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ORIGINAL ARTICLE

Effects of asynchronous acorn production by co-occurring *Quercus* trees on resource utilization by acorn-feeding insects

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Abstract To clarify the effects of asynchronous seed production among tree species on the population of seed predators, we investigated the relationship between the annual variation in production of mature acorns and the insect damage in those acorns of two sympatric oak species, *Quercus variabilis* Blume and *Quercus serrata* Thunb. ex Murray, over 4 years at two study sites. The annual variation in acorn production was noticeable, with a coefficient of variation (CV) at the two sites of 1.05 and 0.80 for *Q. variabilis* and 0.87 and 0.73 for *Q. serrata*. Annual fluctuation in acorn production by *Q. serrata* was synchronized between the two sites. Since annual fluctuation in acorn production was not synchronized between the two species, the CVs for the total acorn production by both oak species (0.83 and 0.62 at the two sites) were lower than those for *Q. variabilis* and *Q. serrata* alone. The rate of predation by the specialist predators (*Curculio* weevils) on the acorns of both species was not related to the annual acorn crop size. Prolonged diapause of *Curculio* weevils might stabilize their populations. The rate of acorn predation by the generalist predators (tortricid moths) was also not related to the annual crop size. Asynchronous acorn production by the two oak species would help to stabilize the population.

Keywords Acorn predation · Asynchrony · *Curculio* · *Cydia* · Mast seeding

Introduction

Acorns, the seeds of *Quercus* species, are a rich source of food for many animals. Of these predators, insects are the most important for both pre- and post-dispersal phases of acorn development, and have large effects on the regeneration process of *Quercus* species (Matsuda 1982; Fujii 1993; Maeto 1993; Fukumoto and Kajimura 2005; Pulido and Díaz 2005).

Large fluctuations among years in acorn production occur in the genus *Quercus* (Sork et al. 1993; Koenig et al. 1994; Crawley and Long 1995; Maeto and Ozaki 2003; Espelta et al. 2008); years with particularly high acorn production are referred to as "mast seeding" years (Janzen 1971; Silvertown 1980; Kelly 1994). For insect predators, acorns are therefore unpredictable food resources with large annual fluctuations. The magnitude of the annual fluctuation in acorn production can be associated with the dynamics of insect predators. *Quercus* species often co-occur in temperate forests, and share the same insect seed predators (Ueda 2000; Shibata et al. 2002; Ueda and Osumi 2003). Synchronous acorn production between populations of sympatric tree species that share the same seed predators has the potential advantage of predator satiation (Janzen 1971; Silvertown 1980), thereby ensuring that at least some seeds will survive. Recently, asynchronous acorn production was reported in North America between 1-year species, which mature their acorns in the year after flowering, and 2-year species, which mature their acorns in the next year after flowering (Sork et al. 1993; Koenig et al. 1994; Liebhold et al. 2004; Kelly et al. 2008).

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However, we found no information in the research literature on how asynchronous acorn production by sympatric species affected resource utilization by acorn-feeding insects.

Quercus variabilis Blume (a 2-year species) and *Quercus serrata* Thunb. ex Murray (a 1-year species) co-occur in the temperate deciduous forests of central Japan (Fukumoto and Kajimura 2005). Detailed studies of the biology of acorn-feeding insects have been carried out previously (Fukumoto and Kajimura 1999, 2001). Here, we investigated the relationships between the annual variation in the production of mature acorns and insect damage to the acorns of both oak species over 4 years at two study sites. We analyzed the annual synchrony of acorn production between the two species and the yearly changes in acorn predation by each insect. On the basis of the results of this monitoring, we discuss potential mechanisms capable of stabilizing the insect population size as a function of the biology of acorn-feeding insects.

Materials and methods

Study site and methods

We carried out our study in the secondary forests in the Nagoya University Campus (site A) and in Higashiyama Park (site B), both in Nagoya City, Aichi Prefecture, central Japan (35°10′N, 136°58′E, 50 m a.s.l.). The forests consist mainly of deciduous oaks (*Q. variabilis* and *Q. serrata*) and Japanese red pine (*Pinus densiflora* Sieb. et Zucc). Table 1 summarizes the tree density, diameter at breast height, and total basal area of *Q. variabilis* and *Q. serrata* at the two study sites. The mean annual precipitation and temperature at the nearby Nagoya Weather Station are about 1,500 mm and 15.1°C (the highest monthly mean is 32.3°C in August and the lowest, 0.1°C in January), respectively (National Astronomical Observatory 2001). The two sites lie only about 1.5 km apart, and have similar climatic conditions.

