Acorn defenses to herbivory from insects: Implications for the joint evolution of resistance, tolerance and escape

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Abstract

Acorn predation by insects and its effects on seedling establishment were investigated among three co-occurring oak species (*Quercus variabilis*, *Q. serrata* and *Cyclobalanopsis glauca*) in a subtropical evergreen broadleaved forest, Southwest China. All oak species had high tannin concentration (over 10%) but differed in acorn mass and germination schedule. We hypothesized that the defensive traits in acorns (e.g. seed mass, tannins and germination schedule) act together to reduce damage from insect seed predators. *Q. variabilis* had significantly lower predation (51.2%) than either *Q. serrata* (71.4%) or *C. glauca* (73.8%). Seedling establishment decreased with increasing injury for all oak species studied. As much as 43% of insect infested acorns germinated and established as viable seedlings despite extensive acorn mortality due to insect seed predators. The larger seed mass of *Q. variabilis* appears to tolerate insect infestation and retain enough stored reserves for seed germination and early growth of seedlings. Autumn germination also benefited *Q. variabilis* and *Q. serrata*, allowing escape from both direct and ancillary effects of insect feeding by fast reserve shifting to immediate germination of mature acorns. Our results indicate that large seed mass, tannin and autumn germination act together to ameliorate effects of insect seed predation, and the joint evolution of resistance and tolerance (as well as escape through autumn germination) in acorns may be the selective consequences driven in part by interactions with insect seed predators.
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1. Introduction

Investigation of the evolution of plant defenses to herbivory requires characterization of existing plant traits and then reconciliation of these traits with the forces of natural selection that are (and presumably were) operating in the system. Evolutionary categories recently receiving attention are ''resistance'' (i.e. confrontational mechanisms that reduce the amount of damage a plant experiences) and ''tolerance'' (i.e. accommodating or repairing the detrimental effects of herbivore damage) (e.g. Rosenthal and Kotanen, 1994; Strauss and Agrawal, 1999; Stowe et al., 2000; Leimu and Koricheva, 2006, and references therein). However, distinguishing plant tolerance from plant resistance is often difficult (e.g. van der Meijden et al., 1988; Fineblum and Rausher, 1995; Mauricio et al., 1997; Leimu and Koricheva, 2006). Moreover, it is poorly understood how plant tolerance, resistance and other defensive mechanisms function together in response to herbivory (e.g. Harris, 1980; Strauss and Agrawal, 1999; Mauricio, 2000; Stowe et al., 2000). Seed predation by animals is a specific form of herbivory termed granivory, and plays an important role in seedling establishment, plant colonization and diversity, and the coevolutionary interactions between seeds and animals (e.g. Janzen, 1971; Crawley, 2000; Hulme and Benkman, 2002). Seeds complexly package many traits, including those for defense, dispersal and germination, and these traits are expected to collectively maximize fitness by minimizing damage by seed predators, maximizing dispersal and germination, etc. (e.g. Harris, 1980; Vander Wall, 2001; Hulme and Benkman, 2002). Therefore, the interactions between plant seeds and their seed predators provide a model system to explore how plant traits interact and evolve in response to seed predators.

Seed predation differs from general herbivory in that seed predators often kill individual seeds while herbivores impose relatively low damage on individual plants or their tissue

(Strauss and Zangerl, 2002). Subsequently, the cost of seed predation is much higher than that of herbivory because seed predation can disproportionately reduce plant fitness by directly killing a majority of seeds. Therefore, plant defense to seed predators may be more stringently selected than that derived from selection in response to general herbivores (e.g. browsers) (Hulme and Benkman, 2002). For many seed plants, especially large-seeded plants, the damage caused by insect seed predators is often very extensive prior to dispersal (Crawley, 2000; Hulme and Benkman, 2002, and references therein). The probability for a given seed to survive to become a one-year-old seedling may be largely dependent on its ability to defend, tolerate or escape damage by predators. However, few studies have examined how seed predators influence the evolution of defensive traits in plant seeds and fruits, in contrast to the extensive literature examining plant-herbivore interactions (Stowe et al., 2000; Strauss and Zangerl, 2002, and references therein).

