Annual variability in sound acorn production was regulated by a generalist seed predator weevil in *Quercus serrata*

Kimiko Hirayama^{1*}, Kenta Mizo¹, Manaka Tatsuno², Mizuki Yoshikawa², Chieri Tachikawa²

¹ Graduate School of Life and Environmental Sciences, Kyoto Prefectural University,

Hangi-cho 1-5, Shimogamo, Sakyo-ku, Kyoto, Japan

² Faculty of Life and Environmental Sciences, Kyoto Prefectural University,

Hangi-cho 1-5, Shimogamo, Sakyo-ku, Kyoto, Japan

*Corresponding author: Kimiko Hirayama

Email: khirayam@gmail.com

Tel & Fax: +81757035682

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Abstract

Highly variable and synchronous seed production within a population ('masting') could be from either synchronised high annual variability in floral initiation ('flower masting') or synchronised floral abortion until maturity ('fruit maturation masting'). We investigated the demographic processes of the female organs from flowering to seed maturity, including each type of insect damage identified, in *Quercus serrata* in six individuals within a stand from 2014 to 2020, western Japan. Although the annual production of sound acorns was significantly correlated with that of female flowers, the annual variability in sound acorn production within an individual was significantly higher and their synchrony increased, compared to those of female flowers. The annual production of female flowers was positively correlated with the temperature difference in April between the previous and flowering years. However, their fluctuation was low, which was neither affected by seed and flower production in the previous year nor contributed to predator starvation. Key-factor analyses revealed that reproductive loss due to oviposition and sap suction by *Mechoris ursulus*, a generalist seed predator weevil for oak species, was the largest and most important factor that contributed to the annual variation in the total pre-dispersal loss of *Q. serrata*. The survival rate from female flowers to sound

acorns was strongly predicted by the temperature in June, corresponding to the emergence of adult *M. ursulus*. This study suggests that highly variable and synchronous sound seed production can be proximately regulated by seed predation when the main predator is a generalist.

Keywords

annual variability in seed production, seed predator, oak species, masting

Statements and Declarations

We have no conflict of interest to declare.

Introduction

Highly variable seed production, which synchronises among individuals within a population, usually termed ‘masting’, has been observed in many long-lived plant species (Kelly 1994, Kelly and Sork 2002). Because masting requires plants to delay reproduction, it is assumed that masting occurs as a selective advantage through ‘one or more economies of scales’, such as

predator satiation and pollination efficiency, in which an occasional large reproductive effort is more efficient than regular smaller ones (Norton and Kelly 1988, Kelly and Sork 2002). In contrast to the ultimate-level hypothesis, masting is regulated by proximate-level mechanisms, such as responses to variability in internal resources and weather cues, which do not necessarily require ultimate-level benefits (Crone and Rapp 2014, Pearse et al. 2016). Identifying the factors that proximately produce variability in seed production would lead to an understanding the adaptive meaning of masting.

Pearse et al. (2016) suggested that the production of a mast seed crop can be the product of either high initial flower production ('flower masting') or high proportion of flowers maturing into seeds ('fruit maturation masting'). In flower masting, the success rate of pollination and maturation into fruit will be high during high-flowering years, induced by weather cues or resources. In fruit maturation masting, flower or seed abortion during pre-dispersal stages, owing to factors not related to flowering size, e.g., weather condition during pollination and/or fruit growing, causes variation in seed crops, which may occur even in the absence of any selective advantage (Espelta et al. 2008, Perez-Ramos et al. 2010). In addition, Montesinos et al. (2012) reported not all mast flowering episodes resulted in mast seeding.

Therefore, to determine the real factors causing masting and their relative contribution, clarifying the demographic process of female reproductive organs from flowering to seed maturity in each individual within a population in the long term, together with the effects of weather and resources, would be needed.

For fagaceous species, whose masting behaviour has been reported in many previous studies (e.g., Sork et al. 1993, Kelly and Sork 2002, Shibata et al. 2002, Kon et al. 2005, Espelta et al. 2008, Perez-Ramos et al. 2010, Koenig and Knops 2014, Koenig et al. 2015, Pesendorfer et al. 2016, Schermer et al. 2019, Moreira et al. 2019), predation pressure on their female reproductive organs (i.e., acorns) is known to be high (Kon et al. 2005, Hirayama et al. 2017, Xiao et al. 2017, Bogdziewicz et al. 2018). Kon et al. (2005) investigated the relative contribution of pollination failure and insect predation to the annual fluctuation of seed crops for *Fagus crenata* by monitoring the female reproductive organs from flowering to seed maturity in five beech forests. They indicated that the effect of insect predation on seed production was larger than that of pollination failure, although both factors significantly affected fluctuations in seed production. As in their study, the quantitative evaluation of insect predation on the demographic process during the pre-dispersal stage would be important for

understanding masting behaviour in fagaceous species, although few studies have reported on it (Fukumoto and Kajimura 2005, Hirayama et al. 2017).

Previous studies indicated that pre-dispersal predation in fagaceous species occurs soon after flowering up to maturity by various insects and that oviposition by adult insects and predation by hatched larvae usually occur at specific periods during the pre-dispersal phase (Fukumoto and Kajimura 2001, Hirayama et al. 2017). Koenig et al. (2003) suggested that seed predator characteristics, such as size, mobility, abundance, lifespan, and degree of specialisation, act as selection pressures in the seed production patterns of plants. Therefore, distinguishing each type of insect damage and evaluating its effect on the demographic process during the pre-dispersal stage might explain the real cause of fluctuations in seed production of fagaceous species.

