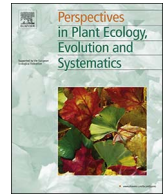


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Embryo size as a tolerance trait against seed predation: Contribution of embryo-damaged seeds to plant regeneration

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ABSTRACT

Embryo damage in seed predation is a common occurrence and has been generally considered equivalent to seed death. We hypothesize that seeds with proportionally larger embryos (radicle plus plumule) provide greater tolerance to seed damage by rodents, allowing successful germination. To test this hypothesis, we examined germination and estimated the contribution of embryo-damaged seeds to plant regeneration by comparing the dispersal patterns of intact and embryo-damaged seeds and the ecophysiological responses of their emerged seedlings in two oak species of contrasting embryo size.

Our results show that embryo size was positively correlated with seed size in both oak species, but one (*Quercus lobata*) had proportionally longer embryos than the other (*Q. agrifolia*), revealing inter-specific differences in embryo size. Probability of embryo excision behavior (partial seed damage to extirpate the embryo) was positively associated with seed size but intensity of damage was relatively constant across all sizes. The species with proportionally longer embryos showed a stronger capacity to regenerate from embryo damage because longer embryos experienced reduced probability of total (lethal) embryo damage by rodents. Seed size and thus intraspecific embryo size only increased germination success in the species with shorter embryos, allowing larger seeds to escape full embryo damage.

Seedlings from intact seeds performed better (greater plant biomass and higher chlorophyll and nitrogen index) than those from embryo-damaged seeds. However, seedlings from embryo-damaged seeds showed higher anthocyanin content, a possible response to seed damage. Intact and embryo-damaged acorns showed similar dispersal patterns by rodents (e.g. seed caching behavior and dispersal distances). Importantly, seed retrieval by rodents was significantly lower for embryo-damaged seeds, allowing greater seed survival and supporting the expectation that embryo excision behavior is a strategy to store seeds for longer periods. We conclude that tolerance to embryo damage is an important reproductive strategy that enables plant recruitment. Embryo size could play a crucial role in the evolutionary and ecological responses of seeds to animal predation.

1. Introduction

Seed predation is an important selective pressure driving the evolution of seed traits (Janzen, 1969, 1971). Coevolution between seeds and their foragers through adaptation to reciprocating selection pressures may determine the development of mutualisms from antagonisms (Thompson, 1982). Seed-animal interactions can be particularly complex given the dual role of some seed foragers (e.g. rodents) as seed dispersers and predators (McEuen and Steele, 2005). Changes in seed traits (e.g., size, shape or chemistry) or in seed foraging behavior (e.g., seed selection, seed handling or hoarding behavior) can modify the sign and strength of the interaction and, hence, its position along the

mutualism–antagonism continuum (Karst et al., 2008; Chamberlain and Holland, 2009; Perea et al., 2013). Therefore, animal-dispersed seeds are expected to evolve traits that will enhance effective seed dispersal (i.e., seedling establishment away from parents) while minimizing seed predation (McEuen and Steele, 2005). Simultaneously, seed foragers will develop behavioral strategies to maximize rewards from seeds (Vander Wall, 1990; Jansen et al., 2006; Lichti et al., 2015), setting up the potential for a coevolutionary arms race.

Embryo excision is a well-known strategy performed by several rodent species (mostly squirrels; Sciuridae), which consists of extirpating (or damaging) the embryonic parts (radicle and plumule) of the seed to prevent germination and ensure long-term seed storage

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(Wood, 1938; Fox, 1982; McEuen and Steele, 2005; Smallwood et al., 2001; Steele et al., 2001a, 2006; Xiao et al., 2009, 2010; Xiao and Zhang, 2012a, 2012b; Yi et al., 2013). This embryo damage is common in nut-bearing trees, particularly in oak (genus *Quercus*) seeds, and has been, in general, considered equivalent to seed death (Andersson and Frost, 1996; Steele et al., 2001a; Branco et al., 2002; Steele, 2008; Xiao et al., 2009; Mendoza and Dirzo, 2009; Hou et al., 2010; Perea et al., 2011a; Perea et al., 2012a; Yang and Yi, 2012). However, other studies have documented the survival and germination of embryo-damaged acorns, with significantly lower germination rates as compared to intact acorns (Wood, 1938; McEuen and Steele, 2005; Xiao et al., 2009; Cao et al., 2011; Xiao and Zhang, 2012a, 2012b; Zhang et al., 2014). Interestingly, McEuen and Steele (2005) showed that although germination and radicle production are possible in embryo-damaged acorns, no seedlings successfully produced stems and leaves and, thus, their contribution to recruitment seems unlikely. In contrast, Cao et al. (2011) showed relatively high germination rates, and even successful seedling establishment, for artificially-damaged embryo acorns, which suggests a possible tolerance mechanism against embryo damage. However, potentially adaptive tolerance traits in seeds have been poorly investigated in the context of seed predation (but see Mendoza and Dirzo, 2009). As a result, our understanding of the possible adaptive traits responsible for embryo damage tolerance is still very limited. Research aimed at filling this lacuna may shed some light on the coevolutionary dynamics of seed predation.

Critical to the understanding of the consequences of partial embryo damage are the size of the embryo and the proportional magnitude of damage. However, to our knowledge, no study has explored the quantitative and qualitative contribution of embryo-damaged seeds to recruitment throughout the whole dispersal process, from seed removal to seedling establishment. A more comprehensive approach with experimental and field data is needed to help disentangle the ecological and evolutionary implications of embryo damage for plant regeneration.

