Effects of Seed Size and Chemical Variation on Seed Fates in a Deciduous Oak Species *Quercus serrata*

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Keywords: counter-directional effect, intraspecific variation, seed characteristics, seed predation, tannin

Received 3 December 2009; accepted 1 February 2010

Abstract

Relationships between seed traits (size and tannin content) of individual seeds and their seed fates (dispersal and survival) were examined by the combination of a large-scaled field experiment and a nondestructive tannin estimation method using seeds of a deciduous oak *Quercus serrata*. The field experiment revealed that large and low-tannin seeds tended to be dispersed well and, contrary to this, small and high-tannin ones tended to survive well. These findings demonstrated the presence of two counter-directional effects of seed size and tannin content on seed fates.

Introduction

Plants in stages from seed dispersal to seedling establishment are subject to be damaged by a lot of factors: seed consumers, decomposers, and unfavorable situations, such as shortage of light and soil drought (Moles and Westoby, 2004). These factors may affect seed fates and, subsequently, the recruitment of plant populations. Various seed traits, such as seed size and chemical compositions, are supposed to have considerable impacts on seed fates via interrelations with the biotic and abiotic environmental factors.

Seed traits are not uniform even within species. Indeed large intraspecific variations have been reported in some seed traits. A number of previous studies documented those in seed size and examined effects of seed size on seed fates based on intraspecific variation (e.g. Gómez, 2004). Intraspecific variations in the content of seed chemical constituents have also been reported (e.g. Sork et al., 1983). However, effects of seed chemical content on seed fates have not been examined yet in individual seed scale, though chemical contents may affect their seed fates like seed size.

Tannins are one of the most popular plant secondary metabolites, which act as a defense chemical against herbivory and fungal attack. Some of oak species include high level of tannins in their seeds (Shimada and Saitoh, 2006). Recently we found a large intraspecific variation in acorn tannin content in a deciduous oak species *Quercus serrata* within a local population and, further, within individual mother trees (mean ± SD, 6.6% ± 3.5; range, 0.7-27.1%; Takahashi & Shimada, unpublished data). Such large differences in tannin content may likely have substantial influences on seed fates even in the individual seed scale.

The objective of the present study is to examine the effects of individual seed characteristics, such as size and tannin content, on seed fates using seeds of *Quercus serrata* by the combination of a large-scaled field experiment and a nondestructive tannin estimation method, which we have recently developed.

Materials and methods

This study was conducted in the Takizawa Research Forest of Iwate University (Iwate pref., 39° 46' 31" N, 141° 9' 27"E, c.a. 200m a.s.l.). We selected 34 trees of *Q. serrata* in this site, whose crowns did not overlap each other. Preliminary survey revealed that two species of wood mice, *Apodemus speciosus* and *A. argenteus*, inhabited in this site. Both species are major predators and dispersers of acorns (Kikuzawa, 1988).

Seed traps were set up under each sample tree to collect acorns. They were in a rectangle form and covered the crown projection area of each tree as large as not intermixing acorns with ones from neighbor *Q. serrata* trees. Acorns were collected every three or four days from September to November in 2007 and sorted into five categories as sound, damaged by insects, immature, maldeveloped, and infected by fungi. Only sound acorns which were not damaged by consumers and free from deterioration were stored at 5 ºC until the following treatment: measuring seed traits and attaching tapes to trace.

Tannin content of individual acorns were estimated with the near infrared spectroscopy calibration model, which we have developed (Takahashi et al., unpublished data). Each acorn was placed in a water bath maintained at 25 ºC for at least 20 min to bring the sample temperature to 25 °C. After the temperature adjustment, near infrared spectrum of each acorn was obtained with a modified FQA-NIRGUN instrument (FANTEC, Kosei, Japan). This portable near infrared spectrophotometer operates in transmittance mode, in which absorbance of light penetrating through a sample is measured. A standard reference was measured prior to every sample measurement. Transmittance readings were converted to absorbance values. After the pretreatment for the absorbance spectra, tannin content in individual acorns was estimated with the calibration model. All the samples were weighed individually after spectra acquisition.

After measuring seed characteristics these acorns were marked with identifiable number and tape. Then, marked acorns were returned under the seed traps where each acorn was collected. The study site was intensively searched for the marked acorns from May to June in 2008. Status of the seed discovered was recorded. We defined an acorn whose hypocotyl emerged as “survived”, that is, success in early establishment. In addition, the places where the marked acorns were found were located for all the marked acorns regardless of their conditions of survival. We defined the acorns found outside the seed traps of their maternal trees as dispersed.

We analyzed relationships between seed characteristics and individual seed fates (dispersal or survival). Relationship between seed traits and dispersal was analyzed using the dataset of all samples. Missing acorns were categorized as dispersed, because they could not be detected under the seed traps in spite of intensive search. Relationship between seed traits and survival (success in early establishment) was analyzed using the dataset of all sample acorns excluding missing ones. To examine the effects of seed characteristics on seed fates in the individual seed scale, we analyzed the relationships between seed fate and seed characteristics (acorn size and tannin content) by multiple logistic regression analysis using maternal trees as a random effect. The null samples whose tannin content failed to be estimated by near infrared spectroscopy were excluded from the data beforehand.