In this study, we investigated the demographic processes from flowering to seed maturity, including each type of insect damage identified, for six individuals of *Quercus serrata* within a forest stand from 2014 to 2020. First, we analysed intra-individual variability and inter-individual synchrony within a population in both annual flower and sound acorn production in relation to weather and resources, examined in previous studies as mentioned above. Second,

key factor analyses were conducted to assess the relative importance of each demographic factor that can contribute to annual fluctuations in sound acorn production during the pre-dispersal stage in individuals. Based on these results, we proposed a novel mechanism affecting annual variability in seed production in plant species whose main seed predator during the pre-dispersal stage is a generalist: insect predation can proximately induce highly variable and synchronous sound seed production within a population.

Materials and Methods

Study site and species

We conducted our study at the Kamigamo Experimental Station, Kyoto University (35°4'21"N, 135°45'43"E; 145 m a.s.l.) in western Japan, which has hot and humid summers and moderately cold winters. The rainy season occurs annually during the transition from spring to summer, from the beginning of June to the middle of July. Based on the data recorded from 1986 to 2015 at the station office (142 m a.s.l.), the mean annual temperature and precipitation were 14.7°C and 1578 mm, respectively (Kamigamo Experimental Station, unpublished data). The forest soils were Inceptisol (Soil Survey Staff 2010) derived from Mesozoic sedimentary rocks

(Geological Survey of Japan, AIST 2015). The study area was covered with a secondary forest dominated by *Chamaecyparis obtusa*, *Q. serrata*, *Q. glauca*, and *Ilex pedunculosa*.

Q. serrata is a deciduous oak native to East Asia that belongs to the subgenus *Quercus* section *Prinus* (Iwatsuki et al. 2006). This species is widely distributed in temperate regions and is often found in secondary forests in Japan. *Q. serrata* is monoecious, anemophilous, flowers in spring (during late April and early May in the study site; K. H., personal observation), and requires one year to mature acorns. According to the observation of flower buds using a stereomicroscope, Hashizume et al. (2003) found that differentiation of primordia of staminate inflorescences within the buds occurred from late June to late August of the previous year of flowering, and pollen grains were formed in early or middle April of the following year. They also reported that the differentiation of pistillate flowers was initiated in early August of the previous year of flowering, perianth differentiation occurred in late August, young pistillate flowers grew rapidly in mid-April in the following year, and pistil differentiation was observed approximately 10 days before anthesis. After flowering, fruit development occurred until late September; first, the cupules, which enclose the acorns, develop and then enlarge, and after that,

the acorns protrude from the cupules and grow rapidly from mid-August (Matsuda 1982, K. H., unpublished data). Mature acorns mainly fall in mid-October.

During the stages after flowering up to maturity, the female reproductive organs of *Q. serrata* are continuously attacked by various insects, either larvae or adults, during specific periods (Fukumoto and Kajimura 2001, Hirayama et al. 2017). At the study site, we observed that female reproductive organs produced galls due to cynipid wasps approximately from early June, damaged due to sap suction by adults of weevils (mainly *Mechoris ursulus* (Roelofs)) approximately from early July, oviposited by *Kobuzo rectirostris* (Roelofs) approximately from middle August, oviposited by *M. ursulus* approximately from late August, and oviposited by *Curculio* spp. approximately from September (K. H., personal observation). We also observed female reproductive organs damaged by moth larvae of various species: *Pammene nemorosa* Kuznetsov, *Cydia danilevskyi* (Kuznetsov), and *Assara inouei* Yamanaka were mainly identified, while many other unidentified species feeding on the female reproductive organs of *Q. serrata* appeared to exist (K. H. personal observation).

Sampling and classifying design of female reproductive organs

128 We selected six *Q. serrata* individuals (diameter at breast height (DBH) $\pm$ SD, 35.4 ± 6.8 cm;
129 height, 18.4 ± 2.2 m; canopy area, 45.2 ± 42.2 m²). These trees were within a natural stand
130 where a number of *Q. serrata* trees were mixed. Regarding fagaceous species within the stand,
131 *Q. glauca*, *Q. sessilifolia*, and *Castanopsis cuspidata* were also mixed to a lesser extent. We set
132 three seed traps (0.5 m² surface area with a circular mouth) under the crown of each sampled
133 tree on 13 May 2014. Each seed trap was made of polyethylene cloth (mesh size, 1 mm) and
134 positioned approximately 1.2 m above the ground. The contents of the traps were collected
135 twice a month from May 2014 to March 2021, and all female reproductive organs (both
136 pistillate flowers and acorns) of *Q. serrata* were sorted in the laboratory. We first classified the
137 organs into four categories based on the size (length and width of the organs) and the condition
138 of the organs: (A) sound (attaining mature acorn size [13 mm in length, 7 mm in width] with
139 sound cotyledons), (B) immature with no signs of damage (failing to attain mature seed size
140 and/or with undeveloped cotyledons, including pistillate flowers); (C) organs with some signs
141 of damage other than being broken (exhibiting a gnaw mark, a penetrating hole, larval frass,
142 deformation, and/or discolouration; mainly caused by insects), and (D) the organs that were
143 broken (mainly caused by vertebrate predation), as described by Hirayama et al. (2017). The

organs classified into category (D) were low in our study system (0–1.4 % of all female reproductive organs falling during one year in each tree).

When we classified the organs into category (C), we dissected them and observed them using a stereomicroscope. Based on larval faeces, feeding traces, penetration and oviposition scars, and/or larvae inside, we classified the damage into the following types: (a) sap suction by adult weevils, mainly by *M. ursulus*, (b) damaged by moth larvae, (c) oviposition by *M. ursulus*, (d) oviposition by weevils other than *M. ursulus*, mainly by *K. rectirostris*, (e) damaged by cynipid wasps, and (f) others, as described by Hirayama et al. (2017). In addition, we reared the larvae from the female reproductive organs and observed the feeding and/or oviposition patterns of the adults on the organs (K. H. personal observation). Based on this, we confirmed our classification of insect damage types. For each type of insect damage, the mean $\pm$ SE of the length of the organs was recorded, which reflected the developmental stage of the organs (Matsuda 1982, K. H. unpublished data). These measurements for each of the types of damage were as follows: (a) 5.82 ± 0.06 cm, (b) 9.13 ± 0.28 cm, (c) 13.29 ± 0.13 cm, (d) 12.11 ± 0.29 cm, and (e) 4.64 ± 0.06 cm, respectively. They were determined to be statistically different from each other based on Tukey's multiple comparison test ($P < 0.05$) after conducting a linear mixed

model (LMM) with the length of acorns as the response variable and each type of insect damage as the explanatory variable, with each individual tree as a random factor.

