



Acorn – weevil interactions in a mixed-oak forest: Outcomes for larval growth and plant recruitment



Alberto Muñoz^{a,c,*}, Raúl Bonal^{b,c}, Josep Maria Espelta^c

^aDepartamento de Didáctica de las Ciencias Experimentales, Facultad de Educación, Universidad Complutense de Madrid, Madrid, Spain

^bGrupo de la Biodiversidad Genética y Cultural, Departamento de Ecología, Instituto de Recursos Cinegéticos (CSIC-UCLM-JCCM), Ciudad Real, Spain

^cCREAF, Cerdanyola del Vallès 08193, Spain

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ABSTRACT

Weevils are the most important pre-dispersal acorn predators in the Mediterranean region, where oaks often form mixed forests and different weevil species can coexist. The performance of weevil larvae depends in great extent on their feeding activities inside the infested acorns that, in turn, are known to reduce the viability of acorns. In this paper, we have analysed the interactions among the weevil community and four oak species (*Quercus pyrenaica*, *Quercus suber*, *Quercus faginea* and *Quercus ilex*) coexisting in a Mediterranean mixed-oak forest. DNA sequencing of weevil larvae revealed four different weevil species (*Curculio elephas*, *Curculio glandium*, *Curculio pellitus* and *Curculio venosus*) infesting the acorns of the four oak species. Oak species differed in acorn size, and weevil species also differed in body size. Weevil species showed some degree of specificity among the four oak species, but specificity was not related to variations in acorn size. By contrast, larval development and seedling recruitment were mostly driven by inter-specific differences in larval and acorn size. Larger seeded species suffered less seed damages by weevils (i.e. embryo predation and cotyledon consumption), thus reducing the impacts of acorn infestation in seedling emergence and seedling size. Larval development for the largest weevil species *C. elephas* was constrained by cotyledon depletion in all acorn species. Yet, this pattern was not observed for other weevil species. Larval size of the same weevil species also varied among different oak species after controlling for the amount of cotyledon eaten by larvae, thus, variation of other acorn traits among acorn species (e.g. chemical composition) may also have consequences for the performance of weevil larvae. It is likely that other variables operating at population level, such as temporal and spatial changes in acorn production or phenological variations of weevils and oaks, are also implicated in the complex functioning of these outstanding mixed-oak forests where natural regeneration seems to be threatened.

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1. Introduction

Pre-dispersal seed predation by insects is a major source of seed crop losses in many plant species and constitutes an important selective pressure on life-history traits of plants (Crawley and Long, 1995; Whitney and Stanton, 2004; Carlson and Holsinger, 2010). Seed weevils are prominent pre-dispersal predators that are usually specialised in exploiting the seeds of one or few plant species closely related (Desouhant et al., 2000; Hughes and Vogler, 2004; Espelta et al., 2009a; Hosaka et al., 2009; Bonal et al., 2010a; Ramírez and Traveset, 2010). For example, in temperate oak forests

* Corresponding author at: Departamento de Didáctica de las Ciencias Experimentales, Facultad de Educación, Universidad Complutense de Madrid, C/ Rector Royo Villanova s/n Ciudad Universitaria, E-28040 Madrid, Spain. Tel.: +34 91 3946245.

E-mail address: alberto.munoz.munoz@edu.ucm.es (A. Muñoz).

(*Quercus* spp.) weevils (*Curculio* spp.) may infest a significant proportion of the acorn crop (Leiva and Fernandez-Ales, 2005; Bonal et al., 2007; Espelta et al., 2009a). This reduces the oak reproductive output because weevil larvae feed on the acorn cotyledons, thus diminishing the amount of reserves available for early development of seedlings (Bonal et al., 2007; Bonal and Muñoz, 2008, 2009). In addition, larvae may depredate the seed embryo, thus impeding seed germination (Branco et al., 2002; Bonal et al., 2007; Lombardo and McCarthy, 2009).

Acorn weevil larvae are trophic specialists that have to complete their development within a single acorn, so that acorn size may constrain the final larval size, which is a key life-history trait in most insects. Particularly, larval size in *Curculio* weevils is an accurate individual fitness proxy, strongly related with larval survival, adult size and future potential fecundity (Desouhant et al., 2000; Bonal et al., 2011). In some occasions several larvae have to share the same acorn, thus competing for a limited amount

or seed resources (Bonal and Muñoz, 2008, 2009). The dependence of larval size on acorn size allows certain evolutionary mechanisms in oaks to reduce insect fitness and infestation rates. For instance, weevil-infested acorns can be prematurely abscised before they are full-grown, limiting the resources available and impeding larvae to reach their potential size (Bonal and Muñoz, 2008). Oaks could thus reduce infestation by reducing acorn size, however, this can be detrimental for seedling growth since acorn size may also determine seedling size and survival (Bonal et al., 2007; Sage et al., 2011). In contrast, a larger acorn size can also increase its tolerance to predation, as embryo is more likely to survive at infested large seeds (Bonal et al., 2007; Espelta et al., 2009b). Thus, the interactions between weevils and oaks occur within complex evolutionary scenarios where contrasting selective pressures can act on both sides (Crawley and Long, 1995; Hughes and Vogler, 2004; Bonal et al., 2007).