Oak species (*Quercus sensu*), including about 450 species, are very important hardwoods in many temperate and sub/tropical forests across the Northern Hemisphere (Chun and Huang, 1998). Feeding by insect seed predators, e.g. weevils and moths, can cause heavy losses (up to 100%) to acorn crops prior to dispersal (e.g. Crawley and Long, 1995; Fukumoto and Kajimura, 2001; Xiao et al., 2001, 2004b; Yu et al., 2001, 2003; Branco et al., 2002; Maeto and Ozaki, 2003; Leiva and Fernández-Alés, 2005). Defensive mechanisms may include seed mass, time to germination and confrontational chemistry. Tannins, a group of phenolic compounds are believed to be a resistant trait to defend acorns from insect and vertebrate seed predators (e.g. Fox, 1982; Weckerly et al., 1989; Steele et al., 1993; Smallwood et al., 2001; Vander Wall, 2001), while large seed mass (often several grams) in acorns could tolerate partial consumption by seed predators, because some predator-damaged acorns can germinate (e.g. Oliver and Chapin, 1984; Kaushal and Kalia, 1989; Weckerly et al., 1989; Andersson, 1992; Steele et al., 1993) and even establish as viable seedlings (e.g. Fukumoto and Kajimura, 2000; Branco et al., 2002; Leiva and Fernández-Alés, 2005). In addition, autumn dormancy in red oaks (subgenus *Erythobalanus*), in contrast to autumn germination in white oaks (subgenus *Quercus*), may be an adaptive trait to reduce instant consumption and enhance acorn scatter-hoarding/dispersal by seed-caching rodents (e.g. Fox, 1982; Smallwood et al., 2001). These findings show that no single defensive trait (i.e.

resistance, tolerance, escape, etc.) in acorns prevents feeding by seed predators. Thus, we hypothesize that these defensive traits in acorns should function together to minimize predator damage and maximize plant fitness.

As part of a large program, three co-occurring oak species, *Quercus variabilis*, *Q. serrata* and *Cyclobalanopsis glauca*, have been studied in a subtropical evergreen broadleaved forest, Southwest China since 2000 (Xiao et al., 2001, 2003, 2004a, 2004b). Acorns of *Q. variabilis* and *Q. serrata* often germinate soon after falling on the ground while those of *C. glauca* remain dormant until the following spring. The acorn mass also differs among the three oak species, but the differences are small for other seed traits, e.g. tannin concentration and nutrient composition (Table 1). Our previous and ongoing studies indicate that, at least two weevil species (*Curculio haroldi* and *Mechoris ursulus*) and one moth species (*Cydia* sp.) are predispersal seed predators that feed on the acorns of the three oak species, and *C. haroldi* is the dominant insect seed predator (Zhishu Xiao, unpublished data). Typically, adult female weevils puncture the acorn to feed and usually lay one to several eggs in a nearly developed acorn. Larvae hatch and feed within that acorn until the mature larvae exit the acorn and burrow into the soil to enter dormancy for several months or over one year (Z.-S. Xiao, unpublished data). Adult weevils that feed but do not oviposit in the acorns injure the tissue, but leave the seeds relatively intact.

In this study, we investigated acorn predation by insects, and its effects on seedling establishment in the three co-occurring oak species. Here, we addressed the following questions: (1) does insect infestation vary significantly across the three oak species with high tannin concentration (over 10%) but different in acorn mass and germination schedule? (2) How does damage by insects affect acorn germination and seedling establishment? Lastly, we discussed how the defensive traits in acorns (e.g. tannins, seed mass and germination schedule) act together in response to seed predators.

