

Satiation of predispersal seed predators: the importance of considering both plant and seed levels

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Abstract Plants can reduce the fitness costs of granivory by satiating seed predators. The most common satiation mechanism is the production of large crops, which ensures that a proportion of the seeds survive predation. Nevertheless, satiation of small granivores at the seed level may also exist. Larger seeds would satiate more efficiently, enhancing the probability of seed survival after having been attacked. However, a larger seed size could compromise the efficiency of satiation by means of large crops if there were a negative relationship between seed size and the number of seeds produced by an individual plant. We analyze both types of satiation in the interaction between the holm oak *Quercus ilex* and the chestnut weevil *Curculio elephas*. Both crop size and acorn size differed strongly in a sample of 32 trees. Larger crop sizes satiated weevils, and higher proportions of the seeds were not attacked as crop size increased. Larger seeds also satiated weevil larvae, as a larger acorn size increased the likelihood of embryo survival. Seedling size was strongly related to acorn size and was reduced by weevil attack, but seedlings coming from large weeviled acorns were still larger. The number and the size of the acorns produced by individual trees were negatively related. Larger proportions of the crop were infested in oaks producing less numerous crops of larger acorns. However, contrary to expectations, these trees did not satiate more effectively at the seed level either. Effective satiation by larger acorns was precluded by larger multi-infestation rates associated to smaller seed crops, in such a way that the proportion of attacked seeds that survived did not vary among trees with different acorn sizes. These results highlight the need of considering satiation by means of large crops and large seeds in studies of predispersal seed predation. Long-term monitoring on individual oaks will help to assess whether there is a trade-off between the number and the size of the acorns

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and, if it existed, how it could condition the fitness consequences of both types of satiation.

Keywords Seed size · Seed number · Predispersal seed predation · Satiation · Multi-infestation · Granivorous insects · *Curculio* · *Quercus*

Introduction

Seed consumption (granivory) causes fitness costs to plants, as it reduces their reproductive output. Plants have evolved both resistance and satiation strategies to reduce these fitness costs. Resistance mechanisms preclude consumption and include physical barriers like hard seed coats, awns or characteristic shapes (Harper et al. 1970; Janzen 1971; Kelrick et al. 1986; Díaz 1996; Hulme and Benkman 2002), or chemical defences such as toxic or deterrent compounds (Janzen 1971, Díaz 1996, Hulme and Benkman 2002). Satiation does not prevent consumption but reduces its negative consequences (Stowe et al. 2000), and may be achieved by large seed crops (Crawley 1997).

In the case of the strategies against granivory, resistance/satiation trade-offs are evident. The formation of physical barriers or the synthesis of chemical defences requires resources that cannot be employed elsewhere, so that large investments on the protection of individual seeds impair the capacity of producing large seed crops (Hulme and Benkman 2002). Satiation of granivores has been considered almost exclusively from the point of view of the mother plant. It has been estimated as the number of seeds saved depending on crop size, considering all the seeds consumed by granivores to be killed. However, many species of granivorous insects do not always consume seeds completely (see Oliver and Chapin 1984; Dalling et al. 1997; Mack 1998; Siscart et al. 1999; Branco et al. 2002; Sousa et al. 2003). Attacked seeds whose embryo is not predated and that retain enough reserves for seedling development after consumption may be viable (Oliver and Chapin 1984; Branco et al. 2002; Sousa et al. 2003). Both embryo survival and the amount of reserves left would increase with seed size (Dalling et al. 1997; Mack 1998; Sousa et al. 2003). Thus, besides the widely considered satiation at the plant level, satiation at the seed level should be taken into account.

Plants could thus reduce the negative fitness consequences of granivorous insect attacks by both satiating with large crops and large seeds. However, several studies have found negative relationships between seed size and the number of seeds produced (Eriksson and Jakobsson 1999; Parciak 2002; review in Sakai and Harada 2001). Such an inverse relationship might preclude the combination of both types of satiation by the same individual plant. Moreover, a smaller number of seeds at a plant level could increase the likelihood for a seed to suffer multi-infestation, as this risk could increase when the number of seeds available for the insects decreases (Desouhant et al. 2000). If large-seeded individuals also produce smaller seed crops, the increased effectiveness of satiation at the seed level could be impaired by an increased number of larvae per seed, as more seed tissue would be needed to satiate them.

