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Dispersal timing, palatability and caching of acorns of *Aesculus turbinata* Bl.

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Runninghead: Acorn dispersal on *Aesculus turbinana*

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Abstract

Aesculus turbinata acorns were dispersed earlier than other acorn-producing species and are removed completely by rodents, although the acorns are unpalatable. The dispersal timing and low palatability to rodents on *A. turbinata* acorns promote the seed caching by rodents, facilitating the seedling emergence is possible even in lower-seeding years.

Keywords: *Aesculus turbinata*, rodent, seed palatability, seed dispersal timing, mast seeding

Introduction

The production of large seeds by species promotes the evolution of the cycles of mast-and total non-seeding, since larger seeds undergo more predation by insects and mammals, and mast seeding prevents complete removal by predation (Kelly & Sork 2002). There are a large number of mast-seeding trees, including species in genera *Fagus*, *Castanea*, *Corylus avellana* and *Quercus* (Koenig et al. 1994; Kon et al. 2005). These taxa all produce large fruits such as acorns or nuts, and exhibit large yearly fluctuations in fruit production from year to year. *Aesculus turbinata* is a common riparian species in Japanese natural forests and produces insect-pollinated large acorns, but total non-seeding years of *A. turbinata* have not been reported. *A. turbinata* develops riparian forest, and also cohabits with the other acorn-producing trees in *F. crenata* forests.

The success of trees that undergo mast seeding is commonly explained by the predator satiation hypothesis, which includes the prediction of seedling establishment, animal pollination, animal dispersal and accessory costs (Liebhold et al. 2004; Fenner & Thompson 2005). Rodents often cache the acorns below the ground surface (Vander Wall 1994). If the palatability of acorns is low, then the acorns remain beneath the ground surface to germinate even in years yielding fewer seeds. To test these hypotheses, we examined: 1) the seed dispersal timing of common tree species which produce acorns, 2) the optimal burial depth of acorns for seed germination of *A. turbinata*, 3) the germination ability of acorns of *A. turbinata* which were partially cut so as to simulate partial herbivory, and 4) the palatability to rodents of *A. turbinata* acorns.

Methods

The acorn dispersal period was studied in a mountainous area, Niigata Prefecture in central Japan (36°55'N, 138° 39'E; 775 m in altitude). The mean annual temperature is 18.1°C, and

annual precipitation is ca 1,500 mm. The snow-free period is from May to November, and is approximately matches the period of high activities of rodents. The natural vegetation is categorized as cool temperate deciduous forest. In this area the dominant tree species is an acorn-producing species *Fagus crenata*. Other common trees are: *A. turbinata*, *Castanea crenata*, and *Quercus mongolica* var. *grosserrata*, all of which produce large fruits. The ground surface was covered sparsely with herbs. At this site we established 21 1 m × 1 m seed traps before seed dispersal of *F. crenata* began in this forest. Seven seed traps were set up along three lines, at 10 m intervals. The seeds captured in the traps were collected at 1-4 week intervals from early August to early December in 1993 and 1994. The end of acorn production on the tree canopies was confirmed by a pair of field glasses.

Forty seeds of *A. turbinata* were buried at each of five soil depths (0, 5, 10, 20, and 50 cm) in early November 1993 in the areas where the seed traps established. All seeds were collected from the adjacent area. Observations continued until no more seedlings were observed. Tap water was sprayed at 2-3 day intervals to ensure full germination.

To determine the germination capability of seeds damaged by rodent feeding, 120 seeds were cut by a pair of clippers and buried 5 cm deep in soil on December 14th, 1993. Each seed was weighed before and after cutting, and the weight loss post-cutting was calculated. The weight loss ranged from 0% to 68%. Seed germination was observed as in the seed burial experiments described above. Differences in the germination percentages between burial depths and between seed weight loss amounts were confirmed by the χ^2 -test.

To investigate the food preferences of rodents, fruits of two different species were given concurrently to a single mouse in a cage, in various pairs of the four species: *Fagus crenata*, *Castanea crenata*, *Quercus mongolica* var. *grosserrata*, and *A. turbinata*. The two mice studied were: a 12.2-g male *Apodemus argenteus* and a 37.6-g female *Apodemus speciosus*. Both mice are common in Japanese broad-leaved forests and are known to be major acorn

consumers and dispersers (Miyaki and Kikuzawa 1988; Irie and Tsuyuzaki 2007). We gave equivalent weights of acorns of two species chosen at random, and recorded which acorns were firstly eaten by mice. Three replicates on each combination were made.