2. Methods

Experiments were performed in the Banruosi Experimental Forest (altitude 700–1000 m, 31°4′N, 103°43′E) of Dujiangyan City, Sichuan Province, Southwest China, with a mean annual temperature of 15.2 °C and an annual precipitation of 1200–1800 mm (Chen, 2000). Common tree species include *Casta-nopsis fargesii*, *Q. variabilis*, *Q. serrata*, *Pinus massoniana*, *Acer*

Table 1
Acorn traits in the three study oak species: *Q. variabilis*, *Q. serrata* and *C. glauca* (from Xiao et al., 2001, 2003)

Description (germination schedule)	Q. variabilis (autumn germination)	Quercus serrata (autumn germination)	C. glauca (autumn dormancy)
Dry mass (g)	1.71	0.77	0.47
Protein (%)	5.92	6.07	4.80
Fat (%)	3.94	3.02	1.88
Starch (%)	54.17	54.01	55.42
Crude fiber (%)	2.87	3.41	2.24
Tannin (%)	11.68	10.62	11.05

Note: Seed nutrient compositions, i.e. protein, fat, starch and tannin, were provided by Center of Grain Quality of Ministry of Agriculture, China.

catalpifolium, *L. harlandii*, *Phoebe zhennan*, *C. glauca*, and *Camellia oleifera*.

2.1. Pre-dispersal seed predation by insects

Acorns of the three oak species studied here become mature in October with *Q. variablis* being the earliest. In late October of 2002, mature acorns were randomly collected on the ground under the canopy of at least five individuals of each of the three oak species. A random sub-sample was taken without replacement and dissected individually to determine predation rate and potential damage to a given acorn by insects, i.e. weevils and moths. Number of eggs or larvae found in a given acorn was recorded. Insect damage was categorized as: (1) undamaged, sound; (2) low-damaged mostly with a sound embryo and over 50% of cotyledons undamaged by insects, detected by puncture evidence of adult weevil feeding but without exit holes (and may still contain insect eggs or young larvae); (3) high-damaged mostly with a damaged embryo and over 50% of cotyledons damaged by insects, detected by presence of mature larvae or exit hole(s). Acorn length, width and fresh mass were also measured in relation to insect damage. The sample size of dissected acorns for each oak species is 168 (*Q. variabilis*), 168 (*Q. serrata*) and 164 (*C. glauca*), respectively.

2.2. Effects of insect damage on seedling establishment

Treatments consisting of undamaged, low-damaged and high-damaged acorns were established for each oak species by external examination of the acorns. Undamaged acorns appeared sound, low-damaged acorns exhibited a surface puncture, but no exit holes, and high-damaged acorns had an exit hole(s). Generally, insect-infested acorns with one or several exit holes have higher damage (mostly with a damaged or dead embryo and over 70% of cotyledons consumed by insects) than those without exit hole(s) (see also Weckerly et al., 1989; Branco et al., 2002; Xiao et al., 2003), and they can be determined by carefully identifying the oviposition holes or exit holes on the acorn surface (Xiao et al., 2003). In November of 2002, a rodent-proofed soil-sand-mixed seedbed (area 9 m × 1.2 m) was established near the study forest, and then 100 acorns per damage level for each oak species were planted 1–3 cm deep, with a proportional spacing distribution in the seedbed. We recorded the number of seedlings emerging in mid-July of 2003, and then we examined the survival of 1-year seedlings and measured shoot height and root length for each seedling 3 months later (i.e. mid-November).

2.3. Data analysis

Pearson χ^2-test was used to test the difference of insect predation among oak species and also for the differences in frequency of number of eggs or larvae per acorn among oak species by pooling the data with two or more eggs or larvae. One-way ANOVA along with LSD test was used to test for differences in acorn length, width and fresh mass among the

levels of insect damage, and also among the three oak species for a given damage level.