Analyses

Annual variability in the number of female flowers and sound acorns

We defined the sum of the number of female reproductive organs that fell into the seed traps for each individual (total area, 1.5 m²) in a year (flowering to the end of the following March) as the annual number of female flowers. To detect intra-individual variability in the production of female flowers and sound acorns, we calculated the coefficient of variation for the annual numbers of female flowers and sound acorns during the seven-year observation for each of the six individuals (CV_i) and their means ($\overline{CV_i}$). To identify inter-individual synchrony in the production of female flowers and sound acorns within a population, we calculated pairwise correlation coefficients of the female flower and sound acorn numbers (both log-transformed after adding 1 to reduce the correlation between the mean and the variance and avoid excluding zero data) during the seven years for each pair of all individuals (Pearson's correlation coefficient; r_p), and then obtained the means of all these pairs ($\overline{r_p}$), as suggested by Koenig et

al. (2003). To obtain 95% confidence intervals in $\overline{CV}_i$ and $\overline{r_p}$ values, we performed sets of 1000 bootstrap trials, in which the annual number of female flowers and sound acorns were randomly replaced from the observed values for each individual over a seven-year period.

We performed a generalised linear mixed model (GLMM) with a log link and negative binomial error distribution to evaluate whether the annual number of sound acorns per individual is related to female flowers. The annual number of sound acorns (non-log-transformed) was designated as the response variable. The annual number of female flowers, which were log-transformed after adding 1, was the explanatory variable, and the individual tree was treated as a random factor. To explore the effect of the previous flower and/or acorn production per individual on their current amount, we also conducted GLMM analyses with a log link and negative binomial error distribution. The annual numbers of female flowers or sound acorns (non-log-transformed) in the year (t_i) were designated as the response variables, whereas those in the year before (t_{i-1}) were designated as the explanatory variables. These explanatory variables were log-transformed by the addition of 1. Individual trees were treated as random factors.

To assess whether the annual fluctuation in the number of female flowers per individual was related to pre-dispersal insect damage, we performed two GLMM analyses with logit link and binomial error distribution, in accordance with Shibata et al. (2002). In the first analysis, to examine whether individual-level predation satiation occurred in years with high production of female flowers, the proportion of the female organs damaged by insects during one year per individual was designated as the response variable, and the log-transformed annual number of flowers per individual was the explanatory variable. In the second analysis, to examine whether annual fluctuations in the production of female flowers per individual contribute to the individual-level predator starving effect, the proportion of the female organs damaged by insects during one year per individual was designated as the response variable, and the log-transformed ratio of the annual number of female flowers per individual in the year (t_i) to the year before (t_{i-1}) was designated as the explanatory variable. In both analyses, the number of broken acorns (mainly due to vertebrate predation) was excluded from calculating the proportion of the female organs damaged by insects, and the individual tree was treated as a random factor. When the annual number of female flowers per individual was zero, the data were excluded from the analysis.

207

208 *Relationships between weather variables and the annual production of female flowers and*
209 *survival rate from female flowers to sound acorns*

210 We obtained daily precipitation data and mean daily temperature (average of the daily
211 maximum and minimum values) from 2012 to 2020 from the Kamigamo Experimental Station
212 office. Weather variables were chosen considering the differentiation process of the
213 reproductive organs in flower buds, as mentioned above (Hashizume et al. 2003), for the
214 analyses of annual variability in female flower number per individual; monthly average
215 temperature (average of mean daily temperatures for one month), and precipitation from April
216 to September one year before flowering and from March to April in the flowering year were
217 considered. We also calculated the difference between a year and its previous year for all
218 variables, according to methods described by Kelly et al. (2013), who suggested that the
219 differential cue might cause masting behaviour. We checked for multicollinearity among all
220 variables using a variance inflation factor (VIF), where a $VIF > 10$ was considered to indicate
221 multicollinearity (Quinn and Keough 2002). If one variable was highly correlated with another
222 variable based on the VIF value, we adopted one variable of the two (Online Resource 1). We

then performed GLMM models, which were a log link and negative binomial error distribution, with the annual number of female flowers per individual (non-log-transformed) as the response variable, each adopted weather variable as the explanatory variable, and the individual tree as a random factor. We selected five weather variables based on a comparison of the models using the Akaike information criterion (AIC); the lower the AIC value, the better the model. We then created GLMM models based on a subset of the five selected variables. The best model was determined using the AIC value, as calculated from the R package MuMIn (Barton 2020), which calculates all possible models extracted from the full model. When there were models with fewer parameters whose ΔAIC was < 2 from the top model, we adopted the simplest model (with the fewest parameter) as the best model. This was because models with ΔAIC between 0 and 2 were considered to have equivalent and substantial empirical support (Burnham and Anderson 2002).

For the analyses of survival rate from female flowers to sound acorns per individual per year, we chose average daily temperature and total precipitation during the flowering periods of *Q. serrata* (15 April to 10 May based on K. H., personal observation) and the monthly values from April to September based on the phenology of the acorn development (Matsuda

1982, K. H. unpublished data; Online Resource 2). The VIF value indicated that all variables were less than 10, which confirmed that multicollinearity among these weather variables was not a serious concern. We constructed GLMM models, which were a log link and negative binomial error distribution, with the annual number of sound acorns (non-log-transformed) as the response variable and each weather variable as the explanatory variable. The annual number of female flowers was an offset variable, and the individual trees were treated as random factors. We determined the best model, which describes the relationship between the survival rate of female flowers and weather variables using the same method in the analyses of annual variability in female flower number as mentioned above.