To verify the changes in the feeding patterns of the mice when different numbers of seeds were given, 1, 3 and 5 acorns of *A. turbinata* were given to each mouse on separate occasions. The acorns were weighed before feeding and 24 hours after, and the proportion of seed weight loss was calculated. The intact acorn weight averaged $21.0 \text{ g} \pm 5.5$ (standard deviation). As seeds that were not exposed to mice spontaneously lost 6% in weight over the same 24 hours, this weight loss was accounted for by multiplying the seed weight of all seeds after feeding by 1.06. Differences in feeding patterns between seed density and granivorous damage were confirmed by one-way ANOVA. All statistical analyses used the software package R (ver. 2.9.0) (R Foundation for Statistical Computing, Vienna).

Results

Before the seed traps were set up, none of the common species dispersed any acorns. *Fagus crenata* produced no acorns in 1994, i.e., in non-seeding year, whereas in 1993 they dispersed $15 \pm 28/\text{m}^2$ seeds. The dispersed seed density of *A. turbinata* was $0.33/\text{m}^2$ in 1993 and $1.52/\text{m}^2$ in 1994, indicating that seed production fluctuated annually but less so than in *F. crenata*. The seed dispersal periods of *A. turbinata* were roughly two weeks from early September to late September in these two years (Fig. 1). The other acorn-producing trees dispersed seeds later than *A. turbinata*, although their acorns were not captured by the seed traps. *A. turbinata* completed its seed dispersal before the other acorn-producing species began to disperse their acorns, and no fruits were produced by any shrubs and herbs during the dispersal periods of *A. turbinata*. *A. turbinata* acorns therefore comprised major food resources for rodents during its acorn dispersal period. Field observations confirmed that all

acorns of *A. turbinata* had disappeared from the ground surface soon after the dispersal.

The seed germination percentages at depths 0, 5, 10, 20 and 40 cm were respectively 45%, 100%, 95%, 50% and 40%, differing significantly between the burial depths (χ^2 -test, $P < 0.01$); seeds buried 5 cm deep were most likely to germinate. At 0 cm deep, i.e., on the ground surface, germination was ca 40%. The germination percentage fell gradually with increasing burial depths. Seed burial clearly assisted seedling emergence.

The germination percentages decreased gradually with increasing the weight of hand cut seeds, imitated herbivorous damages (χ^2 -test, $P < 0.01$). Uncut seeds with no weight loss all germinated (100%, using 40 seeds), 54.6% of the 39 seeds with 0-20% weight cut out germinated, 13.2% of 38 seeds losing 20-40% weight, and only 2.3% of 43 seeds losing 60-80% weight did so.

The palatability trials of the four species of acorn to the tow wood mouse species gave clear results. A total of 60 trials were conducted with various combinations in pairs of acorns of *A. turbinata* and the other three species. Acorns of *A. turbinata* were not eaten after 24-hr feeding when acorns of two species were given at the same time. Given a choice, the mice never selected *A. turbinata* acorns. Their favorite acorns were *F. crenata*. When a single acorn on *A. turbinata* and no others of other species was given to one mouse, the mouse ate 40-80% portions of acorns and thus they did not ate an entire seed (Fig. 2). When 3 and 5 seeds of *A. turbinata* were given at the same time, they ate an entire seed and did not eat remainders. These observations suggested that seeds of *A. turbinata* remained under the soil after caching when the acorn density of *A. turbinata* was low due to changes in the seed feeding patterns of rodents.

Discussion

Low palatability has advantages on granivory avoidance (Kerly & Erasmus 1991; Tsuyuzaki

& Takahashi 2007). During the periods of acorn dispersal of *Aesculus turbinata*, however, the acorns were a single food available to rodents and were completely removed from the ground surface in spite of their low palatability, indicating that the timing of acorn dispersal by *A. turbinata* promoted seed removal and caching by rodents. This seasonal disharmony of seed production is observed also in sympatric bird-dispersal species, most of which produce juicy and/or oily fruits (Skeat 1987; Nishi & Tsuyuzaki 2004). Our study confirms that the timing of dispersal also affects seed cache patterns by rodents. The low palatability to rodents of *A. turbinata* acorns led to only partial eating of the acorns when seed density was low, i.e., the mice did not eat the entire seed. When the seed density was high, i.e., 3-5 seeds were given, the mice ate a few seeds completely but did not eat the rest. Therefore, even in less-seeding years, acorns of *A. turbinata* should remain under the ground surface due to caching.