Results

Total number of collected *Q. serrata* acorns was 45,335. Number of sound acorns, infested by insects, immature, maldeveloped, and infested by fungi were 19,606, 19,456, 6,027, 223, and 23, respectively. A half of total sound acorns were used as samples in the seed fate analyses (9,803). After removal of the null samples, 8,988 of the marked acorns were supplied for further analyses. Acorn weight varied from 0.10-4.49 g (2.11 g ± 0.55 SD). Tannin content varied from 0.001 % to 31.48 % (5.19% ± 2.42 SD). The relationship between tannin content and weight of acorns was not significant ($r = -0.0056$, $P = 0.5934$).

We could find 4,280 acorns (47.6 % of all the acorns) among 8,988 of the marked ones. Among them 176 acorns (2.0 %) were proved to be dispersed, and the rest (4,104 acorns, 45.7%) were found at the site where the marked acorns had been returned. A total of 766 acorns (8.5 %) successfully germinated, which consisted of eight acorns (0.1 %) that were dispersed and 758 ones (8.4 %) that were not dispersed. 4,708 acorns (52.4 %) were missing, and they were regarded as being dispersed.

Both of acorn weight and tannin content in individual acorns had significant relationships to whether an acorn was dispersed or not ($n = 8988$; whole model: $\chi^2 = 1623.0$, $P < 0.0001$; tannin content: β coefficient = 0.1024, $P < 0.0001$; seed weight: β coefficient = -0.4288, $P < 0.0001$). Seed dispersers tended to disperse larger-sized and lower tannin acorns. Similarly, acorn weight and tannin content showed negative and positive correlations with survival of acorns, respectively ($n = 4280$; whole model: $\chi^2 = 651.2$, $P < 0.0001$; tannin content: β coefficient = -0.0805, $P < 0.0001$; seed weight: β coefficient = 0.7843, $P < 0.0001$). Namely, small-sized and higher tannin acorns tended to survive better.

Discussion

In this study the relationship between seed traits and seed fate was examined in the scale of individual seeds. We discovered that tannin content and seed size of individual acorns have significant impacts on seed fate. This is the first study to demonstrate the effects of seed chemical traits on seed fate in the individual seed scale.

Detection ratio of marked acorns in this study (47.6 %) was similar to those of previous studies (53.9 – 71.5 %, Sork, 1984; 54.4 – 95.0 %, Hoshizaki and Hulme, 2002). Dispersal ratio (54.3 %) was thought to be ordinary comparing with those of previous studies (7.0 – 93.1 %, Sork, 1984; 30.1 – 77.7 %, Hoshizaki and Hulme, 2002), although the ratios largely differed among maternal trees or years. Survival ratio (8.5 %) was higher than that in Hoshizaki and Hulme (2002) (0.08 – 2.9 %). It might result from predator saturation caused by mast seeding in this year.

The field experiment revealed that acorns with lower tannin content and larger size were more likely to be dispersed. This result seems to be reasonable for seed dispersers, because they tend to prefer less tannin and large acorns, which are better in food quality and feeding efficiency. A question occurs from this result: can wood mice detect tannin content without removing pericarps and seed coats? Grey squirrels can distinguish between acorns of red and white oak, which differ widely from each other in tannin content. Grey squirrels may be able to distinguish acorn groups with odor of tannins and /or tannin-related materials (Steele, 2001). The relationship between chemical content and odor of acorns in our study system needs to be examined. The relationship between seed dispersal and seed size has been reported in a number of previous studies. Large sized foods tend to be removed better and hoarded rather than consumed instantly. The result of the present study showed the same tendency.

For seed survival, acorns with smaller size and higher tannin content tended to survive better. This result was consistent with selective consumption by the Japanese wood mouse according to tannin content (Takahashi and Shimada 2008). Tanniferous acorns may have higher probability to survive through selection by consumers, since consumers generally avoid negative effects of tannins.

Large seed size generally brings some benefits for survival from unfavorable conditions, such as competition with existent vegetation (Jakobsson and Eriksson, 2000), drought (Leishman and Westoby, 1994). In these studies, however, changes in predation risk according to seed size were not considered. Actually, predation risk often increases with seed size. In the case of cache dispersal seeds by rodents (*Q. ilex*), large size invites higher predation risk than small size, whereas it increases germination rate and seedling survival in acorns (Gómez, 2004). He suggested that seed size effects work on fitness in two different ways: large seeds suffer high selective pressure of seed consumers before germination; and, in contrast, they have advantage in seedling establishment (after germination). Indeed, in this study we found that larger seeds seemed to suffer higher predation risk than smaller ones.

In this study, seed characteristics that were advantageous for dispersal (large size and low tannin) were opposite to those for survival (small size and high tannin). This finding demonstrated the presence of two counter-directional effects of seed size on dispersal and survival. Similarly, two counter-directional effects of tannin content for dispersal and survival might exist. Namely, acorns with low tannin tended to be dispersed, but to be predated. Advantageous seed traits might be determined through the balance of these two counter-directional effects. In the case of high predation pressure by seed consumers like our study, acorns with higher tannin content and in smaller size would be favorable in the early seedling establishment stage. Contrary to this, in the case of low predation pressure, acorns in larger size would be favorable, and ones with lower tannin content might have some benefits, if tradeoff in resource use exists between tannin and any other traits related with seed survival. We suppose that these counter-directional effects of seed traits on seed fates may generate and maintain large intraspecific variation of seed traits in *Q. serrata*.

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