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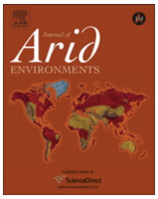

Effects of seed beetles on the performance of desert legumes depend on host species, plant stage, and beetle density

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ABSTRACT

Seeds of many arid habitat plants have a water-impermeable coat and can germinate only after being scarified. Bruchine seed beetles are important parasites of legume seeds in these environments, but their effect on germination can be unpredictable. Beetles deplete seed resources and can kill the embryo but also scarify seeds. We investigated the effects of a generalist parasite, *Stator limbatus*, on the germination and growth of two common legumes in the Sonoran desert, catclaw acacia (*Acacia greggii*) and blue paloverde (*Parkinsonia florida*). Feeding damage from a single larva greatly increased germination of paloverde but not acacia. This benefit was reduced if seeds were attacked by multiple larvae. Beetle-damaged seeds of both hosts germinated more quickly than did control seeds. Infestation by beetles reduced seedling size, though effects were greater for paloverde than for acacia. Our results demonstrate that the effect of *S. limbatus* can be highly host-specific. In addition, beetle infestation may enhance or reduce seedling recruitment, depending on the availability of other scarifying agents and the number of larvae per seed. Such contingencies make it difficult to predict the net effect of seed beetles on efforts to control invasive legume hosts or establish native hosts during aridland restoration.

1. Introduction

Seed germination is influenced by many abiotic and biotic factors, including rainfall, temperature, soil properties, leaf litter, burial depth, and vegetative cover (Bewley and Black, 1994). The timing of germination can have profound effects on seedling survival and later life-history traits in plants (Kalisz, 1986). Determining the factors that affect germination and early seedling growth is thus necessary to predict the establishment and regeneration of plants in native habitats and for choosing appropriate plants to restore degraded lands (Sy et al., 2001). Many desert legumes play an important role in restoration ecology because they can tolerate aridity, fix atmospheric nitrogen, and provide food, microhabitats, and shade for a diversity of organisms (Barnes, 2001; Camargo-Ricalde et al., 2004; Rohner and Ward, 1999).

In arid and semi-arid environments, germination and seedling growth are often limited by water availability (Bowers et al., 2004). Many arid habitat legumes produce seeds with an impermeable coat, so that seeds can germinate only after damage to the seed coat (scarification) that allows water imbibition. Seeds of many arid habitat plants have evolved in association with a variety of scarifying agents, including fire, floods, soil abrasion, and soil microorganisms (Bewley and Black, 1994). Germination and seedling recruitment may also be improved by ingestion and defecation of seeds by mammals and birds (Miller, 1994a; Rohner and Ward, 1999; Traveset et al., 2001). Finally, scarification can be mediated by insect damage, which often produces holes in the seed testa (Mucunguzi, 1995; Takakura, 2002).

Seed beetles (Coleoptera: Chrysomelidae: Bruchinae) are especially common predators and parasites of legume seeds in desert and tropical environments, and many are highly host-specific (Ramirez and Traveset, 2010). Females generally lay eggs on or inside fruits, or they glue their eggs directly to seeds that are exposed in dehiscent pods or are found on the soil surface (Southgate, 1979). Larvae typically bore into the seed and complete development within a single seed. In some cases, seed-beetle larvae may attack a majority of seeds in the local plant population, but infestation rates of some hosts can be chronically low (Miller, 1994a; Takakura, 2002).

The net effects of seed beetle infestation on the germination and recruitment of host legumes can be unpredictable (Southgate, 1979). In some cases, the insect clearly acts as a seed predator;

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larval feeding effectively kills the embryo or removes so much endosperm that the seed cannot germinate (Camargo-Ricalde et al., 2004; El Atta, 1993; Tomaz et al., 2007). Larval feeding may also create openings for pathogenic bacteria and fungi (Chang et al., 2011; Cipollini and Stiles, 1991; Mucunguzi, 1995). Even if germination occurs, prior infestation of seeds may distort the development of cotyledons or prevent the formation of true leaves (Hegazy and Eesa, 1991). Depletion of cotyledon reserves may slow plant growth and hence reduce the probability of establishment. Beetle damage may even negatively affect non-infested seeds developing in the same pods as infested ones, e.g., by mediating allocation of resource among seeds within the fruit (De Menezes et al., 2010).

Despite these detrimental effects of seed-beetle damage, some proportion of infested seeds will germinate successfully in most host populations (Halevy, 1974; Hoffman et al., 1989; Mack 1998; Miller, 1994b,c). The fate of a damaged seed often depends on its size relative to that of its parasite, as well as the number of larvae per seed (Fox et al., 2010). If beetle damage acts as a scarifying agent, it can have a large, positive effect on the frequency of germination (Arévalo et al., 2010; Mucunguzi, 1995; Nakai et al., 2011). In one study, beetle infestation was considered a prerequisite to successful germination (Takakura, 2002). Because their effects on host performance can be so variable, bruchine beetles have been implicated in aiding the spread of undesirable, invasive legumes (Arévalo et al., 2010) and, conversely, have been proposed as biological control agents for such invasive hosts (van Klinken and Flack, 2008).