For each oak species, Pearson chi-square test or Fisher's Exact test were used to test for differences in seedling emergence and survival among the levels of insect damage, and also among the three oak species for a given damage level. χ^2-Test was used to test the difference in seedling emergence or survival from either low- or high-damaged acorns between any two oak species using differences in seedling emergence or survival of undamaged seeds as a null distribution of expected probabilities. One-way ANOVA along with LSD test or independent sample *t*-test were used to test for differences in shoot height, root length and the ratio of root length to shoot height among the levels of insect damage, and also among the three oak species for a given damage level.

3. Results

3.1. Pre-dispersal seed predation

Pre-dispersal predation of acorns by insects was significantly different among the three oak species ($\chi^2 = 20.826$, d.f. = 2, $P < 0.001$): *Q. variabilis* (51.2%) was significantly lower than either *Q. serrata* (71.4%) ($\chi^2 = 9.412$, d.f. = 1, $P = 0.002$) or *C. glauca* (73.8%) ($\chi^2 = 18.040$, d.f. = 1, $P < 0.001$), but there was no difference between *Q. serrata* and *C. glauca* ($\chi^2 = 0.156$, d.f. = 1, $P = 0.693$) (Fig. 1). Insect-infested acorns consisted primarily of highly damaged compared to low-damaged acorns for all three oak species ($P < 0.001$) (Fig. 1). Frequency of number of eggs or larvae per acorn was not different ($\chi^2 = 3.701$, d.f. = 2, $P = 0.157$) among oak species, though a few *Q. variabilis* acorns contained more than two eggs or larvae (Fig. 2). Acorn length and fresh mass gradually decreased with increasing insect damage for *Q. variabilis* ($P < 0.05$) and *C. glauca* ($P < 0.001$), but only acorn mass was significantly reduced in highly damaged acorns for *Q. serrata* ($P < 0.001$) (Fig. 3). Acorn width was similar in relation to insect damage ($P > 0.2$) for the three oak species (Fig. 3). For a given damage level, *Q. variabilis* acorns had the largest seed mass and width, and *Q. serrata* acorns had the largest length, while all three parameters were smallest in *C. glauca* (all $P < 0.001$).
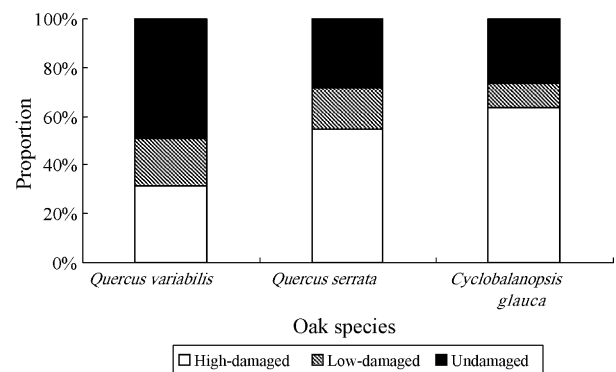

Fig. 1. Relationship between acorn damage level and pre-dispersal seed predation by insects in the three oak species, *Quercus variabilis*, *Q. serrata* and *Cyclobalanopsis glauca*.
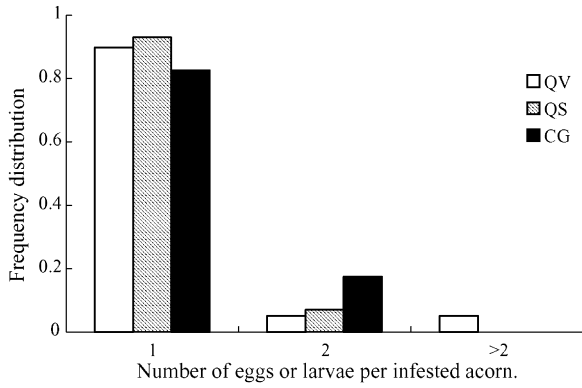
Fig. 2. Frequency distribution of number of eggs and/or larvae found in acorns of the three oak species, *Q. variabilis* (QV), *Q. serrata* (QS) and *C. glauca* (CG).