Relative contribution of each type of reproductive loss during the pre-dispersal phase

Key factor analysis (Podoler and Rogers 1975) was used to estimate the relative contribution of factors that influenced plant reproductive potential to the observed variation in total pre-dispersal losses. The reproductive losses due to factor k_i and the total pre-dispersal loss (K) were calculated for each year in each individual tree as follows:

$$k_i = \log_{10}(N_{i-1} + 1) - \log_{10}(N_i + 1)$$

255 $K = \sum_{i=1}^n k_i$

256 where N_i is the number of female reproductive organs that remained after mortality due to
 257 factor i (the number per total area of 1.5 m² per individual), and n represents the number of
 258 factors. We added 1 to those numbers before log-transformation to avoid excluding zero data.
 259 The slope of the regression of k_i on K was used to determine the relative impact of each factor
 260 on the total variation in the reduction of potential reproductive output (Jordano 1989, Traveset
 261 1994, Fukumoto and Kajimura 2005, Hirayama et al. 2017): the higher regression value
 262 contributes more to changes in the total mortality (Podoler and Rogers 1975). In this study, to
 263 identify the slope of the regression between k_i and K , we performed a LMM with each k_i as
 264 the response variable, K as the explanatory variable, and the individual tree as a random factor.

265 Based on the phenological observation (K. H. personal observation) and size of the
 266 organs suffered from each type of insect damage, as mentioned above, we determined the
 267 seasonal order of factors damaging the organs as follows:

- 268 (1) damaged by cynipid wasps
 269 (2) sap suction by adult weevils, mainly by *M. ursulus*
 270 (3) damaged by moth larvae

271 (4) oviposition by weevils other than *M. ursulus*, mainly by *K. rectirostris*

272 (5) oviposition by *M. ursulus*

273 Damage caused by other insects and vertebrate predation was assumed to be lower in order than
274 insect damage because it usually occurred when the acorns had reached maturity. Meanwhile,
275 reproductive loss due to abortion of pistillate flowers and immature acorns was assumed to
276 occur before insect damage in the analysis.

277 All analyses were performed using R 4.1 (R Core Team 2021).

278

279 **Results**

280 **Annual variability in the numbers of female flowers and sound acorns**

281 The annual numbers of sound acorns exhibited higher inter-year variation than those of female
282 flowers for all individual trees (Fig. 1). $\overline{CV}_t$ for the number of sound acorns was significantly
283 higher (1.51) than that for the number of female flowers (0.50) based on their 95% confidence
284 intervals using the bootstrap method (Table 1). The annual number of sound acorns was
285 significantly correlated with that of female flowers (Fig. 2 and Online Resource 3). However,
286 there were many cases where the production of sound acorns was very low despite the large

production of female flowers in a year. Synchrony was stronger in the production of sound acorns (0.68) than that of female flowers (0.32), although average pairwise correlations in both productions were significantly positive (Table 1). There were no significant effects of annual production of female flowers or sound acorns on their production in the following year (Online Resource 3 and 4).

The proportions of insect-damaged organs to the production of female flowers ranged from 0.18-0.83 (Fig. 3) for individual trees over the seven years. While the GLMM analysis indicated that their proportions significantly decreased with increasing the annual number of female flowers, change in annual numbers of female flowers between successive years did not significantly affect their proportions (Fig. 3 and Online Resource 5).

Relationships between weather variables and the annual production of female flowers and survival rate from female flowers to sound acorns

For the annual number of female flowers per individual, in the models selected based on AIC values, five weather variables which were highly correlated with them were: the change in average April temperature from one year before flowering to the flowering year ($\Delta\text{AprT}(t_i)$),

the precipitation in May in one year before flowering, the change in average May temperature from two years before flowering to one year before flowering, the average temperature in April the year before flowering, the average temperature in April in the flowering year (Online Resource 6). Among them, $\Delta\text{AprT}(t_i)$, which was positively related to the annual number of female flowers, was selected as the best model for predicting their production (Online Resource 7 and Table 2).

For the survival rate from female flowers to sound acorns per individual, in the models selected based on AIC values, the five weather variables which were highly related to them were: the average temperature in June, the average temperature during the flowering period from 15 April to 10 May, the precipitation in April, the average temperature in April, and the average temperature in May (Online Resource 8). Among them, the average temperature in June, which was positively related to the survival rate, was selected as the best model for the prediction (Online Resource 9 and Table 2).

Relative contribution of each type of reproductive loss during the pre-dispersal phase

Except in 2014 and 2020, when the production of sound acorns was high for all individuals, the number of female organs tended to be greatly reduced by sap suction by adult weevils (Fig. 4, stage 3-4) and by oviposition by *M. ursulus* for all individuals (stage 6-7). Reproductive losses due to abortion of pistillate flowers and immature acorns (stage 1-2) and oviposition by weevils other than *M. ursulus*, mainly by *K. rectirostris* (stage 5-6), were not significantly related to total pre-dispersal loss, while reproductive losses due to almost all types of insect damage were significantly related to the total pre-dispersal loss (Table 3). Among the types of insect damage, the slope of the regression on the total pre-dispersal loss was the highest in oviposition by *M. ursulus*, followed by sap suction by adult weevils, mainly by *M. ursulus* (Table 3 and Online Resource 10).

