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Large acorns benefit seedling recruitment by satiating weevil larvae in *Quercus aliena*

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Abstract Plants can enhance their seed viability and survival through reducing the fitness costs of herbivory by satiating seed predators at either plant or seed level, or both. The former satiates with production of large crops while the latter with large-sized seeds, enhancing the probability of seed survival. We analyzed both types of satiation in the interaction between the *Quercus aliena* and the weevil *Curculio* spp in 2 years with different crop size and acorn size. Larger crop size seemed to satiate less effectively weevils due to higher proportions of the seeds were attacked in oaks producing more crops of smaller acorns. However, prematurely abscission of infested acorns in large crop year might compensate this ineffectiveness. Larger acorns in lean year well satiated weevil larvae, as a larger acorn size increased the likelihood of embryo survival and seedling establishment. Although effective satiation by larger acorns would be negated by smaller seed crops, the proportion of attacked acorns that survived increased with large acorn size in lean year. These results highlighted the importance of annual variation in acorn size of *Quercus aliena* in satiating and defending weevil larval predations, consequently in successful seedling recruitment and establishment.

Keywords Acorn · Defense traits · Acorn infestation · Acorn size/mass · Seedling establishment

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Introduction

Seeds of many plants suffer very heavy pre-dispersal predation by animals (Crawley 2000; Branco et al. 2002). Lots of seed-eating animals exert strong selective pressures on plants by greatly reducing seed crops, and thereby lowering plant fitness and fecundity (Steele et al. 1993; Siemens et al. 1994). Plants, however, evolve a number of morphological and chemical characteristics that serve as defense mechanisms against seed predators and dispersers (Harborne 1991; Steele et al. 1993; Hughes and Vogler 2004), in which some plant defenses appear only when the plant is attacked (Howe and Westley 1988; Schultz 1988). Generally, plants can employ two general strategies to defend themselves against herbivory: they can either reduce the amount of damage they experience (resistance), or they can tolerate herbivore damage (Fineblum and Rausher 1995).

Acorn bearing oaks are one of the most important forest trees in the world (Takahashi and Shimada 2008). Because of its large in amount and richness in nutrients, such as large amounts of protein, carbohydrates, and fats, as well as the minerals, acorns are very attractive to animals and suffer heavy predation by a number of consumers. Wild creatures, including birds, small and large mammals as well as insects, i.e., larvae of weevils, *Curculio sp*. make acorns as an important part of their diet and efficiently consumed them. In most cases, the larvae of some weevils live in young acorns of *Quercus* species, consuming the kernels as they develop (Brown 1980). It is well documented that resistance and tolerance are often considered to be alternative defense strategies for plants (Siemens et al. 2003). Resistance mechanisms avoid consumption and include a number of physical barriers or chemical defenses (Harper et al. 1970; Janzen 1971; Kelrick et al. 1986; Díaz 1996; Hulme and Benkman 2002). However, satiation does not prevent consumption but tolerates weevil's damage and reduces its negative consequences (Stowe et al. 2000; Bonal et al. 2007), and may be achieved by large seed crops or large seeds (Crawley 1997). They might function together or solely to reduce the fitness costs of granivory and then minimize predator's damage and maximize plant fitness and fecundity. The probability for a given seed to survive to become a 1-year-old seedling may be largely dependent on its ability to defend or tolerate damage by predators (Xiao et al. 2007).

Many tree species, e.g., oak trees can produce massive crops of large seeds at irregular intervals (Vander Wall 2002; Xiao et al. 2005; Jansen et al. 2006; Li and Zhang 2007). This "mast seeding" phenomenon has been widely explained by the hypothesis of "predator satiation hypothesis" (Janzen 1970; Kelly 1994; Kelly and Sork 2002) that mast seeding can produce massive crops which swamp local seed eaters with food and allow seeds to escape predation and successfully establish (Sork 1993). Plants producing large seed crops in synchrony with conspecifics are predicted to experience less pre- and post-dispersal seed mortality and have higher seedling recruitment than plants that produce nonsynchronous seed crops (Janzen 1970; Ims 1990). On the other side, most field and laboratory studies accumulated that acorns with large size/mass are not always consumed completely by insects and may still possess the ability to germinate and produce viable seedlings (Oliver and Chapin 1984; Soria et al. 1996; Siscart et al. 1999; Branco et al. 2002; Yi and Zhang 2008), indicating the capability of oak acorns to tolerate and satiate predation by insects at seed level. Recent studies on seed dispersal by rodents have shown that large seeds (Forget et al. 1998; Vander Wall 2003; Xiao et al. 2006) are more likely to be removed and then hoarded, rather than eaten in situ. Larger acorns are therefore assumed to facilitate post-dispersal acorn survival and seedling establishment and recruitment for most oak species. However, it has not been explicitly addressed whether producing large acorns could be an effective satiation strategy for oak regeneration due to a trade-off between the production of large acorns and acorn crops. This study focused on the annual variation in seed rain, seed size, seed mass, infestation rate, tannin concentration, germination rates, to explore the potential defensive mechanisms of *Q. aliena*, the most important oak species in a wide area of eastern Asia (e.g., China, Japan, and Korea). We aim to test the hypothesis that acorns with large size or mass in the lean year are responsible for tolerance/resistance to weevil larval predation, and serves as the main role in defending insect predation.