We selected five trees of *Q. variabilis* and five of *Q. serrata* at site A, and five *Q. variabilis* and 14 *Q. serrata* at site B. We chose trees whose canopies did not overlap with trees of the same species, but one pair of neighboring *Q. serrata* at site B overlapped their canopies slightly. We established four 0.5-m^2 seed traps (0.25 m^2) under each tree canopy. The seed traps at site A were plastic containers raised about 0.2 m above the ground, whereas those at site B were made from nylon cloth and were positioned about 0.8 m above the ground. Our previous research (Fukumoto and Kajimura 2005) has demonstrated that there is no difference in the efficiency of acorn collection between the two types of trap. Sampling periods at site A were 31 May–21 December 1997, 11 April–20 December 1998, 9 April–17 December 1999, and 13 April–23 December 2000; at site B they were 15 June–19 December 1997, 12 April–25 December 1998, 15 April–19 December 1999, and 18 April–22 December 2000.

Table 1 Tree density, diameter at breast height, and total basal area of *Quercus variabilis* and *Quercus serrata* at two study sites

	Site A	Site B
Tree density (no./ha)		
Q. variabilis	200	300
Q. serrata	260	600
Diameter at breast height (mean ± SD) (cm)		
Q. variabilis	22.0 ± 7.3	17.1 ± 9.2
Q. serrata	25.7 ± 8.3	12.0 ± 5.6
Total basal area (m^2/ha)		
Q. variabilis	8.4	4.7
Q. serrata	14.8	4.1
Q. variabilis/*Q. serrata*	0.57	1.15

We collected the contents of the traps once every 1 or 2 months. Then, we dissected the acorns and classified their internal condition as sound (a mature acorn with sound cotyledons), aborted (an immature acorn with undeveloped cotyledons), insect-infested (an acorn with penetrating holes or the presence of eggs, larvae, adults, or larval feces), or degenerated (a mature acorn with evidence of desiccation or fungal attack). Aborted acorns and immature insect-damaged acorns were removed from our sample. Insects were identified to the species level from their eggs, larvae, adults, or larval feces. We identified tortricid moths and *Curculio* weevils only to the family and genus level, respectively, because their eggs, larvae, and larval feces were too similar to let us confirm finer taxonomic distinctions in these groups.

Data analysis

The rate of acorn predation by each insect species or group was the number of infested acorns divided by the total number of mature acorns in our sample. In this study, acorns damaged by two insects or insect groups simultaneously were counted twice. To assess whether mast seeding in *Q. variabilis* and *Q. serrata* would be an effective strategy against generalist acorn-feeding insects, we calculated the rate of combined acorn predation as the total number of infested acorns divided by the sum of mature acorns of *Q. variabilis* and *Q. serrata* combined. Because the total basal area differed between the two oak species at both sites, we weighted the number of mature acorns of *Q. variabilis* by multiplying the number of mature acorns of this species by the ratio of total basal area