Our hypothesis is that seeds with proportionally larger embryos will provide greater tolerance to embryo damage, increasing germination and establishment rates. We also hypothesize that, regardless of embryo size, intact seeds will produce more vigorous seedlings (larger and healthier) than embryo-damaged seeds. Additionally, we aim to quantify the embryo damage behavior of four rodent species on two California oak species that differ in embryo size. We specifically examine several factors potentially involved in embryo damage behavior, including seed size, acorn species and rodent behavior. Beyond the analyses of such factors, we examine the ecological consequences thereof, by comparing the dispersal patterns of intact and embryo-damaged seeds (dispersal distance, microsite of deposition, seed caching and recovery, and final seed fate). By integrating all these aspects, from seed removal to seedling establishment, with contrasting seed predators and oak species, we attempt to provide novel insights into the ecological and evolutionary implications of embryo damage for plant reproductive success.

2. Materials and methods

2.1. Study area and species

The study was conducted at the Jasper Ridge Biological Preserve (JRBP), located in the interior foothills of the Santa Cruz Mountains, Northern coastal California, USA (37.40°N, 122.23°W). JRBP is a 480-ha research preserve where elevation ranges from 66 to 207 m a.s.l., under a coastal Mediterranean climate, with warm, dry summers and cool, wet winters. Mean annual precipitation is 605 mm and average daily temperatures range from 2 to 4 °C (winter) to 25–27 °C (summer) (Zavaleta and Kettlely, 2006). JRBP supports diverse vegetation types, including grassland, woodland, chaparral and forest. Oak-dominated systems (woodlands and savannas) are the most common vegetation

type in JRBP. Oak systems are dominated by coast live oak (*Quercus agrifolia* Née), valley oak (*Q. lobata* Née), and blue oak (*Q. douglasii* Hook. and Arn.). *Quercus agrifolia* is an evergreen red oak (sect. *Erythrobalanus*) whereas *Q. lobata* and *Q. douglasii* are closely-related, deciduous white oaks (sect. *Leucobalanus*). Compared to live oak, the latter two have lower tannin content and larger acorns (Koenig, 1991; Koenig and Faeth, 1998). *Quercus lobata* and *Q. agrifolia* are both considered slow-germinating species, germinating in November–February, approximately 2–5 months after seed drop (Matsuda and McBride, 1989).

Livestock (mostly cattle) was removed from JRBP in 1973, and black-tailed deer (*Odocoileus hemionus*) is the only ungulate present. Rodents are common in the area with a variety of species foraging on acorns (*Peromyscus* spp., *Sciurus* spp., *Neotoma* spp., *Otospermophilus* spp.). Among them, tree squirrels (*Sciurus* spp.) in North America are considered important acorn foragers and dispersers that perform embryo excision behavior (Fox, 1982; Steele et al., 2006). Three species of tree squirrels are present in Jasper Ridge (Jasper Ridge camera-trap monitoring of mammals; www.jrbp.stanford.edu): the native Western gray squirrel (*Sciurus griseus*) with few individuals in the dense forests of Jasper Ridge, and two introduced tree squirrels, the Eastern fox squirrel (*S. niger*) and the Eastern gray squirrel (*S. carolinensis*). Fox squirrels are by far the most abundant tree squirrel in the study area (oak savannas and open woodlands).

2.2. Acorn collection and characterization

Acorns of one deciduous (*Q. lobata*) and the evergreen oak (*Q. agrifolia*) were collected in the study area during September–October 2014 and 2015, from at least 14 different trees. We classified acorns into two categories: 1) Intact acorns (i.e., sound acorns with no damage), and 2) Embryo-damaged acorns, with the apical part of the acorn showing clear damage by rodents (gnawed; Fig. A1). Intact acorns were also tested for viability by a flotation method, following Perea et al. (2012b). Acorns were stored at 4 °C in plastic bags for approximately 15 days, and they were weighed (precision 0.01 g) before use.

To characterize intact acorns we randomly selected 100 sound acorns (fifty of each species), and measured length and maximum width (precision of 0.01 mm). Then, we cut the acorns longitudinally to measure the embryo length (radicle plus plumule), using a digital caliper with a 0.01 mm precision. We then obtained the embryo:seed length ratio (r), as shown in Fig. A1 (Supporting Information). To estimate average rodent damage on the embryo, we carefully selected 50 embryo-damaged acorns (25 of each species) where the apical edge of the pericarp (acorn apex) remained undamaged (see Fig. A2, Supporting Information). Then, we measured the length of the apical damage on the acorn (distance from the pericarp apex to the first undamaged point of the cotyledons; Fig. A2). These acorns were weighed and planted in the greenhouse to examine potential ability of naturally embryo-damaged acorns by rodents to produce seedlings.

2.3. Acorn germination and seedling emergence

Two plantation experiments were conducted. First, we planted 50 naturally embryo-damaged acorns by rodents (25 of each species; Fig. A2) to examine germination success. We also simulated embryo damage by rodents for another 80 intact acorns (40 of each oak species) by cutting 12% of the acorn length from the apical part, following the average rodent damage found in the naturally embryo-damaged acorns. We planted these 130 embryo-damaged acorns (50 naturally damaged and 80 simulated), together with 80 control seeds (intact acorns; 40 of each species) in individual containers 10 cm long x 10 cm diameter, filled with a substrate of 70% peat and 30% perlite. Acorns were partially covered in the substrate (1–2 cm) and kept under the same environmental conditions in Stanford University Plant Growth Facilities

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