Materials and methods

Study site and oak species

Acorns of *Q. aliena* investigated in this study maturate in the Tianchi Mountain National Forest Park (altitude 950–1860 m, 34°12′–34°18′ N, 111°42′–111°52′ E) of Luoyang City, Henan Province. Weevil species (*Curculio sp.*) are pre-dispersal seed predators that feed on acorns of the oak species. Female weevils lay one or several eggs (up to seven) in the cotyledon of acorns. Weevil larvae hatch from eggs a few days after they are laid and the larvae progress through 5 instars inside the acorn. Throughout their development, the weevil larvae feed on the acorn despite the presence of ellagic and gallic acid tannins while at the same time excreting frass (Oak 1993). Acorns of *Q. aliena* do not send up a green shoot in the fall, instead, a thick taproot grows down several cm into the soil.

Seed rain

Twenty-four oak trees were randomly chosen and labeled in our study area in 2007 and 2008. Acorns were collected using seed traps that were placed under the oak canopies. Seed traps, excluding terrestrial vertebrate predators, were designed and randomly located to capture acorns (according to Skalski 1987). Avian predation is regarded as less influence on potential losses of acorns because few bird species were witnessed in the experiment sites during our survey, and most of them are small-sized passerines unable to swallow the entire acorns. 1 m × 1.2 m polyester net (2-mm mesh) was fastened on a 0.5 m^2 metal frame to make a concave seed trap, preventing acorn rebounding after falling. The frame was set on a thin wooden rod about 1.2 m above the ground to prevent predation by terrestrial vertebrates. Traps were established to catch acorns and other debris while letting rainfall easily pass through. Seed traps were set up 1–2 m away from the tree trunk under the crown of the selected oak trees just before acorns ripened. The number of traps per tree was proportional to its canopy surface, in all of them it was covered between 1.5 and 2% of the canopy (Pulido and Diaz 2005). Traps were left in place until all ripe acorns had fallen from the trees. In order to assess whether acorns were removed from the traps by birds or other vertebrate animals, acorns were marked with a tiny tag, and placed in pairs within seed traps at the beginning of seed rain, and none of them were removed during the course of the study.

Acorn classification and pre-dispersal predation by insects

Seed traps were sampled periodically. First acorns were collected on 24 August both in 2007 and 2008, and from that date onwards seed traps were checked every day until acorn rain ceased in later September. In each visit, traps were emptied and their content taken to the laboratory and deposited separately. The sample from each seed trap was visually classified into four categories: (1) sound, no obvious oviposition puncture on pericarp, (2) immature, undeveloped acorns enwrapped in cupule, (3) insect depredated, having obvious puncture on pericarp or showing emergence holes, and (4) cupules. Sound and infested acorns collected every day were individually placed in-doors in plastic plates with 4 cm × 3 cm × 3 cm grids. Acorns were checked daily to detect and count weevil larvae exited from acorns (number of larvae of Lepidoptera were neglected due to very low level of infestation rate), each larva was weighted to the nearest 0.1 mg using a precision balance. Thirty days after all the larvae had escaped from acorns, acorn traits (length, width, and mass), number and site of emergence holes per acorn, and number of larvae per acorn were measured. Infestation rate was calculated on each individual tree sample. All acorns were dissected and categorized according to Xiao et al. (2007) as following: (1) intact or sound; (2) lightly damaged mostly with a sound embryo and over 50% of cotyledons undamaged by insects, detected by puncture evidence of adult weevil feeding but without emergence holes (and may still contain insect eggs or young larvae); (3) severely damaged mostly with a damaged embryo and over 50–100% of cotyledons damaged by insects, detected by presence of mature larvae or emergence hole (s). Husk thickness of sound acorns was measured using a digital caliper. Tannin concentration in basal and apical end per sound acorn (sample size = 6 in 2007 and 2008, respectively) of the oak were measured using Folin-Denis method according to AOAC (1990).