The physical and chemical protection of oak *Quercus* spp. seeds is usually weak, whereas satiation of oak seed predators by means of large crops is widespread (Crawley 1997; Hulme and Benkman 2002). Usually, satiation in oaks has been

studied at the population level giving rise to the concept of “masting”. Masting consists in large seed crops synchronized among trees and separated by a variable number of low crop seasons (reviews in Kelly (1994) and Kelly and Sork (2002)). The proportion of seeds (acorns) consumed or attacked by granivores, especially insects, is generally much lower in mast than in lean years (Crawley and Long 1995). On the other side, it is known that acorns are not always consumed completely by insects, so that infested acorns can germinate and produce viable seedlings (Oliver and Chapin 1984; Soria et al. 1996; Siscart et al. 1999; Branco et al. 2002). Larger acorns could have higher chances of satiating developing insect larvae before they reach the embryo (Siscart et al. 1999). However, it has not been explicitly addressed whether producing large acorns could be an effective satiation strategy, and whether satiation at this level could interact with satiation by means of large crops. The aim of the present study was to analyze both types of satiation at individual trees.

We carried out a study with the holm oak *Quercus ilex* and its more prevalent predispersal seed consumer, the chestnut weevil *Curculio elephas*, a specialist insect whose larvae develops inside the acorns. We specifically tested (1) whether large seed crops could satiate weevils by comparing the proportion of acorns attacked among isolated trees differing in the number of acorns produced; (2) whether large acorns could satiate weevil larvae; (3) whether there is a negative relationship between the number and the size of the acorns produced; and (4) whether the number of acorns produced by a tree influenced the likelihood of multi-infestation and the amount of cotyledon left uneaten in the infested acorns. On this basis, we will compare the relative contribution of both satiation strategies in terms of the final reproductive output of holm oaks.

Material and methods

Study area

The study was carried out in the Cabañeros National Park (Ciudad Real province, central Spain; 39°24' N, 3°35' W). The vegetation of the Park is Mediterranean, being oaks (*Quercus suber*, *Q. ilex*, *Q. faginea* and *Q. pyrenaica*) the main tree species. Our study site was located in the flat lowlands of the Park, whose tree populations are dominated by holm oaks *Quercus ilex*. The original tall shrubland with scattered trees that occupied these lowlands (Jiménez 1998) was cleared and ploughed long before the declaration of the National Park in 1995, as it happened in most part of the Iberian Peninsula from the Middle Ages onwards (Díaz et al. 1997; Pulido et al. 2001; Pulido and Díaz 2002). The resulting landscape is savannah-like, with holm oak trees scattered within a grassland matrix. The study site had a surface of 7 ha, with a mean tree density of 13.28 trees/ha.

Study species

The holm oak is the most widespread tree species of the Iberian Peninsula, extending over more than five million hectares (Blanco et al. 1997). It is a Mediterranean evergreen oak whose crops can be very large (up to 38,000 acorns/tree), although with a strong inter-annual variability (Rupérez 1957; Herrera et al. 1998). Holm oak acorns are eaten by a large variety of animals, from insects to ungulates

(Díaz et al. 1993, 1995; Díaz and Martín 1998; Leiva and Fernández-Alés 2003, 2005; Gómez 2004a; Pulido and Díaz 2005). Acorn size is extremely variable, with values ranging between 1 and 14 g (Rupérez 1957; Pulido and Díaz 2002, Gómez 2004b). The embryo is located at the pointed, distal end of the acorn. Most seed biomass is composed by the two large cotyledons, which constitute the reserves for seedling development. Mean acorn mass varies among populations (Rupérez 1957) and among individuals within populations (Soria et al. 1996; Leiva and Fernández-Alés 1998), whereas intraindividual variation is very low (Soria et al. 1996; Leiva and Fernández-Alés 1998).