The interactions between weevils and oaks in multi-specific scenarios, where several weevil species co-occur with several oak species, can be even more complex than in pair-wise assemblages (Lombardo and McCarthy, 2008; Fukumoto and Kajimura, 2011; Espelta et al., 2009b). That is because acorn size and acorn chemical composition differ among oak species (Herrera and Pellmyr, 2002; Ofcarcik and Burns, 2006; Pérez-Ramos et al., 2008; Espelta et al., 2009a), and both seed traits determine the source of food for weevil larvae and the reserves from which seedlings develop. Moreover, different weevil species may also differ in larval size (Espelta et al., 2009a; Pélisson et al., 2011) and may have different nutritional requirements. Thus different acorn species may constrain differently the development of different weevil species, their damage on acorns, and the performance of seedlings. For example, in mixed forests those oak species that have got smaller acorns benefit from a reduced infestation, by excluding larger weevil species because small seeds do not provide a minimum food supply for their larvae (Espelta et al., 2009a).

In the Mediterranean region, weevils are the most important pre-dispersal acorn predators (Siscart et al., 1999; Espelta et al., 2009b; Bonal et al., 2010a). In that region oaks often form mixed forests with 2–4 species (Blondel and Aronson, 1999; Gómez-Aparicio et al., 2008; Pérez-Ramos et al., 2008; Espelta et al., 2009b) where several weevil species can coexist (Espelta et al., 2009a; Pélisson et al., 2011; Bonal et al., 2011). Here, we have studied the weevil community of a Mediterranean mixed forest where four oak species (*Quercus ilex*, *Quercus faginea*, *Quercus suber*, *Quercus pyrenaica*) co-occur. All oak species start growing their acorns usually in September and then they are attacked by adult weevils, which emerge in spring or late summer depending on the species (Bonal et al., 2010a). Female weevils climb to the tree canopy, mate and use their specialised snout to drill a small puncture in the acorn to introduce the ovipositor and lay usually one egg (Menu, 1993; Bonal et al., 2007, 2010a). However, subsequent ovipositions by the same or other females can occur and more than one larva can develop together within the same seed (Desouhant et al., 2000; Bonal et al., 2007, 2010b; Bonal and Muñoz, 2008). Once hatched inside the acorn, the larvae start feeding on the cotyledons until completing its development or until all the food resources of the acorn are depleted (Bonal et al., 2007; Bonal and Muñoz, 2009). Then, the larva drill an exit hole through the seed coat and bury to over winter underground. Most acorn mass is composed by two cotyledons, which constitute the food resource for weevil larvae, but also the reserves for seedling early growth. If the larval feeding tunnels reach the embryo, the acorn is killed, whereas if not the acorn may germinate and produce a viable seedling depending on the amount of cotyledon eaten by the larvae (Siscart et al., 1999; Bonal et al., 2007; Espelta et al., 2009a).

We used DNA taxonomy for weevil larvae identification to analyse the specificity and infestation patterns of weevil species for

certain oak species and the outcome of their interactions for each one. In terms of weevil performance we specifically assessed (1) whether acorn size differs between the four oak species, (2) the inter-specific differences in larval size, (3) to what extent acorn size and cotyledon depletion conditions larval growth depending on the species of oak and weevil involved, (4) whether the conversation of acorn tissue biomass to larval biomass differs between oak species. In terms of plant performance we analysed, (5) whether embryo predation rates and cotyledon consumption differ between oak species and (6) in which extent different oak species can tolerate weevil infestation, by comparing the success of seedlings produced by infested and sound acorns.

2. Material and methods

2.1. Study area and field sampling

The study was carried out in a 15-ha Mediterranean forest located in the Toledo Mountains (Ciudad Real province, Central Spain) composed by four oak species (*Quercus pyrenaica*, *Q. suber*, *Q. faginea* and *Q. ilex*). At the beginning of the seeding season 2010 (October), we collected a minimum of 150 weeviled acorns from each oak species under the canopies of, at least, 20 different trees per species randomly selected across the study area. Randomization was done by drawing a grid over a map of the study area, and then generating random pairs of coordinates. At each random point we sampled the nearest tree of each oak species. In order to assess the total number of larvae per acorn we made sure that all the collected acorns had still all larvae inside by checking the absence of emergence holes. These acorns are easily recognisable by the female oviposition scars on the seed coat (Bonal et al., 2007, 2010a).

2.2. Acorn monitoring in the laboratory

Acorns were carried to the laboratory and placed outdoors in open plastic vials covered with a mesh to avoid predation from birds or rodents. Each acorn was checked daily to register emerged larvae, which were immediately weighed with a digital balance (precision ± 0.1 mg). We used larval fresh weight because we had previously assessed that larval weight does not change in the first 24 h after leaving the acorn (for similar procedure see Bonal et al., 2007). The total mass of infested acorns was estimated by means of their linear dimensions (length and width, measured with digital callipers ± 0.01 mm) using the equivalence $M = 5.6 \times 10^{-4} LW^2 - 7.13 \times 10^{-8} \times L^2 \times W$, where M is the estimated mass of the acorn and L and W the length and the width of the acorns measured, respectively (see Bonal et al., 2007 for a detailed description of this procedure). Once all larvae had emerged, acorns were dissected to check whether the acorn embryo had been predated. Then, the portions of uneaten cotyledon (if any) were oven dried for 48 h at 80 °C and weighted to the nearest 0.01 g to accurately estimate the proportion of cotyledon eaten by the larvae in each acorn.

A very low proportion of weeviled acorns (<5%) contained also moth larvae (*Cydia* spp. Lepidoptera). Previous studies in Spain have equally reported very low overall infestation rates by moths (<10% Bonal et al., 2007). This percentage is even smaller if we consider just weeviled acorns, as *Curculio* females avoid ovipositing in seeds already occupied by moths (Debouzie et al., 1996) Those acorns infested with *Cydia* were excluded from the analyses.

2.3. Weevil species identification

While adults of several weevil species can be easily identified by morphological characteristics, this is impossible to do at the

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