Effects of insect damage and acorn size on seedling establishment

To test the effects of insect damage and acorn size on seedling emergence and establishment, we set up four treatments consisting of intact, damaged, large, and small acorns collected from no less than five oak trees in field. Intact acorns appear sound without emergence hole and obvious oviposition puncture after 30 days' deposition; however, infested acorns display one or more emergence holes. We randomly selected 100 each acorns for large, small, sound, and infested acorns with different emergence holes both in 2007 and 2008. Large and small acorns were sound acorns and differed greatly in seed size and mass but sound and infested acorns showed no difference in seed size (Table 1). In November 2007 and 2008, 40 flowerpots (diameter = 20 cm, height = 15 cm) each contained with sand (nutrition free) were divided into four groups, and then 100 acorns of each category were uniformly sown 1 cm deep in the flowerpots (10 acorns per flowerpot). All flowerpots were placed into FPG3-300AY-12 lightemitted feeding boxes and artificially watered at regular intervals to keep a relative humidity of 60 ± 10%. No fertilizer was applied throughout the experiments. All the flowerpots were subject to an artificially visible light 800 μmol m^{-2} s^{-1} radiation, 25/15°C and 14 h:8 h photoperiod. We recorded the proportion of seedlings emergence after 10 days' cultivation; survival rates were estimated after 60 days of treatments.

Statistical analysis

Independent Sample *T* Test was used to test the differences in acorn length, width, and fresh mass of intact and damaged acorns between 2007 and 2008. Difference in the number of emergence holes and larvae per acorn between the acorns trapped in 2007 and 2008 were tested using Generalized Linear Models (GLM). Independent Sample *T* Test was applied to test the differences in acorn crops and infestation rates of acorns between 2007 and 2008. The nonparametric Mann–Whitney test was used to test the differences in seedling emergence and survival between intact and damaged as well as large and small acorns of the oak species tested.

Results

Seed rain course

Two years' studies indicated that seed rain of the oak species simultaneously began in late August (24th day), and ended in later September (25th day) (Fig. 1). The acorn crop of *Q. aliena* in 2008 was significantly lower than those in 2007 ($t = -2.113$, df = 46, $P = 0.040$) (Table 1). Length, width, and fresh mass of acorns trapped in 2007 were significantly smaller than those of acorns collected in 2008, both for sound acorns ($t = -10.579$, df = 405, $P < 0.0001$; $t = -11.137$, df = 405, $P < 0.0001$; $t = -5.411$, df = 405, $P < 0.0001$) and infested ones ($t = -11.208$, df = 386, $P < 0.0001$; $t = -7.962$, df = 386, $P < 0.0001$; $t = -3.691$, df = 386, $P < 0.0001$) (Table 1). The temporal changes of the sound acorns, infested acorns, and undeveloped acorns recorded during the seed rain followed an inverse U-shape pattern both in 2007 and in 2008 (Fig. 1). However, infected acorns were dropped prematurely and infested acorn rain was earlier than sound acorn rain in 2007, indicating the premature acorn abscission. Whereas, infested acorns did not drop prematurely and infested acorn rain was concurrently with sound acorn rain in 2008 (Fig. 1).

Pre-dispersal seed predation

In-door dissection of acorns collected from seed traps indicated that pre-dispersal infestation proportions of acorns by weevil larvae were (59.90 ± 16.24)% and (41.27 ± 19.61)% in 2007 and 2008, respectively ($t = 3.039$, df = 46, $P = 0.004$). Length, width, and fresh mass of insect damaged acorns of *Q. aliena* were much larger than those of intact ones in 2007 ($t = 3.143$, df = 454, $P = 0.002$; $t = 3.735$,