Acorns of *A. turbinata* germinated even after 40-60% of their weight had been cut out by hand. When a single acorn was given to one mouse, the amount of the acorn eaten ranged from 40% to 80% by weight, so that a few seeds could still germinate. In fact, we observed that *A. turbinata* seeds partly eaten by rodents often germinated in the fields. *Apodemus* mice often construct the burrows approximately 25 cm deep in forests and grasslands (Wolff 1988). Seeds buried by mice in soils were more likely to germinate than those on the ground surface. Burial of seeds saves them from mammalian predators, at least in the case of *Quercus rubra* (Garcia et al. 2002). Seed burial into caches is likely to confer advantages of both seed germination and saving from predators.

The pollination efficiency hypothesis predicts that mast seeding is derived from increasing pollination success for wind-pollinated perennial plants (Kelly & Sork 2002), but seems inadequate to explain mast seeding for insect-pollination including *A. turbinata*. The resource-matching or weather-tracking hypothesis predicts that, under an unpredictable and

variable climate (as in arid regions), mast seeding occurs when the climate is favorable for seed production (Monks & Kelly 2006). *A. turbinata* is distributed in a cool temperate region, however, in which the climate is relatively predictable and mild. In conclusion, the strategies of seed production by *A. turbinata* differ from other common acorn-producing tree species. The low palatability to rodents of *A. turbinata* seeds and the seed dispersal timing support seedling emergence in years of reduced seeding, due to rodent caching. By this means, *A. turbinata* can flourish with taking weak fluctuations of mast-and non-seeding cycles.

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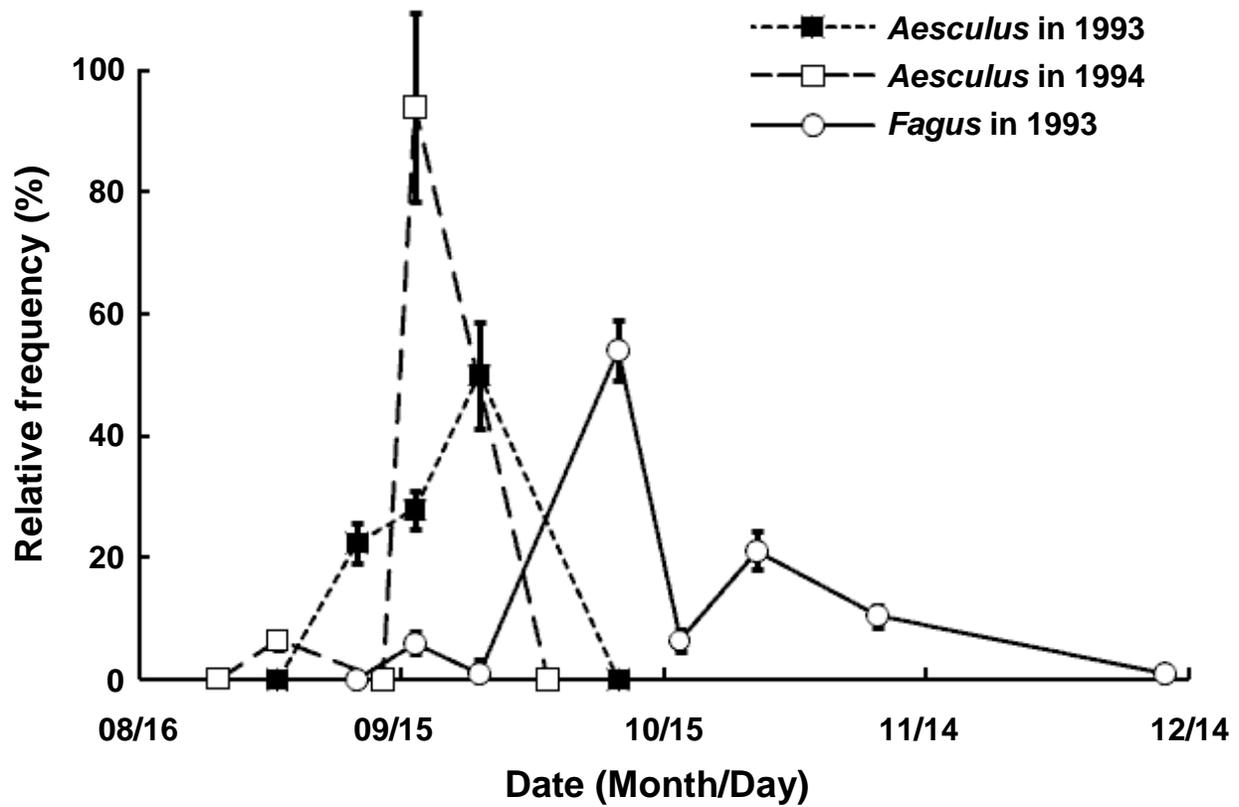


Figure 1. Relative frequencies (mean and standard error) of seeds captured by 21 1m \times 1 m seed traps in 1993 and 1994. No seeds of *F. crenata* were captured in 1994 due to the absence of seeding in that year. Acorns produced by the other species were not captured.

