

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

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Received 2 March 2006; received in revised form 26 June 2006; accepted 26 October 2006

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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Keywords: Seed predation by insects; Seed mass; Germination schedule; Oak species

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

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(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 pre-dispersal 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 *Castanopsis 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)	<i>Q. variabilis</i> (autumn germination)	<i>Quercus serrata</i> (autumn germination)	<i>C. glauca</i> (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.

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