3.2. Effects of insect damage on seedling establishment

For any oak species, the proportion of seedling emergence from undamaged acorns was significantly higher than either low- or high-damaged acorns the following July: *Q. variabilis* ($\chi^2 = 67.4$, d.f. = 2, $P < 0.001$), *Q. serrata* ($\chi^2 = 135.8$, d.f. = 2, $P < 0.001$) and *C. glauca* ($\chi^2 = 42.3$, d.f. = 2, $P < 0.001$) (Fig. 4). It was also true for total survival of one-year seedlings (All $P < 0.001$, Fig. 4). For *Q. variabilis*, the proportion of 1-year seedlings surviving was similar among the levels of insect damage ((86.3% for undamaged, 87.8% for low-damaged and 81.8% for high-damaged; $\chi^2 = 0.450$, d.f. = 2, $P = 0.798$), while seedling survival did decrease with increasing acorn damage for *Q. serrata* ($\chi^2 = 3.382$, d.f. = 2, $P = 0.184$) and *C. glauca* ($\chi^2 = 5.212$, d.f. = 1, $P = 0.022$). There was no difference in seedling emergence or survival from either low- or high-damaged acorns between any two oak species based on the differences in seedling emergence or
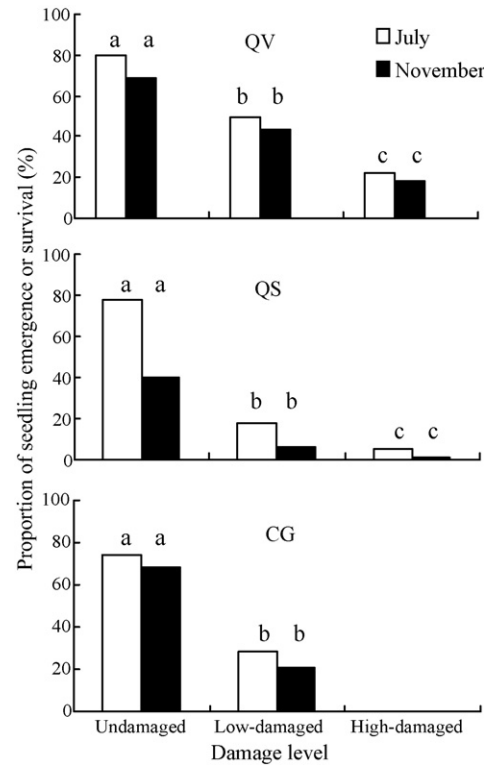

Fig. 4. Seedling emergence (July) and survival (November) with three insect damage levels (undamaged, low-damaged and high-damaged, $n = 100$ per damage level) in three oak species, *Q. variabilis* (QV), *Q. serrata* (QS) and *C. glauca* (CG). Bars with the same letter are not significantly different ($P > 0.05$; χ2-test or Fisher's exact test for a given species).

survival of undamaged seeds as a null distribution of expected probabilities ($P > 0.6$).