Discussion

Although the annual production of female flowers per *Q. serrata* individual significantly influenced the annual production of sound acorns (Fig. 2), the annual fluctuation of female flower production was significantly lower than that of sound acorn production (Fig. 1 and Table 1). Previous studies have suggested that the annual variability of flower production is affected

by weather conditions during floral initiation and development and their internal resource dynamics in plants (Kelly and Sork 2002, Pearse et al. 2016). Miyazaki et al. (2014) demonstrated that nitrogen concentration in the shoot at the time of floral initiation positively correlated with flowering intensity in the following year for the masting species *F. crenata*, supporting the resource budget model, which assumes that the fluctuation of reproductive efforts could be induced by resource depletion after heavy flowering (Isagi et al. 1997, Satake and Iwasa 2000). However, for *Q. serrata*, the annual production of female flowers was not affected by both the annual production of female flowers and sound acorns in the previous year (Online Resource 4), indicating that internal resources were not important for their annual variability. On the other hand, their production was affected by the change in average April temperature from one year before flowering to the flowering year (Table 2). Because April is the period when pistil differentiation in female flowers occurs immediately before flowering (Hashizume et al. 2003), the weak fluctuation of annual female flower production may be induced by a weather cue, as suggested by Kelly et al. (2013).

Both the amplitude of variation and synchrony between individuals increased in sound acorn production, compared with those in female flower production (Fig. 1 and Table1),

350 implying that synchronised floral or seed abortion until maturity would work in sound acorn
351 production patterns in *Q. serrata*. For most of the 1-yr *Quercus* species, which require one year
352 to develop acorns, their annual seed production has a relationship with spring temperatures
353 when pollination occurs (Koenig and Knops 2014): higher spring temperature results in higher
354 phenological synchrony during the flowering season, contributing to increased pollen
355 availability and fertilisation success (Koenig et al. 2015, Bogdziewicz et al. 2020). After
356 fertilisation, acorn development has been reported to be strongly affected by water stress during
357 the summer and/or by resource supply, resulting in in synchronous fluctuation in mature acorn
358 production (Espelta et al. 2008, Perez-Ramos et al. 2010). However, for *Q. serrata*, the survival
359 rate of female flowers was not positively related to spring temperature, nor negatively related
360 to summer precipitation (Online Resource 8). Moreover, reproductive loss due to abortion of
361 pistillate flowers and immature acorns, mainly caused by intrinsic factors (Jordano 1989,
362 Traveset 1994), was not correlated with the total pre-dispersal loss (Fig. 4, Table 3, and Online
363 Resource 10), and the annual production of sound acorns was not affected by either female
364 flowers or sound acorns in the previous year (Online Resource 3). The annual variability in total
365 pre-dispersal loss was significantly influenced by almost all types of insect damage. Therefore,

synchronised floral or seed abortion until maturity in *Q. serrata* is not caused by plant internal mechanisms, such as pollination failure nor resource limitation, but by insect damage.

Among the types of insect damage, reproductive loss, owing to oviposition and sap suction by *M. ursulus*, was the largest and most important factor that contributed to the annual variation of total pre-dispersal loss in *Q. serrata* (Fig. 4, Table 3, and Online Resource 10). In our study area, adult *M. ursulus* began to emerge from middle to late July after one winter (K. H. personal observation). They sucked sap from immature acorns using their proboscis immediately after emerging, and oviposited eggs in each acorn (one egg per acorn) from mid-August (K. H. personal observation). The survival rate from female flowers to sound acorns was strongly predicted by the average temperature in June (Table 2), which corresponds to the emergence of adult *M. ursulus*. The higher temperature in June probably enhanced the emergence of *M. ursulus* adults earlier, resulting in a phenological mismatch between their sap suction behaviour and acorn growth in *Q. serrata*; however, further long-term studies are required to clarify this mechanism.

Even though the effect of insect damage on acorn survival was so large in *Q. serrata*, their weak fluctuation in annual female flower production did not contribute to the predator

382 starvation at the individual level (Fig. 3 and Online Resource 5). Although predator satiation
383 may occur when the amount of annual female flower production exceeded a certain threshold,
384 predation rates were often high even at the high amount of the flower production (Fig. 3 and
385 Online Resource 5). Selection for predator satiation and starvation depends on various factors
386 of seed predators' characteristics, including the size, mobility, abundance, lifespan, and degree
387 of specialisation (Koenig et al. 2003, Bogdziewicz et al. 2021). For species with specialist seed
388 predators, it has been reported that high fluctuations in flowering intensity contribute to
389 starvation and satiation of predators (Kelly and Sullivan 1997, Kon et al. 2015). In contrast, a
390 main seed predator of *Q. serrata*, *M. ursulus*, is a generalist weevil that predaes on various
391 kinds of acorns of oak species (K. H. personal observation, Imai and Hirayama 2013, Hirayama
392 et al. 2017, Hirayama et al. 2019); however, they prefer oak species with scale-like cupules,
393 such as *Q. serrata* (Hirayama et al. 2017). Ims (1990) predicted that the mechanisms that
394 promote within-group reproductive synchrony are unlikely to have evolved when predators
395 have a typical generalist-type of functional response and can switch favourable prey with high
396 offspring densities. Accordingly, for *Q. serrata*, weak fluctuations in annual female flower
397 production, which only correlated with the weather variable, might have adapted to the

generalist seed predator. The result of this study suggests that insect predation during the pre-dispersal stage can proximately induce highly variable and synchronous sound seed production for plant populations, which main seed predator is a generalist.

Author Contributions

KH conceived the ideas and designed methodology; CH, MY, MT and KM collected the data; KH analyzed the data and wrote the manuscript. All authors contributed the drafts and gave final approval for publication.

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Table 1 Mean individual variability ($\overline{CV}_t$) and mean synchrony between trees ($\overline{r}_p$) in the annual number of female flowers and sound acorns of *Q. serrata*.

	Female flowers	Sound acorns
$\overline{CV}_t$	0.50 (0.36-0.58)	1.51 (1.02-1.72)
$\overline{r}_p$	0.32 (-0.16-0.27)	0.68 (-0.16-0.24)

Numbers in parentheses indicate 95% confidence intervals using the bootstrap method.

