M. rubra* on Yakushima Island. We confirmed that pre-dispersal seed predation by insects occurred mainly during the early phase of fruit development and that predation by *T. pancratiastis* possibly had a significant effect on the survivorship of young fruit. We observed that some individuals of *T. pancratiastis* emerged from one fruit and entered into another one. Therefore, individual larvae may have attacked more than one fruit.

The pattern of fruit survivorship was similar among the three female trees sampled: a dramatic decrease occurred just after flowering, followed by a moderate decrease. Predation by *T. pancratiastis* may partly explain this pattern.

The proportion of living fruit attacked by insects was very low throughout the fruiting period, suggesting that some sound fruit remained on the trees. In contrast, much of the aborted fruit suffered from predation. If fruit abortion occurs at random, there should be no difference in the proportions of living and aborted fruit that are attacked. Mother plants may selectively abort attacked fruit. The Yakushima macaque, which is a major seed disperser of *M. rubra* on Yakushima Island, eats and disperses mature fruit from mid-June to early July. Thus, many non-attacked fruit would be dispersed by Yakushima macaque.

M. rubra exhibits mast fruiting. According to the predator satiation hypothesis, the population density of seed predators becomes small in poor harvest years because of starvation, and in a mast year, plants produce many sound seeds that escape predation because the increase in the predator population density can not catch up with the increase in resource abundance. The crop size of five female *M. rubra* was approximately twice as large in 2005 than in 2006, and seed predation on *M. rubra* was 1.5 times higher in 2006 than in 2005. Thus, mast fruiting may have reduced the predation rate.

However, *T. pancratiastis* attacks not only fruit, but also new leaves. *T. pancratiastis* stays in the leaf veins and eats the new leaf tissue. Before pupating, it severs the new leaf in which it occurs and falls to the ground with the leaf tip. On the ground, it makes a nest out of the leaf tip and pupates inside the nest (personal observations). From early June to late June, we collected these nests from the seed traps and reared 283 adult *T. pancratiastis* from 554 pupae. Thus, *T. pancratiastis* may maintain its population density by using new leaves in years of limited fruiting. To evaluate the effect of pre-dispersal seed predation on *M. rubra*, it is important to understand the life history of seed predators and their resource use.

References

Agetsuma N (1995) Dietary selection by Yakushima macaques (*Macaca fuscata yakui*): the influence of food availability and temperature. International Journal of Primatology 16: 611–627.

Ida H, Hotta M, Ezaki Y (2004) Predispersal seed predation by rodents to beechnuts (*Fagus crenata* Blume). Ecological Research 19: 503–509.

Janzen DH (1971) Seed predation by animals. Annual Review of Ecology and Systematics 2: 465–492.

Nakagawa M, Takeuchi Y, Kenta T, Nakashizuka T (2005) Predispersal seed predation by insects vs. vertebrates in six dipterocarp species in Sarawak, Malaysia. Biotropica 37(3): 389–396.

Sun S, Gao X, Chen L (2004) High acorn predation prevents regeneration of *Quercus liaotungensis* in the Dongling Mountain region of North China. Restoration Ecology 12 (3): 335–342.

Tagawa H (1980) Vegetation on the western slope of Mt. Kuniwaridake, Yakushima Island. Science Reports of Kagoshima University 29: 121–137. (in Japanese)