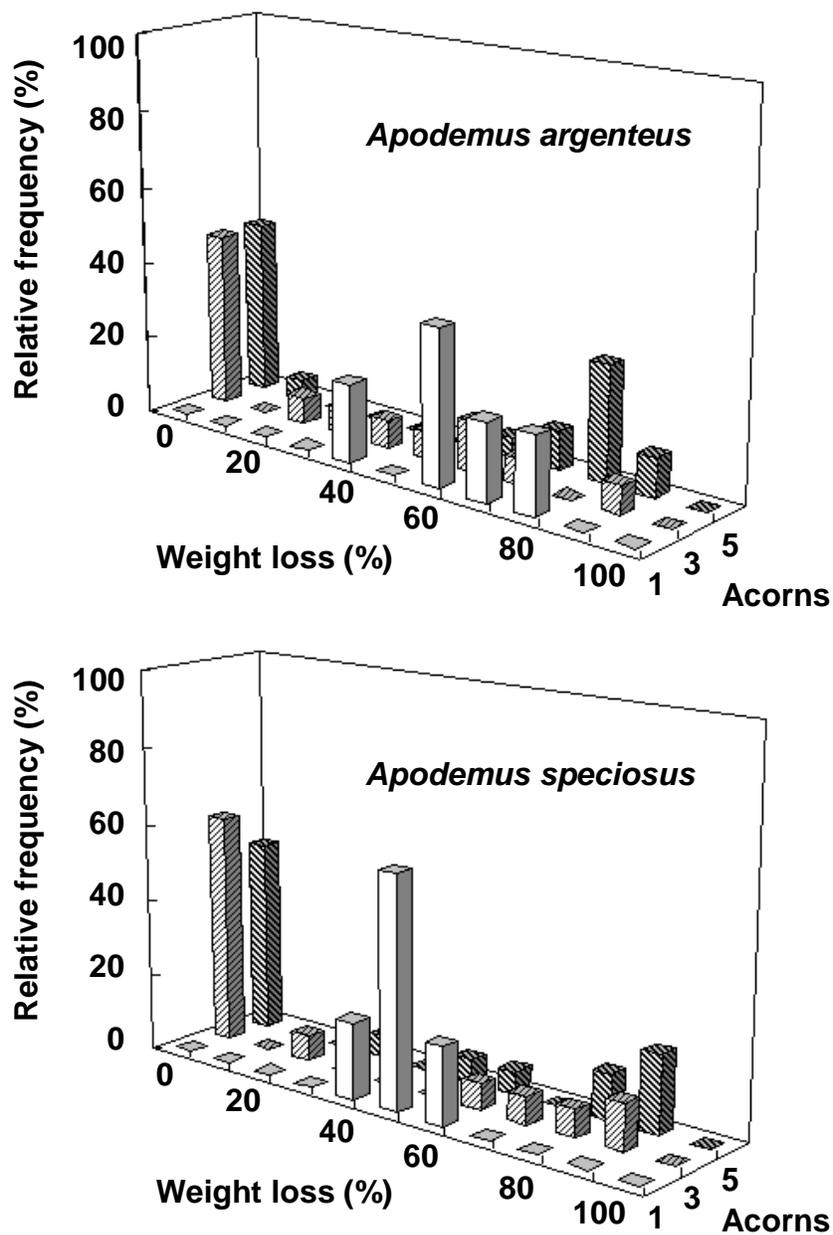


Figure 2. Relative frequency of *Aesculus turbinata* acorns that decreased in weight due to feeding by mice. Open, hatched and closed cumuli respectively indicate the weight loss percentages when 1, 3, and 5 acorns were given to a single mouse. The weight loss patterns differed significantly between one acorn and five acorns given to *Apodemus argenteus* and between one seed and other number of seeds given to *Apodemus speciosus* at $P < 0.01$ (ANOVA).