Table 2 The best model predicting the annual number of female flowers and survival rate from female flowers to sound acorns from the weather variables using a GLMM.

	Estimate	SE	z-Value	P
<i>The number of female flowers</i>				
(Intercept)	6.599	0.142	46.46	<0.001
Changes in average temperature in April from one year before flowering to the flowering year	0.222	0.073	3.06	0.002
<i>The survival rate from female flowers to sound acorns</i>				
(Intercept)	-41.410	4.881	-8.57	<0.001
average temperature in June	1.741	0.222	7.85	<0.001

Table 3 The results of LMMs test indicating the regression of each reproductive loss due to main factors on the total pre-dispersal loss (K).

	Estimate	SE	t -Value	P
<i>Abortion of female flowers and immature acorns</i>				
(Intercept)	0.361	0.060	6.029	<0.001
Total K	-0.019	0.025	-0.783	0.439
Damaged by cynipid wasps				
(Intercept)	-0.015	0.013	-1.135	0.268
Total K	0.026	0.006	4.427	<0.001
Sap suction by adult weevils, mainly by <i>M. ursulus</i>				
(Intercept)	-0.010	0.100	-0.103	0.919
Total K	0.274	0.050	5.445	<0.001
Damaged by moth larvae				
(Intercept)	-0.041	0.039	-1.077	0.288
Total K	0.108	0.020	5.336	<0.001
Oviposition by weevils other than <i>M. ursulus</i> , mainly by <i>K. rectirostris</i>				
(Intercept)	0.036	0.032	1.112	0.273
Total K	0.030	0.017	1.755	0.087
Oviposition by <i>M. ursulus</i>				
(Intercept)	-0.199	0.118	-1.680	0.101
Total K	0.448	0.062	7.218	<0.001

Figure legends

Fig. 1 Annual variability in the number of (a) female flowers and (b) sound acorns for each individual tree.

Fig. 2 The relationship between the annual number of female flowers and sound acorns for each individual tree over seven years. Different letters indicate different individuals. The regression line is a predicted relationships based upon the result of the GLMM ($P < 0.05$) testing the effects of the number of female flowers per year (t_i) on the number of sound acorns per year (t_i). Individual trees were treated as a random factor.

Fig. 3 The relationship of the proportion of the female organs damaged by insects during one year to (a) the annual number of female flowers and (b) the ratio of the number of female flowers in the current year to that in the previous year for each individual. Different letters indicate different individuals. When the number of flowers was zero, the data were excluded. The regression line is a predicted relationships based upon the result of the GLMM ($P < 0.05$)

testing the effects of the annual number of female flowers per year (t_i) on the proportion of the organs damaged by insects during a year (t_i). Individual trees were treated as a random factor.

Fig. 4 Reduction in the number of female reproductive organs for each individual throughout the successive stages for each observed year. Stage 1, female flowers (i.e., initial number of the organs); stage 2, organs remaining after abortion in the immature stage; stage 3, organs remaining after being damaged by cynipid wasps; stage 4, organs remaining after being attacked through sap suction by adult weevils; stage 5, organs remaining after being damaged by moth larvae; stage 6, organs remaining after oviposited by weevils other than *Mechoris ursulus*; stage 7, organs remaining after oviposited by *M. ursulus*; stage 8, organs remaining after other damage mainly due to animals (i.e., number of sound acorns).

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Supplementary Information

Annual variability in sound acorn production was regulated by a generalist seed predator weevil in *Quercus serrata*

Kimiko Hirayama^{1*}, Kenta Mizo¹, Manaka Tatsuno², Mizuki Yoshikawa², Chieri Tachikawa²

¹ Graduate School of Life and Environmental Sciences, Kyoto Prefectural University,
Hangi-cho 1-5, Shimogamo, Sakyo-ku, Kyoto, Japan

² Faculty of Life and Environmental Sciences, Kyoto Prefectural University,
Hangi-cho 1-5, Shimogamo, Sakyo-ku, Kyoto, Japan

*Corresponding author: Kimiko Hirayama

Email: khirayam@gmail.com

Online resource 1 Data of weather variables which were analysed in relation to the production of female flowers.

		Flowering year (t_i)						
		2014	2015	2016	2017	2018	2019	2020
AprT(t_{i-1})	average Apr. temp. in year (t_{i-1})	12.1	12.3	13.5	14.2	12.8	14.5	11.8
Δ AprT(t_{i-1})	change in average Apr. temp. from year (t_{i-2}) to year (t_{i-1})*1	-0.7	0.2	1.1	0.7	-1.3	1.7	-2.6
AprP(t_{i-1})	Apr. precipitation in year (t_{i-1})*2	111.5	85.0	170.0	163.0	149.5	157.0	102.5
Δ AprP(t_{i-1})	change in Apr. precipitation from year (t_{i-2}) to year (t_{i-1})*3	-23.0	-26.5	85.0	-7.0	-13.5	7.5	-54.5
MayT(t_{i-1})	average May temp. in year (t_{i-1})	18.2	17.7	19.1	18.9	19.0	18.0	18.5
Δ MayT(t_{i-1})	change in average May temp. from year (t_{i-2}) to year (t_{i-1})	0.9	-0.5	1.4	-0.2	0.1	-1.0	0.5
MayP(t_{i-1})	May precipitation in year (t_{i-1})	52.0	78.5	133.0	144.0	74.0	214.0	87.5
Δ MayP(t_{i-1})	change in May precipitation from year (t_{i-2}) to year (t_{i-1})*1	-6.0	26.5	54.5	11.0	-70.0	140.0	-126.5
JunT(t_{i-1})	average June temp. in year (t_{i-1})	23.7	22.4	20.9	21.5	20.3	21.5	21.8
Δ JunT(t_{i-1})	change in average June temp. from year (t_{i-2}) to year (t_{i-1})	2.3	-1.2	-1.6	0.6	-1.1	1.2	0.3
JunP(t_{i-1})	June precipitation in year (t_{i-1})*2	169.0	64.5	281.5	261.5	205.0	251.0	140.5
Δ JunP(t_{i-1})	change in June precipitation from year (t_{i-2}) to year (t_{i-1})*3	-117.0	-104.5	217.0	-20.0	-56.5	46.0	-110.5