The chestnut weevil *Curculio elephas* is a granivorous beetle specialized in exploiting chestnuts and acorns (Desouhant et al. 2000; Hughes and Vogler 2004). Like other borer insects, it is a strict predispersal consumer that attacks seeds only when still attached to the parent tree (Hughes and Vogler 2004). *Curculio elephas* is the most prevalent predispersal consumer of holm oak acorns (Rupérez 1957; Vázquez 1998). Reported crop losses due to this species are extremely variable, and can vary between 0% and 100% (Vázquez 1998; Pulido and Díaz 2005). Larvae overwinter in earth cells just below the trees and adults emerge in late summer (Rupérez 1957; Menu 1993). The mobility of adults is generally low and dispersal within the tree under which they emerge is the rule (Coutin 1960; Debouzie et al. 1996), especially if trees are isolated (Menu and Debouzie 1993). In the case of acorns, weevil females make a hole through the cupule and the seed coat using their specialized snout and oviposit inside. The egg is placed in the proximal portion of the acorn, opposite to the position occupied by the embryo. After hatching, the larva starts feeding on the cotyledons until its development, which takes place inside a single acorn, is completed. If the larval feeding tunnel reach the embryo, the seed is killed, whereas if not the seed may germinate and produce a seedling (Soria et al. 1996; Siscart et al. 1999). *Curculio elephas* females usually lay a single egg per seed in chestnuts (Desouhant 1998). No pheromones are deposited on the seeds after laying so that subsequent ovipositions by the same or other females can occur (Desouhant 1998; Desouhant et al. 2000). In these cases, more than one larva develop together within the same seed (multi-infestation).

Sampling methods

We selected at random 32 holm oaks from the 93 present in the study site. The acorn crop of each tree was estimated by mean of seed traps, which consisted of plastic buckets with an opening of 0.12 m² and 0.5 m in depth. Traps were randomly located (following Skalski 1987) under tree canopies in late July 2002. Traps were hanged from the lower branches to avoid predation from large ungulates. No attempt was made to exclude rodents or birds by means of wire mesh, as mesh could have prevented large acorns to fall into the traps. Lack of acorn removal from traps was assessed by placing 200 marked acorns within 100 traps at the beginning of the study (Pulido and Díaz 2005). No acorn was removed by the end of the study. The number of traps per tree was proportional to its surface to cover a similar proportion of the canopy (1.5–2%; see Pulido and Díaz 2005). Canopy surfaces were calculated from the average of three random measures of their diameter, considering canopies as roughly circular (Pulido and Díaz 2005). Traps were checked and their contents taken to the laboratory every 10 days until late December 2002, when seed rain ceased. Propagules were classified following Pulido and Díaz (2005) as non-fertilized

flowers, early-aborted acorns and grown ones, either infested by insects or sound. All grown acorns were finally dissected to confirm their correct classification.

We used the weeviled acorns collected in the seed traps to estimate the effects of weevils on the viability of the attacked acorns. These acorns were divided in two groups, those from which the larvae had already exited and those in which larvae were still inside. Weeviled acorns with exit holes were dissected to check whether the embryo had been predated. The portions of cotyledon uneaten, if any, were oven dried for 48 h at 80°C and then weighted to the nearest 0.01 g. In those acorns from which no larvae had exited yet these measures were also taken, but only after all the larvae had left. In addition, they were used to assess the number of larvae per acorn. These acorns were frequent (62.94%; $n = 1,466$ weeviled acorns) and could be recognized by the small puncture perforated by the female to oviposit, which is easily noticeable. In fact, (83.6%; $n = 1,011$) of acorns classified as infested finally were, and no larvae emerged from those acorns that had been classified as not weeviled ($n = 1,960$). Weeviled acorns were placed individually in plastic vials opened above, which were kept outdoors and covered with a 0.5–1 mm plastic mesh to avoid predation from birds or rodents. Legless larvae could not climb or escape from vials and acorns were checked daily for larval exit. In January, 3 weeks after the last larvae had been registered, all acorns were opened to look for dead larvae and recalculate numbers if necessary. This way of calculating the number of larvae per acorn is precise, as no eggs are laid once seeds have been dropped and no cannibalism occurs between the larvae.

Weevil species identification was done following two procedures. First, both during the study year (2002) and the previous one, larvae from the study trees were placed in plastic bottles filled with sand. Larvae readily excavated a tunnel and pupate underground. We checked the bottles during the following 3 years to identify to species the emerged adults. All individuals from the 2001 and 2002 cohorts (79 and 278, respectively) were *Curculio elephas*. In addition, during 2 years after the study we sampled adults at the experimental oaks both by emergence traps and by branch shaking. All the adults captured (136) were *C. elephas* as well. Finally, our results are in accordance with extensive samplings carried out all over the National Park, where only *C. elephas* was found in the lowland holm oak savannahs (Fernández-Carrillo 1995).