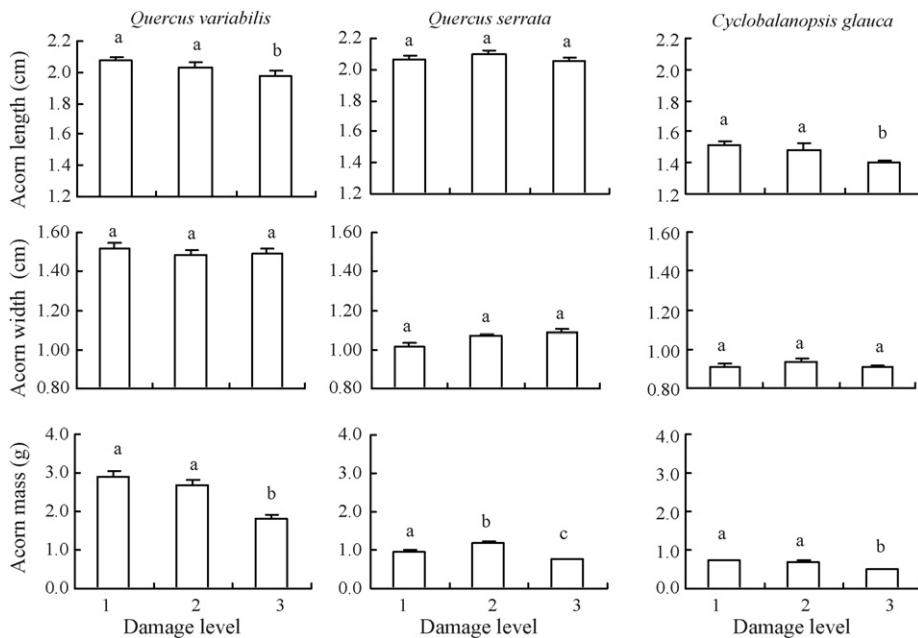For either low- or high-damaged acorns, more seedlings were significantly established from the larger acorns of *Q.*

Fig. 3. Mean (±S.E.) acorn length (cm), acorn width (cm) and fresh seed mass (g) in relation to insect damage in the three oak species, *Q. variabilis*, *Q. serrata* and *C. glauca*. Bars with the same letters are not significantly different ($P > 0.05$; LSD test). Level of insect damage: (1) undamaged; (2) low-damaged; (3) high-damaged.
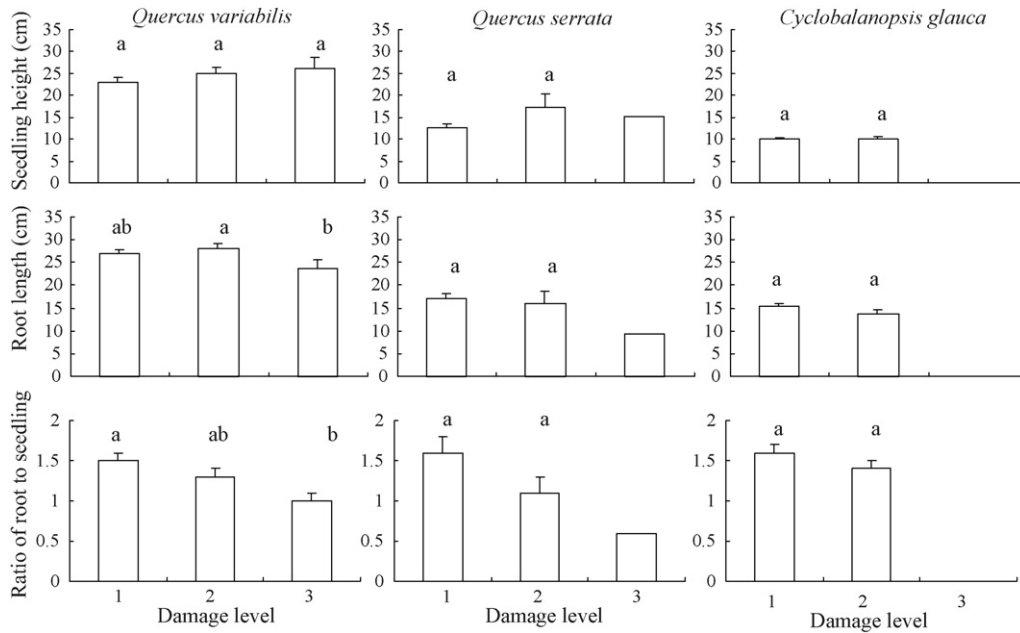
Fig. 5. Effects of insect damage on early growth of seedlings in three oak species, *Q. variabilis*, *Q. serrata* and *C. glauca*. Bars with the same letter are not significantly different ($P > 0.05$; ANOVA with LSD test for a given species). Level of insect damage: (1) undamaged; (2) low-damaged; (3) high-damaged.

variabilis than from that of either *Q. serrata* or *C. glauca* ($P < 0.05$) (Fig. 4). Though seedling establishment decreased with increasing insect damage, many low-damaged acorns (6–43%) and some high-damaged acorns established as viable seedlings after 1 year (0–22%, Fig. 4).