JulT(t_{i-1})	average July temp. in year (t_{i-1})	28.1	25.8	25.6	26.1	26.9	27.9	25.0
Δ JulT(t_{i-1})	change in average July temp. from year (t_{i-2}) to year (t_{i-1})	1.7	-2.3	-0.2	0.5	0.8	1.0	-2.9
JulP(t_{i-1})	July precipitation in year (t_{i-1})	156.5	129.5	447.5	113.0	243.0	487.0	253.0
Δ JulP(t_{i-1})	change in July precipitation from year (t_{i-2}) to year (t_{i-1})	-262.0	-27.0	318.0	-334.5	130.0	244.0	-234.0
AugT(t_{i-1})	average Aug. temp. in year (t_{i-1})	28.6	26.0	26.6	27.3	26.9	27.6	27.7
Δ AugT(t_{i-1})	change in average Aug. temp. from year (t_{i-2}) to year (t_{i-1})	0.8	-2.6	0.6	0.7	-0.4	0.6	0.1
AugP(t_{i-1})	Aug. precipitation in year (t_{i-1})	102.5	458.0	209.0	126.0	139.0	127.0	373.5
Δ AugP(t_{i-1})	change in Aug. precipitation from year (t_{i-2}) to year (t_{i-1})	-46.5	355.5	-249.0	-83.0	13.0	-12.0	246.5
SepT(t_{i-1})	average Sep. temp. in year (t_{i-1})	24.1	21.4	21.3	23.7	21.5	21.9	24.5
Δ SepT(t_{i-1})	change in average Sep. temp. from year (t_{i-2}) to year (t_{i-1})	-0.9	-2.7	-0.1	2.5	-2.2	0.4	2.6
SepP(t_{i-1})	Sep. precipitation in year (t_{i-1})	406.0	112.5	192.0	383.0	173.0	401.0	77.5
Δ SepP(t_{i-1})	change in Sep. precipitation from year (t_{i-2}) to year (t_{i-1})	272.0	-293.5	79.5	191.0	-210.0	228.0	-323.5
MarT(t_i)	average Mar. temp. in year (t_i)	7.1	7.5	8.1	6.2	9.1	7.4	8.6
Δ MarT(t_i)	change in average Mar. temp. from year (t_{i-1}) to year (t_i)	-1.3	0.5	0.5	-1.9	2.9	-1.6	1.2
MarP(t_i)	Mar. precipitation in year (t_i)	167.0	158.0	62.5	68.5	143.5	77.5	99.0
Δ MarP(t_i)	change in Mar. precipitation from	100.5	-9.0	-95.5	6.0	75.0	-66.0	21.5

	year (t_{i-1}) to year (t_i)							
AprT(t_i)	average Apr. temp. in year (t_i)	12.3	13.5	14.2	12.8	14.5	11.8	11.0
Δ AprT(t_i)	change in average Apr. temp. from year (t_{i-1}) to year (t_i)	0.2	1.1	0.7	-1.3	1.7	-2.6	-0.8
AprP(t_i)	Apr. precipitation in year (t_i)	85.0	170.0	163.0	149.5	157.0	102.5	126.0
Δ AprP(t_i)	change in Apr. precipitation from year (t_{i-1}) to year (t_i)	-26.5	85.0	-7.0	-13.5	7.5	-54.5	23.5

Temperature is in °C; precipitation is in mm. Variables marked *1, *2, and *3 were highly correlated with each other and had been found to have a high VIF value (>10). We adopted one variable from each pair.

Online Resource 2 Data of weather variables which were analysed in relation to survival rate from female flowers to sound acorns.

		Flowering and acorn maturing year (t_i)						
		2014	2015	2016	2017	2018	2019	2020
Apr15T (t_i)	Average temp. from 15th Apr. to 10th May in year (t_i)	14.6	16.3	15.5	15.4	15.7	14.8	14.3
Apr15P(t_i)	Precipitation from 15th Apr. to 10th May in year (t_i)	82.5	67.5	106.5	102.0	206.5	59.5	72.5
AprT(t_i)	Average Apr. temp in year (t_i)	12.3	13.5	14.2	12.8	14.5	11.8	11.0
AprP(t_i)	Apr. precipitation in year (t_i)	85.0	170.0	163.0	149.5	157.0	102.5	126.0
MayT(t_i)	Average May temp in year (t_i)	17.7	19.1	18.9	19.0	18.0	18.5	18.5
MayP(t_i)	May precipitation in year (t_i)	78.5	133.0	144.0	74.0	214.0	87.5	116.5
JunT(t_i)	Average Jun. temp in year (t_i)	22.4	20.9	21.5	20.3	21.5	21.8	22.7
JunP(t_i)	Jun. precipitation in year (t_i)	64.5	281.5	261.5	205.0	251.0	140.5	271.0
JulT(t_i)	Average Jul. temp in year (t_i)	25.8	25.6	26.1	26.9	27.9	25.0	24.2
JulP(t_i)	Jul. precipitation in year (t_i)	129.5	447.5	113.0	243.0	487.0	253.0	636.0
AugT(t_i)	Average Aug. temp in year (t_i)	26.0	26.6	27.3	26.9	27.6	27.7	28.7
AugP(t_i)	Aug. precipitation in year (t_i)	458.0	209.0	126.0	139.0	127.0	373.5	17.5
SepT(t_i)	Average Sep. temp in year (t_i)	21.4	21.3	23.7	21.5	21.9	24.5	23.7
SepP(t_i)	Sep. precipitation in year (t_i)	112.5	192.0	383.0	173.0	401.0	77.5	131.0

Temperature is in °C; precipitation is in mm.