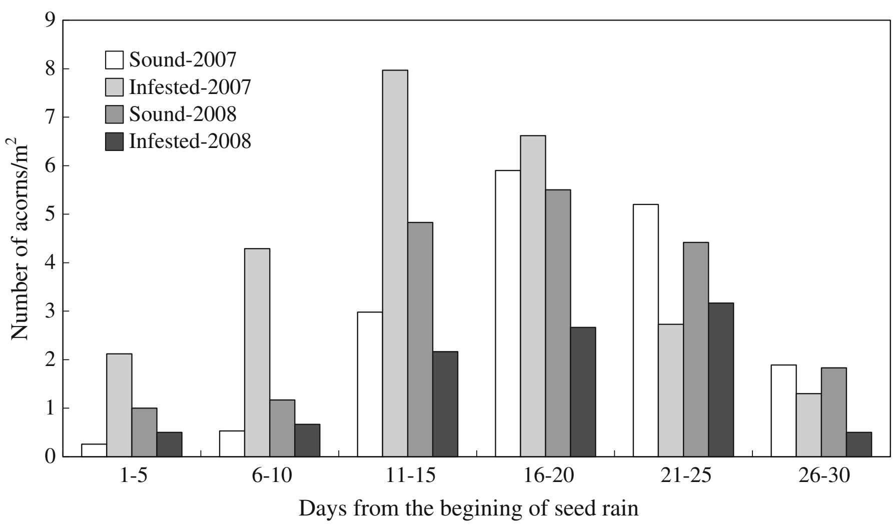


Fig. 1 Accumulative number of infested and sound acorns collected in the traps along the date in 2007 and 2008

Table 1 Variation in acorn crops, acorn traits, and infestation status in 2007 and 2008

Seed features	Year					
	2007			2008		
Intact	All	Large	Small	All	Large	Small
Length	1.91 ± 0.20	2.13 ± 0.18	1.83 ± 0.16	2.34 ± 0.15	2.48 ± 0.06	2.19 ± 0.09
Width	1.35 ± 0.13	1.52 ± 0.09	1.29 ± 0.08	1.65 ± 0.08	1.73 ± 0.06	1.57 ± 0.04
Weight	2.20 ± 0.57	3.12 ± 0.42	1.86 ± 0.30	3.14 ± 0.46	4.30 ± 0.19	2.43 ± 0.26
Sample size (n)	182	112	70	225	143	82
Infested	All	Large	Small	All	Large	Small
Length	2.01 ± 0.18	2.18 ± 0.12	1.81 ± 0.10	2.35 ± 0.18	2.61 ± 0.06	2.26 ± 0.14
Width	1.43 ± 0.14	1.57 ± 0.09	1.28 ± 0.08	1.61 ± 0.12	1.79 ± 0.06	1.55 ± 0.10
Weight	2.58 ± 0.63	3.14 ± 0.39	1.90 ± 0.27	3.01 ± 0.76	4.18 ± 0.41	2.59 ± 0.54
Sample size (n)	272	156	116	116	76	40
Number of larvae per acorn	1.43 ± 0.66			1.93 ± 0.89		
Number of emergence holes per acorn	1.39 ± 0.60			1.90 ± 0.90		
Pre-dispersal infestation (%)	59.90 ± 16.24			41.27 ± 19.61		
Seed crops (acorn/m^2)	41.79 ± 15.56			28.42 ± 17.89		
Non-damaged (%)	40.11			58.70		
Light-damaged (%)	15.51			9.84		
Severe-damaged (%)	44.39			31.46		
	Apical	Middle	Basal	Apical	Middle	Basal
Husk thickness	0.44 ± 0.13	0.42 ± 0.08	0.36 ± 0.06	0.40 ± 0.11	0.40 ± 0.10	0.37 ± 0.08
Tannin content (mg/g)	141.32 ± 4.36		135.39 ± 7.62	134.76 ± 5.21		127.43 ± 3.84
Emergence hole occurrence (%)	26.04	33.14	40.83	32.04	29.13	38.83

df = 454, $P < 0.0001$; $t = 3.878$, df = 454, $P < 0.0001$) but not in 2008 ($t = 0.470$, df = 339, $P = 0.639$; $t = -1.590$, df = 339, $P = 0.113$; $t = 1.156$, df = 339, $P = 0.249$). However, acorn length and width increased with increasing number of emergence holes per acorn in 2008 but not in 2007, indicating larval superparasitism preference for large acorns in 2008. However, fresh mass tended to decrease with increased number of larvae per acorn in 2007 but remained unchanged in 2008 (Table 2). 26.04, 33.14, and 40.83% of emergence holes were found to be at the apical, middle, and basal end of *Q. aliena* in 2007 and a similar pattern was found in 2008 (i.e., 32.04, 29.13, and 38.83%) (Table 1). Both in 2007 and 2008, acorns with single emergence hole accounted for more than 50% of the acorn crops; however, 4.20 and 24.84% acorns with more than three emergence holes were found in 2007 and 2008, respectively (Fig. 2). Numbers of larvae and emergence holes per acorn were different between the two years, respectively ($F = 11.416$, df = 1, $P = 0.001$; $F = 13.108$, df = 1, $P < 0.0001$) (Table 1).