Differences were relatively small in shoot height, root length and ratio of root length to shoot height among the levels of insect damage for seedling growth after one year for the three oak species ($P > 0.05$), but early growth of one-year seedlings significantly increased with increasing seed mass among the three oak species for any given damage level ($P < 0.001$) (Fig. 5). The ratio of root length to shoot height gradually decreased as insect damage increased (Fig. 5).

4. Discussion

Our results show that some insect-damaged acorns (0–43%) could germinate and establish as viable seedlings in the three co-occurring oak species despite extensive acorn injury due to insect seed predators. This indicates that these oak species could, to a degree, survive from damage by insect seed predators. Escape can occur because autumn germination in *Q. variabilis* and *Q. serrata* result in germination and seedling development before later developing larvae are mature (see also in *Q. liaotungensis*, Yu et al., 2003). Thus *Q. variabilis* and *Q. serrata* can begin to transfer the stored reserves into the seedling taproots quickly before insect or other seed predators entirely consume them (see Fox, 1982).

Second, the large seed mass allows toleration of insect infestation by rapidly mobilizing stored reserves. Insect seed predation was relatively high (ca. 30–90%) among years and stands in the study site (Xiao et al., 2001, 2004b, this study), which is similar in other oak species across the world (e.g. Oliver and Chapin, 1984; Steele et al., 1993; Crawley and Long,

1995; Fukumoto and Kajimura, 2001; Yu et al., 2001, 2003; Branco et al., 2002; Maeto and Ozaki, 2003; Leiva and Fernández-Alés, 2005). Steele et al. (1993) showed that tannin concentration was much higher for the apical half (including embryo) than the basal half (containing the cotyledon) of acorns. Thus tannins as a general resistant trait may be more responsible for embryo protection in acorns. If insect feeding does not injure the developing embryo, these partly damaged acorns, combined with large seed mass in acorns (often several grams), can successfully germinate (as also noted by others, e.g. Oliver and Chapin, 1984; Kaushal and Kalia, 1989; Weckerly et al., 1989; Andersson, 1992; Steele et al., 1993) to then establish as viable seedlings comparable to undamaged acorns (e.g. Fukumoto and Kajimura, 2000; Branco et al., 2002; Leiva and Fernández-Alés, 2005, this study). However, establishment rate varies greatly among different species and also depends on the level of insect damage. A larger seed mass would reduce the rate of loss compared to smaller similarly infested seeds. For damaged acorns, our results showed that establishment rate of *Q. variabilis* with the largest seed mass (2.93 g) was significantly higher than that of either *Q. serrata* (0.93 g) or *C. glauca* (0.72 g), and establishment rate from low-damaged acorns was also significantly higher than that from high-damaged acorns for all three oak species. The high tannin concentration (over 10%) in acorns in this study may have delayed cotyledon consumption in the larger seeded early germinating *Q. variabilis* and *Q. serrata* sufficiently to enhance their potential for escape from seed predators in highly damaged acorns, but was insufficient to provide any protection for the smaller seeded later germinating *C. glauca*. Therefore, it may be possible that seed mass and tannins act together to ameliorate effects of insect infestation, particularly in *Q. variabilis*.