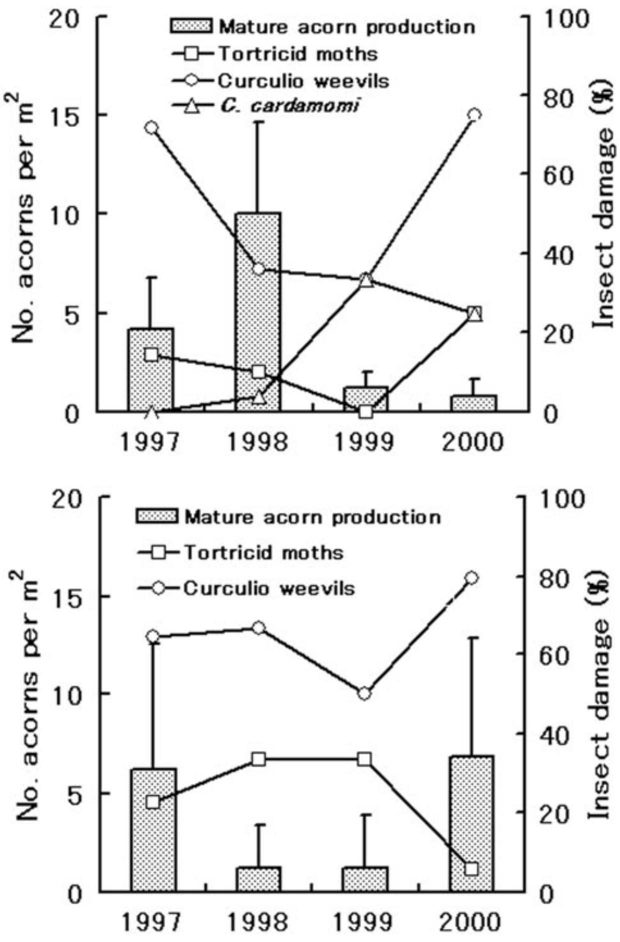

Fig. 1 Annual fluctuations of mature acorn production of *Quercus variabilis* and its insect damage over 4 years at site A (*above*) and site B (*below*). *Bars* on *columns* indicate standard deviation

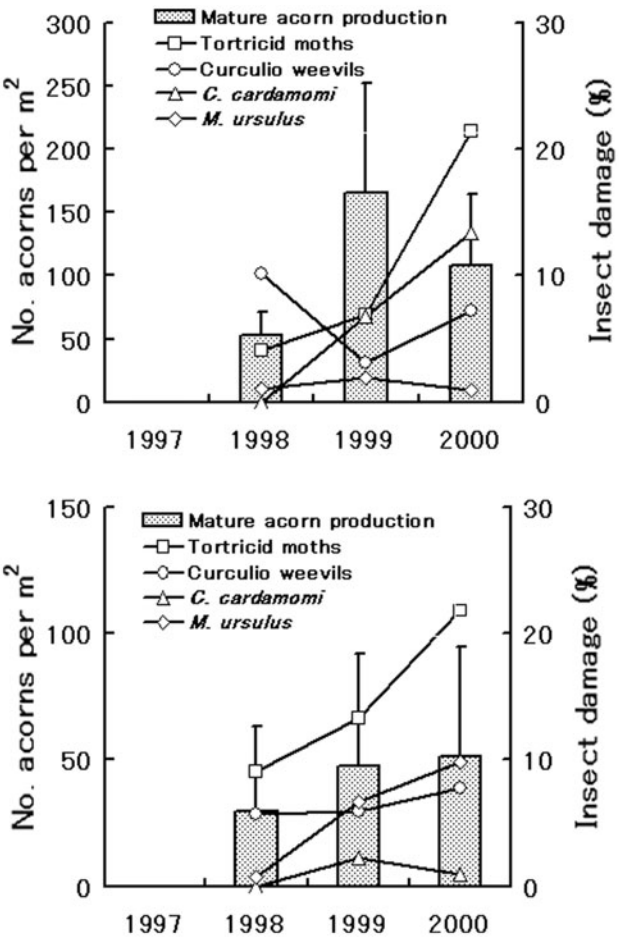

Fig. 2 Annual fluctuations of mature acorn production of *Quercus serrata* and its insect damage over 4 years at site A (*above*) and site B (*below*). *Bars* on *columns* indicate standard deviation

of *Q. variabilis* to that of *Q. serrata* at each study site (see Table 1). To measure the magnitude of the annual variation in acorn production, we used the coefficient of variation (CV) as an index of masting (Silvertown 1980; Kelly 1994), with our calculation based on the mean number of mature acorns for all years. The acorn predation rate was arcsine-transformed and the number of mature acorns produced was log-transformed before statistical analysis. All statistical tests were performed using version 11.5 of the SPSS software (SPSS 2002).

Results

Annual fluctuations in acorn production

The annual variation in production of mature acorns by *Q. variabilis* was noticeable (Fig. 1), with a coefficient of variation (CV) of 1.05 at site A and 0.80 at site B. Large numbers of *Q. variabilis* acorns were produced in 1998 at site A and in both 1997 and 2000 at site B (Fig. 1). The annual fluctuation in acorn production was not synchronized between the two sites ($r = -0.352$, $P = 0.648$).

Quercus serrata produced no mature acorns in 1997 at either site, but acorn production increased thereafter, except in 2000 at site A (Fig. 2). The CVs for the annual variation in *Q. serrata* acorn production were 0.87 at site A and 0.73 at site B. The annual fluctuation in acorn production was synchronized between two sites ($r = 0.994$, $P = 0.006$).