Effects of insect damage and acorn size on seedling establishment

For *Q. aliena*, seedling germination from infested acorns with different emergence hole sites was significantly lower than intact acorns ($Z = -3.782$, $P < 0.0001$) in 2007. Analyses on the correspondent data collected in 2008 demonstrated the same patterns ($Z = -3.784$, $P < 0.0001$). Due to great loss of cotyledon reserves caused by weevil larvae feeding, viability of infested acorns of *Q. aliena* with more than three emergence holes decreased remarkably both in 2007 and 2008 (Fig. 3). However, seedling germination and survival rates in 2008 were much higher than that in 2007 for infested acorns ($Z = -1.855$, $P = 0.064$; $Z = -2.504$, $P = 0.012$) (Fig. 3). No difference was detected in seedling

Table 2 Relationship between acorn traits and the number of emergence holes per acorn trapped in 2007 and 2008 using Spearman correlation

Acorn traits	Number of emergence holes per acorn	
	2007	2008
Acorn length	$y = -0.621x + 2.6817$	$y = 1.7305x - 2.0996$
	$r = -0.152$	$r = 0.370$
	$P = 0.153$	$P < 0.0001$
	$N = 272$	$N = 116$
Acorn width	$y = -0.854x + 2.6589$	$y = 2.3628x - 1.8379$
	$r = -0.119$	$r = 0.301$
	$P = 0.265$	$P < 0.0001$
	$N = 272$	$N = 116$
Acorn weight	$y = -0.3124x + 2.238$	$y = 0.1378x + 1.5559$
	$r = -0.220$	$r = 0.059$
	$P = 0.037$	$P = 0.492$
	$N = 272$	$N = 116$

emergence and survival rates among large, small, and intact acorns both in 2007 ($\chi^2 = 1.286$, df = 2, $P = 0.526$; $\chi^2 = 4.872$, df = 2, $P = 0.088$) and 2008 ($\chi^2 = 1.076$, df = 2, $P = 0.584$; $\chi^2 = 4.927$, df = 2, $P = 0.094$) (Figs. 3 and 4).

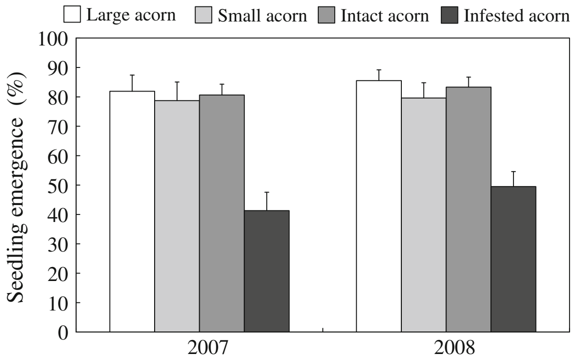
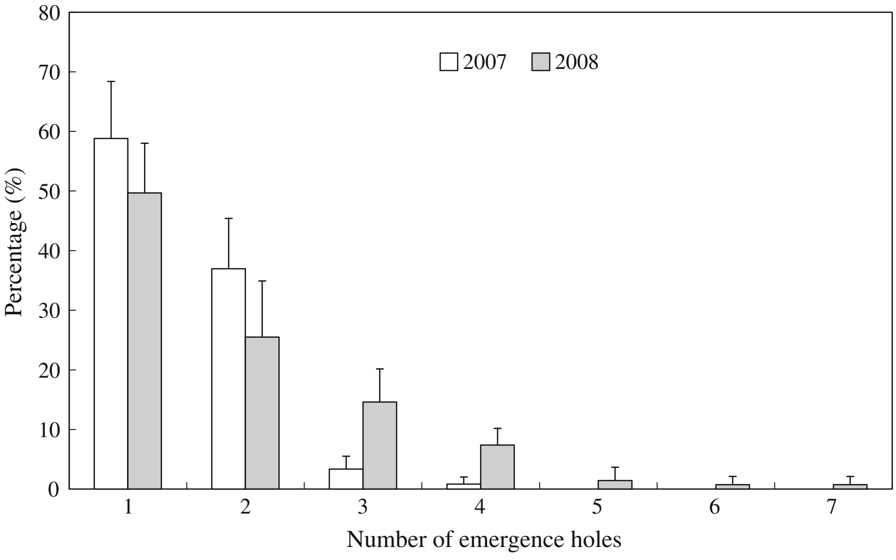