This study examines the effects of seed beetle infestation and damage on two desert legumes: catclaw acacia, *Acacia greggii* Gray (Fabaceae: Mimosoideae), and blue paloverde, *Parkinsonia florida* (Bentham ex A. Gray) S. Watson (Fabaceae: Caesalpinioideae). Both species are common in the southwestern United States and northwestern Mexico. Germination of acacia and paloverde seeds is likely to be enhanced by scarification, which in Arizona may be accomplished by flash floods in gravelly soils, underground weathering, or ingestion by mammals (Longland et al., 2001; Or and Ward, 2003). Seeds of *A. greggii* and *P. florida* are also frequently attacked by a generalist seed beetle, *Stator limbatus* Horn (Fox et al., 1995, 1997; Siemens et al., 1992). This insect has a relatively wide geographic distribution and a broad host range (Stillwell et al., 2007, and references therein), but little is known about this beetle's impact on host performance. To determine the effect of *S. limbatus* on seedling recruitment in *A. greggii* and *P. florida*, we experimentally manipulated densities of *S. limbatus* in seeds and measured effects on both germination and seedling growth.

2. Materials and methods

2.1. Source populations of seeds and insects

Seeds were obtained from three sites in central Arizona: two populations of catclaw acacia and one population of blue paloverde. Seeds of the Oracle population of *A. greggii* were collected from mature pods on >20 trees along Hwy 77 and adjacent roads in Oracle, Pinal County (32.62° N 110.78° W). Seeds of the Phoenix population of *A. greggii* were similarly collected from >20 trees in the Cave Creek area north of Phoenix, Maricopa County (~32.4° N 112.0° W). Seeds of blue paloverde were also collected from >20 trees in Maricopa County (33.79° N 112.12° W). Based on a sample of >900 seeds from each population, average seed mass (±SD) was 195 ± 70 mg for Oracle acacia, 205 ± 72 mg for Phoenix acacia, and 199 ± 50 mg for blue paloverde.

Because the effects of insect damage on seed germination and plant growth may vary depending on the source population of the insect (Fox et al., 2010), we experimentally infested each host population with the same source population of *S. limbatus*. A laboratory population of *S. limbatus* was established >300 beetles that had been collected from >20 *A. greggii* trees at the Oracle site. Female *S. limbatus* oviposit directly onto host seeds inside fruits that have dehisced or have been damaged by other organisms, such as mice or other insects (including other seed beetles, Mitchell, 1977). Hatching larvae burrow into the seed beneath the oviposition site. Because larvae cannot move between seeds, we could control larval density by manipulating the initial number of eggs per seed.

2.2. Treatments

Seeds from each source population were divided among three treatments: control (no manipulation), beetle damage, or scarification. We scarified seeds by removing about 5% of the seed coat with sandpaper, which should promote imbibition of water without affecting the underlying cotyledons. This technique has been widely used for physical scarification of desert legume seeds (e.g., Patane and Gresta, 2006). To produce beetle-damaged seeds, mated pairs of beetles were individually confined with five preweighed seeds in a 30-mm Petri dish. Providing only five seeds per dish caused females to lay multiple eggs per seed. Females were allowed to lay eggs for ~72 h and discarded. Eggs were scraped from seeds to create densities ranging from one to five eggs per seed. Larvae within seeds were reared to adult emergence in a laboratory growth chamber at 30 °C. Because nearly all eggs hatch successfully (>95% of eggs hatch; Fox et al., 2007), the number of eggs on a seed is a good estimate of larval density. Seeds from the three treatments were randomly interspersed in the chamber to ensure that all seeds experienced similar environmental conditions.

After adult emergence from seeds had been completed, we removed beetle frass from seeds by tapping the seed and inserting a small brush into beetle exit holes. Seeds were then reweighed to estimate the amount of mass removed by beetle infestation. Because larval survival can be fairly low in seeds of blue paloverde (Fox et al., 1995; Fox and Mousseau, 1996), we carefully noted the total number of adults emerging from each seed. To remove biases caused by the presence of dead larvae inside seeds, we estimated beetle effects on plant performance using only those seeds from which all beetles emerged successfully as adults.

2.3. Germination and seedling growth

Control, infested, and mechanically scarified seeds were sown in pots in a University of Kentucky greenhouse furnished with supplemental lighting and maintained at 29 ± 1 °C (day) and 27 ± 1 °C (night) and a 15:9 L:D photocycle. Seeds were sown in 13 blocks over a year, with both species and treatments represented in each block. Each pot was filled with loosely packed ProMix® and received a single seed 2.5 cm below the soil surface. Pots were watered daily. Successful germination was noted when seedling tissue became visible above the soil surface. Seeds were classified as having failed to germinate if three months had elapsed with no visible tissue above the soil surface. This protocol would not detect instances in which seeds did germinate but seedlings died before emerging from the soil. However, later inspection of pots with no visible seedlings indicated that such 'cryptic' germination was rare and unlikely to influence any of the treatment effects. Fifteen days after germination, we measured the height of each seedling, carefully washed it to remove clinging soil, and dried it to constant weight at 60 °C. We used an electronic balance to measure above- and belowground dry mass of each seedling.