There was no synchrony in the annual acorn production between *Q. variabilis* and *Q. serrata* ($r = -0.400$, $P = 0.600$ at site A; $r = -0.472$, $P = 0.528$ at site B). The CVs for the annual variation in their combined acorn production were 0.83 at sites A and 0.62 at site B. The annual fluctuation in the combined acorn production by the two tree species was synchronized between the two sites ($r = 0.981$, $P = 0.019$).

Yearly changes in insect damage

Predation of *Q. variabilis* acorns by *Curculio* weevils, with *C. robustus* (Coleoptera: Curculionidae) assumed to be dominant (Fukumoto and Kajimura 2001), ranged from 33.3 to 79.4% (Fig. 1). The rates of predation by *Coccotrypes cardamomi* (Coleoptera: Scolytidae) and tortricid moths, mainly *Cydia glandicolana* (Lepidoptera: Tortricidae) (Fukumoto and Kajimura 2001), were <40% at both sites. The rate of predation by each insect group was independent of the annual fluctuations in the production of mature acorns (Pearson's correlation, $P > 0.05$).

Predation of *Q. serrata* acorns by *Curculio* weevils, with *C. sikkimensis* (Coleoptera: Curculionidae) assumed to be dominant (Fukumoto and Kajimura 2001), ranged from 3.2 to 10.2% (Fig. 2). The rates of predation by tortricid moths, mainly *C. glandicolana* (Fukumoto and Kajimura 2001), increased throughout the study period at both sites, and reached levels >20% in 2000 (Fig. 2). The rates of predation by *C. cardamomi* and *Mechoris ursulus* (Coleoptera: Attelabidae) were both <15% throughout the study period at both sites. The rate of predation by each insect group was independent of the annual fluctuation in the production of mature acorns (Pearson's correlation, $P > 0.05$).

Of the insects identified at our study sites, *C. robustus* was specific to *Q. variabilis*, and *C. sikkimensis* and *M. ursulus* were specific to *Q. serrata* (Fukumoto and Kajimura 1999, 2001). On the other hand, *C. glandicolana* and *C. cardamomi* were known to be generalists at our study sites (Fukumoto and Kajimura 1999, 2001). Among the generalist predators, the rates of predation by tortricid moths and *C. cardamomi* on the combined acorn production of both tree species ranged from 4.7 to 22.6% and from 0 to 13.4%, respectively (Fig. 3). The rates of predation by tortricid moths and *C. cardamomi* were independent of the annual fluctuation in the combined acorn production (Pearson's correlation, $P > 0.05$).

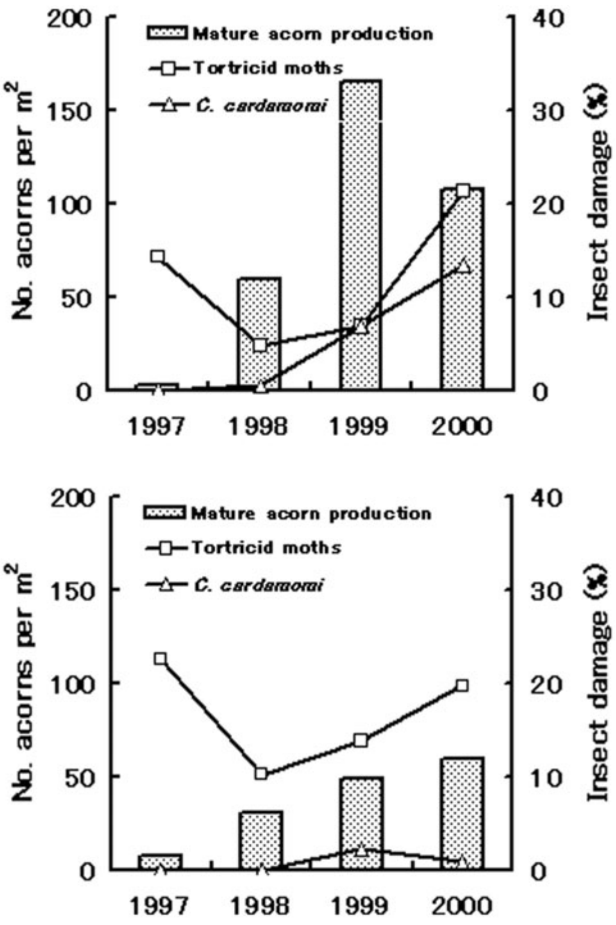

Fig. 3 Annual fluctuations of combined mature acorn production of *Quercus variabilis* and *Quercus serrata* and their insect damage over 4 years at site A (*above*) and site B (*below*)