Fig. 3 Proportion of seedling emergence in large, small, infested, and sound acorns collected in 2007 and 2008

Discussion

Oak species suffer high level of pre-dispersal infestation by insects and post-dispersal predation by small rodents world widely (Johnson et al. 1993; Yu et al. 2003; Maeto and Ozaki 2003; Leiva and Fernández-Alés 2005; Wood 2005; Pons and Pausas 2007; Takahashi and Shimada 2008). Despite extensive acorn damage due to herbivorous species, e.g., larvae of weevil, moths and cynipids, a great portion of infested acorns can successfully germinate and establish as individual seedlings in *Q. aliena* in our studies (Figs. 3 and 4). It can be concluded that the feeding of carpophagous insect larvae does not necessarily destroy the embryo, and that insect

Fig. 2 Frequency distribution of the number of emergence holes in infested acorns collected in 2007 and 2008. Error bars stand for SD, and the same as below in Fig. 3 and 4



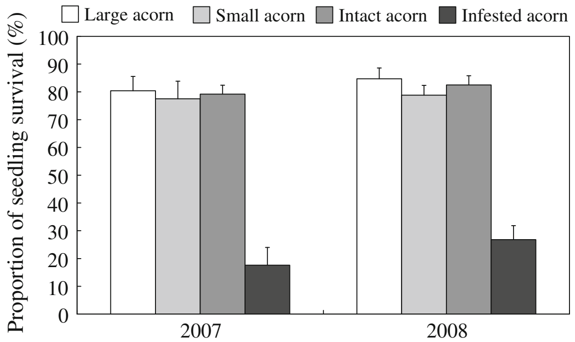


Fig. 4 Proportion of seedling establishment in large, small, infested, and sound acorns collected in 2007 and 2008

infested acorns often retain their germination ability. Our present results are consistent with previous studies on other oak species (Oliver and Chapin 1984; Fukumoto and Kajimura 2000; Branco et al. 2002; Yi and Zhang 2008) that the viability of infested but still viable acorns strongly depends on acorn size and the number of larvae developed in it.

Plants have developed various defensive mechanisms over evolutionary time to decrease the negative effects of herbivorous and granivorous insects by reducing insect growth, fecundity, and/or survival (Strauss and Zangerl 2002). Satiation strategy at the seed level will ensure that a proportion of the seeds survive herbivorous predation (Bonal and Muňoz 2007). Our experiments indicated that larger seeds would satiate more efficiently than small ones, enhancing the probability of seed survival after having been attacked. Acorns with large size/mass allow toleration of insect infestion by rapidly mobilizing stored reserves and show strong immunity to pathogens and fungi for later development of seedlings compared to those possessing a relatively small mass, therefore increased probability for seedling establishment. A significantly negative relationship between acorn mass and the number of emergence holes per acorn found in 2007 but not in 2008 indicated stronger predator satiation of large acorns than small ones (Table 2). Our cultivation experiments reveal that damaged acorns can germinate and produce viable seedlings if the larvae have not killed the germ itself. Some oak species with large acorns can tolerate the presence of a few larvae relatively well. We found that sound and infested acorns of *Q. aliena* trapped in 2008 are significantly larger than those in 2007 (Table 1), this could partially explain the higher proportion of seedling emergence and survival in 2008 due to an increase in the likelihood of embryo survival (Figs. 3 and 4). Weevil larvae usually start feeding at the basal end to the apical end where the embryo is; this feeding behavior is not a consequence of uneven tannin distribution in acorns but mostly related to oviposition behavior of female adult. Thus, a large acorn size increases the probabilities of embryo survival, as the larva may finish its development before reaching and predating the embryo (Bonal et al. 2007).