Third, low-damaged acorns include seeds fed on by weevil adults, seeds where insect progeny mortalities may have

occurred following oviposition, and seeds where insect progeny development may not have been completed prior to germination (see above). The interaction of defensive mechanisms of resistance, tolerance and escape may be particularly important in this damage category in determining fitness. The low-damaged category shows *Q. variabilis* survives well, followed at a distance by *C. glauca* and *Q. serrata* (Fig. 4). The experimental design did not allow differentiation among adult feeding punctures, oviposition with immature larvae, effects of presumed tannin gradients near the embryo, and subsequent embryo mortality due to secondary mortality factors in this category. If seed mass alone were determining seedling survival, then *Q. serrata* should survive better in this category than *C. glauca*. It did not. We believe this category would reward additional study. Others have also noted successful acorn germination following insect infestation and recognized these factors (e.g. Oliver and Chapin, 1984; Branco et al., 2002).

In addition, our results also showed that insect feeding had little effect on early growth of young seedlings for the three oak species. This result is not completely consistent with other similar studies (e.g. Oliver and Chapin, 1984; Fukumoto and Kajimura, 2000; Branco et al., 2002), which showed that early growth of young seedlings was greatly reduced with increasing acorn damage. Generally, cotyledon damage would be expected to increase susceptibility of acorns and resulting seedlings to subsequent mortality factors. Thus, seedling growth is expected to decline with increasing damage to the seed (e.g. Oliver and Chapin, 1984; Fukumoto and Kajimura, 2000; Branco et al., 2002). Our results indicate that seeds that survive damage to germinate and grow until July are comparable to those from undamaged seeds (Fig. 5) and most effects of damage on seedling growth may already have been expressed as mortality during the intervening period (Fig. 4). We do note that *Q. variabilis* root growth is significantly less and that *Q. serrata* root growth appears less (insufficient numbers for statistical testing) in high-damaged seeds. The major impact of weevil infestation in this study is expressed in increased mortality and less evident in the quality of seedlings that survived to germinate from infested seeds.

"When resistance and tolerance may both evolve in response to the same selection pressure, i.e. consumer damage, their evolution is most appropriately considered jointly" (Stowe et al., 2000, p. 578). Acorn-feeding insects such as weevils and moths are largely dependent on acorns as a food source. However, tannins in acorns did not completely deter feeding, oviposition and subsequent feeding by progeny of insect seed predators, and thus we contend additional escape (e.g. autumn germination) and accommodative traits (large seed mass) evolved in response to predator damage. Our results support our hypothesis that these defensive traits (e.g. tannin, autumn germination and large seed mass) act together to ameliorate effects of insect seed predation, and the joint evolution of resistance and tolerance (as well as escape through autumn germination) in acorns may be the selective consequences driven in part by interactions with insect seed predators.

In this study, at least three acorn traits can be set as defensive traits relative to insect damage: tannin, large seed mass and germination schedule. Besides pre-dispersal seed predators, however, many seed-eating animals serve as post-dispersal seed predators (e.g. rodents), including disperser and nondisperser species. Maintaining the delicate balance between rewarding dispersers and discouraging embryo-destroying consumption from all predators would appear to affect tannin (discourages consumption but could increase caching) and autumn germination (escapes nondispersers but limits dispersal window) traits. Moreover, incremental variations of seed mass may change rodent responses, e.g. rodents prefer to harvest and then cache larger seeds but increase instant consumption of smaller seeds (e.g. Xiao et al., 2004a, but see Moles et al., 2003; Gómez, 2004), though rodent mass typically allows complete consumption of individual seeds in the size range studied here. Finally, previous studies indicate that rodents can effectively discriminate insect-damaged acorns from undamaged acorns, and scatter-hoard more undamaged acorns (e.g. Steele et al., 1996; Smallwood et al., 2001; Xiao et al., 2003, 2004a,b). Thus, lower predation by insects can cause more undamaged acorns to be removed and cached by rodents, while higher predation by insects can lead to higher instant consumption of acorns including insect larvae (Xiao et al., 2003, 2004b). Therefore, a more complex web relationship appears to exist among acorns, insects and rodents than previously elucidated. Further studies to simultaneously consider how acorns, insects and rodents interact and how selection by both insect and rodent seed predators influence the evolution of defense to plant herbivory in oak species are warranted.

Acknowledgements

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