Discussion

Asynchrony of the annual fluctuation of acorn production between *Q. variabilis* and *Q. serrata*

Large fluctuations in acorn production among years occur in the genus *Quercus* (Sork et al. 1993; Koenig et al. 1994; Crawley and Long 1995; Maeto and Ozaki 2003; Espelta et al. 2008). The predator-satiation hypothesis, a powerful hypothesis for explaining the selective advantages of mast seeding, proposes that mast seeding is an adaptation against predators: satiating predators by producing more seeds than they can consume during occasional mast years ensures that some seeds will survive, whereas starving predators by producing fewer seeds than the predator population requires for a high survival rate in the intervening periods prevents predator populations from being sustained at high levels (Janzen 1971; Silvertown 1980). Synchronous acorn production between populations of sympatric species sharing the same seed predators would, in theory, offer the advantage of increasing the likelihood of predator satiation (Janzen 1971; Silvertown 1980). However, we observed no annual synchrony in acorn production between *Q. variabilis* (a 2-year species) and *Q. serrata* (a 1-year species) at our study sites (Fig. 3). Sork et al. (1993) and Liebhold et al. (2004) also reported asynchronous acorn production between 1-year species and 2-year species of North American oaks that shared the same acorn predators. One probable explanation for asynchronous acorn production between 1-year and 2-year species relates to differences in their endogenous reproductive dynamics (i.e., differences in the duration of their reproductive cycle). Sork et al. (1993) also clarified that past acorn production had a major impact on the size of the current acorn crop because oak species have an inherent reproductive cycle. For example, *Quercus alba* (a 1-year species) had a 4-year cycle, *Quercus velutina* (a 2-year species) had a 2-year cycle, and *Quercus rubra* (a 2-year species) had a 4-year cycle. To clarify the masting frequencies of *Q. variabilis* and *Q. serrata* in our study area, we should collect a longer time series of data on annual acorn production of these species.

Resource utilization by acorn-feeding insects in relation to their biology

In our study sites, *M. ursulus* was a specialist predator of the acorns of *Q. serrata* (Fig. 2). Acorn damage by *M. ursulus* in 1998 was low at both sites. Since the low production of *Q. serrata* acorns in 1997 would have starved some of the *M. ursulus* that would otherwise have emerged in 1998 (Fukumoto and Kajimura 2001), the population of *M. ursulus* was greatly reduced in 1998. Thus, mast seeding by *Q. serrata* would be an effective means of controlling *M. ursulus* populations.

In contrast, the population of *Curculio* weevils on *Q. serrata* did not decrease in 1998, although the dominant species (*C. sikkimensis*) was a specialist on *Q. serrata* in our study sites (Fukumoto and Kajimura 2001). Since not a few individuals of *Curculio* weevils spend two or more winters in diapause before emergence (Menu 1993; Menu and Debouzie 1993; Menu et al. 2000; Maeto and Ozaki 2003), prolonged diapause would allow some *Curculio* weevils to avoid starvation in years with poor acorn production, thus stabilizing the weevil population.

As most tortricid moths do not exhibit prolonged diapause (Fukumoto and Kajimura 2001; Maeto and Ozaki 2003), starvation would occur in years with poor acorn production. However, there was no synchrony in annual acorn production between *Q. variabilis* and *Q. serrata* at either of our study sites, and the CVs for the combined acorn production of the two *Quercus* species were lower than those for the individual *Quercus* species. Thus, asynchronous acorn production of these sympatric species would tend to stabilize populations of generalist insects such as the tortricids.

The rate of predation by *C. cardamomi* was also independent of the annual fluctuation in total acorn production of the two tree species (Fig. 3). The rates of predation by this beetle in 1997 and 1998 were extremely low, even though this species is a generalist acorn predator. *C. cardamomi* also attacks post-dispersal *Quercus* acorns (Ueda 1995) and has a wide range of alternative host plant species, such as bracken fern (*Pteridium aquilinum* L.) (Gray 1972), the crown of strawberry, and the bark of Japanese red pine (Nobuchi 1981). Ueda (1995) also reported that *C. cardamomi* could produce two generations within a year. Thus, predation patterns by *C. cardamomi* could not be explained by annual fluctuations in production of mature acorns, since the presence of alternative food resources would also affect the dynamics of *C. cardamomi* populations.

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