A negative relationship between seed size and the number of seeds produced has always been identified in various tree species (Eriksson and Jakobsson 1999; Parciak 2002), and the proportion of acorns attacked by insects is generally much lower in mast than in lean years (Crawley and Long 1995). These facts indicate that the satiation effect at the seed level could be negated by low seed crops, larger proportion of infested acorn, and an increased number of larvae per seed. We actually found a negative relationship between seed size and the acorn crops in 2007 and 2008, but we do not witness a negative correlation between seed crop size and the rate of injury by the weevils (Table 1), whereas this phenomenon is widely reported in many temperate tree species (Crawley and Long 1995; Shibata et al. 1998, 2002). This inconsistency with previous results might be explained by the prolonged lifecycle (diapause) of weevil larvae (Maeto and Ozaki 2003), i.e., weevil populations exactly remain high during mast year so that the rate of acorn injury remains high even in rich crops. Although the negative relationship between acorn crop and size would preclude the effectiveness of satiation at seed level, low infestion rate in large-acorn (lean) year would alternatively increase satiation effect of larger acorns. Although predation satiation in mast year will be affected by prolonged diapause of predators (Maeto and Ozaki 2003), effective satiation by larger acorns might be enhanced by lower infestation rates associated to smaller seed crops.

Despite low proportion of infested acorns in large-acorn year 2008, superparasitism occurred and definitely provoked an increase in the number of larvae per acorn, consequently the likelihood for a larva to finish its development before reaching the embryo decrease because of increasing conspecific competition for limited food (Bonal and Muňoz 2008). This can be partially explained by the fact that the number of emergence holes and weevil larvae per acorn trapped in 2008 was larger than those trapped in 2007 (Table 1), suggesting that larger acorns will attract one female weevil to lay much more eggs or a few females to lay eggs into the same acorn (multi-infestation or superparasitism). A positive relationship between acorn size (length and width) and the number of emergence holes per acorn found in 2008 but not in 2007 further upholds the above suggestion. To distinguish if this multi-infestation is due to oviposition preference in larger acorns or, in alternative, if lower mortality of embryos and young larvae occurs in larger acorns due to lower intraspecific competition, we provided female weevil adults with paired small (5) and large (5) acorns to see their oviposition preference. Our results indicated that female weevils significantly preferred for large acorns to lay more eggs. Superparasitism can be largely attributed to multi-oviposition rather than lower mortality of embryos or young larvae in large acorns in our studies.

However, superoviposition in some larger acorns allows a proportion of acorns to escape oviposition and predation by weevils, resulting in low infestion rate in 2008. It seems like that multi-infested acorns will reduce the chance of seedling emergence as compared to acorns infested by single weevil larva and have negative influence on satiation effectiveness of large acorns. However, our results found larval sizes in multi-infested acorns (>4 larvae) decline dramatically compared with those weeviled by single or two larvae and retaining a larger absolute amount of cotyledon uneaten. Furthermore, seedling emergence and survival are higher in infested acorns trapped in 2008 than those with correspondent emergence holes in 2007 due to difference in cotyledon remains, one acorn with six emergence holes even successfully germinated in 2008. Multi-infestation does not necessarily reduce seedling emergence in acorns covarying with large sizes, and compensates the negative effect of smaller seed crops with larger seeds. Oak trees *Q. aliena* producing larger acorns should have been more effective satiating at the seed level. On the other hand, large crops with small acorns seem to serve as an alternative defense mechanism against weevil predation as *Q. aliena* acorns infested by weevils are prematurely abscised in 2007 (Fig. 1). The premature abscission of infested seeds had been suggested as a plant defense that might have negative consequences for insect fitness (Yu et al. 2003; Bonal and Muňoz 2008), larval mortality would increase to a great extent because larvae would suffer from intense predation by vertebrate post-dispersal acorn consumers that do not discriminate weevil infested acorns. Hence, variation in acorn size/mass and subsequent predator satiation may serve as an important role in resisting weevil infestion in acorns of *Q. aliena*.

In summary, the evolutionary defensive mechanisms in the oak acorns may be the results of natural selection driven in part by mutual interactions between acorns and seed predators. Our results first evidence that *Q. aliena* maximize their viability through satiating larval feeding via annual variation in acorn sizes, a unique evolutionary mechanism to resist predators at seed level. The defensive mechanisms of large seed satiation may be particularly important and active in determining acorn fitness in response to selection pressure.

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