Online Resource 3 The results of GLMMs testing the effects of the number of female flowers per year (t_i), in year (t_{i-1}) and the number of sound acorns per year (t_{i-1}), on the number of sound acorns per year (t_i). Individual trees were treated as a random factor.

	Estimate	SE	z-Value	P
(Intercept)	-7.66	3.11	-2.46	0.014
$\log_{10}$ [the number of female flowers in year (t_i) +1]	3.94	1.08	3.64	<0.001
(Intercept)	6.441	2.463	2.61	0.009
$\log_{10}$ [the number of female flowers in year (t_{i-1}) +1]	-1.325	0.891	-1.49	0.137
(Intercept)	3.352	0.619	5.41	<0.001
$\log_{10}$ [the number of sound acorns in year (t_{i-1}) +1]	-0.474	0.558	-0.85	0.40

Online Resource 4 The results of GLMMs testing the effects of the number of female flowers per year (t_{i-1}) and the number of sound acorns per year (t_{i-1}) on the number of female flowers per year (t_i). Individual trees were treated as a random factor.

	Estimate	SE	z-Value	P
(Intercept)	6.176	0.699	8.83	<0.001
$\log_{10}$ [the number of female flowers in year (t_{i-1}) +1]	0.147	0.250	0.59	0.56
(Intercept)	6.757	0.202	33.53	<0.001
$\log_{10}$ [the number of sound acorns in year (t_{i-1}) +1]	-0.222	0.165	-1.34	0.18

Online Resource 5 The results of GLMMs testing the effects of the annual number of female flowers per year (t_i) and the ratio of the annual number of female flowers per year (t_i) to the year before (t_{i-1}) on the ratio of the organs damaged by insects during a year (t_i). Individual trees were treated as a random factor.

	Estimate	SE	<i>z</i> -Value	<i>P</i>
(Intercept)	-0.474	0.620	-0.76	0.44
$\log_{10}$ [the number of female flowers in year (t_i)]	-0.132	0.218	-0.61	0.54
(Intercept)	-0.800	0.085	-9.42	<0.001
$\log_{10}$ [the number of female flowers in year (t_i) / year (t_{i-1})]	-0.099	0.142	-0.70	0.49

Online Resource 6 Five explanatory variables selected based on lower AIC of GLMM models which tested the relationship between the annual female flowers and each of weather variables. Individual trees were treated as a random factor. See Online Resource 1 for an abbreviation of the weather parameters.

	(Intercept)	Estimate	SE	<i>z</i> -Value	<i>P</i>	AIC
$\Delta\text{AprT}(t_i)$	6.599	0.222	0.073	3.064	0.002	632.7
$\text{MayP}(t_{i-1})$	7.224	-0.006	0.002	-2.925	0.003	633.5
$\Delta\text{MayT}(t_{i-1})$	6.555	0.269	0.147	1.837	0.066	637.2
$\text{AprT}(t_{i-1})$	9.366	-0.213	0.119	-1.783	0.075	637.5
$\text{AprT}(t_i)$	4.650	0.151	0.088	1.712	0.087	637.7

Temperature is in °C; precipitation is in mm.

Online Resource 7 The top models extracted from the full model using the selected five explanatory variables are shown based on the results of AIC values. Numerical values indicated estimated values of the models. See Online Resource 1 for an abbreviation of the weather parameters.

(Intercept)	AprT(t_{i-1})	Δ MayT (t_{i-1})	MayP(t_{i-1})	AprT(t_i)	Δ AprT (t_i)	AIC
6.599					0.222	632.7
5.448			-0.005	0.133		633.0
7.224			-0.006			633.5
6.909			-0.003		0.143	633.6
3.776	0.308		-0.011			633.8
6.568		0.136			0.189	633.8

Temperature is in °C; precipitation is in mm.

Online Resource 8 Five explanatory variables selected based on lower AIC of GLMM models which tested the relationship between the survival rate from female flowers to sound acorns and each of weather variables. Individual trees were treated as a random factor. See Online Resource 2 for an abbreviation of the weather parameters.

	(Intercept)	Estimate	SE	<i>z</i> -Value	<i>P</i>	AIC
JunT(t_i)	-41.407	1.741	0.222	7.850	<0.001	323.9
Apr15T(t_i)	20.998	-1.609	0.292	-5.511	<0.001	338.9
AprP(t_i)	1.512	-0.037	0.007	-4.954	<0.001	339.2
MayT(t_i)	34.766	-2.063	0.519	-3.979	<0.001	344.7
AprT(t_i)	6.761	-0.783	0.192	-4.075	<0.001	346.4

Temperature is in °C; precipitation is in mm.

Online Resource 9 The top models extracted from the full model using the selected five explanatory variables are shown based on the results of AIC values. Numerical values indicated estimated values of the models. See Online Resource 2 for an abbreviation of the weather parameters.

(Intercept)	Apr15T(t_i)	AprT(t_i)	AprP(t_i)	MayT(t_i)	JunT(t_i)	AIC
-22.960	1.397	-0.758		-1.285	1.449	322.5
-41.410					1.741	323.9
-32.790			-0.011		1.409	323.9
-48.670	0.637		-0.016	-0.517	1.727	324.4
-26.430				-0.517	1.488	324.5
-23.640	1.401	-0.750	-0.001	-1.260	1,455	324.5

Temperature is in °C; precipitation is in mm.

Online Resource 10 The relationship between the sum of reproductive loss during the pre-dispersal phase and the proportion of each reproductive loss for each individual over seven years. Different letters indicate different individuals. When the number of flowers was zero, the data were excluded.