Germination of weeviled acorns and seedling performance were studied in an outdoor common garden experiment. We took at random 150 acorns from which weevil larvae had already emerged and 150 sound acorns from six of the study trees. Trees were selected to differ as widely as possible in their mean acorn size. In addition, each selected tree had to provide enough weeviled and sound acorns at the same time. The number of experimental acorns was slightly unbalanced among trees and acorn types due to acorn availability. They were planted in 12 rows separated 15 cm, each row being randomly assigned to either sound or weeviled acorns. In each row we buried 25 acorns at a depth of 2 cm with a separation of 10 cm. Prior to planting in January 2003, all acorns were measured (length and maximum width) to the nearest 0.01 mm with a digital caliper. Sound acorns were weighted fresh to the nearest 0.01 g, whereas the fresh mass of weeviled acorns was estimated from their linear measurements (see below). The experiment lasted 1 year, after which we checked whether acorns had germinated and emerged, and we harvested all the seedlings, including the stems and the first 10 cm of the root system. The remains of the cotyledons were discarded, and seedlings were carefully cleaned from sand and

dust, oven dried at 80°C for 48 h and then weighted to the nearest 0.01 g. From the seedlings of the common garden experiment we could not recover the whole root system but the first 10 cm. In order to estimate total root biomass from the biomass of the first 10 cm we planted 100 acorns in plastic tubes 1 m long which allowed the proper recovery of the whole root system. Root dry mass was strongly related to the mass of the first 10 cm (root mass (g) = -0.019 (0.03 SE) + 2.25 (0.12 SE) (mass of the first 10 cm of root (g)); $R^2 = 80\%$; $P \ll 0.0001$; $n = 77$).

Data analysis

Satiation at the tree level was analysed by regressing the total number of grown acorns produced by each tree and weevil infestation rates. These rates were calculated as the proportion of grown acorns that were infested (Pulido and Díaz 2005). The total number of acorns produced and infested per tree was computed from the average number of acorns of each type collected per trap, multiplied by the ratio between the surface of the canopy and the surface sampled by each trap. In order to assess the repeatability of the measure on the total number of acorns per tree we performed a one-way ANOVA with tree as the classification factor and traps as sampling units. This analysis showed that estimates of seed production were highly repeatable within trees ($F_{32, 158} = 5.42$; $P < 0.0001$), as variance among traps within trees was significantly lower than variance among trees.

A logistic regression was used to analyze whether embryo predation depended on acorn size and on the number of growing larvae. Fresh weight of weeviled acorns obviously depends on the amount of cotyledons already eaten by larvae. Hence, we developed a method for estimating such weights prior to infestation from linear dimensions. The length and maximum width of all weeviled acorns were measured with a digital caliper to the nearest 0.01 mm. Acorns are bullet-shaped, so that its weight can be estimated by subtracting from the weight of a cylinder a variable weight depending on the shape (pointedness) of the acorn, that can be in turn derived from the ratio between its length and maximum width. In algebraic terms:

$$W_{ac} = (D_{ac}\pi L(W/2)^2) \cdot (1 - D_{ac}(L/W))$$

where W_{ac} is the weight of the acorn (g), D_{ac} is the density of the acorn tissues, and L and W are the length and maximum width (mm), respectively. The first term is the weight of a cylindrical acorn, and the second term is a correction factor for shape. The development of this model gives the function $W_{ac} = k_1LW^2 - k_2L^2W$, whose parameters k_1 and k_2 can be estimated empirically by means of iterative algorithms (Distribution Fitting Analysis, StatSoft Ltd). We used a collection of 4,000 sound acorns of different shapes and sizes measured to the nearest 0.01 mm (width and length) and weighted to the nearest 0.01 g (fresh weight). Half of these acorns selected at random were used to estimate the model parameters, and the other half to estimate the predictive power of the resulting function by comparing actual weights with weights predicted from linear dimensions.

We used log-linear models to compare the germination rates and seedling emergence rates between the sound and weeviled acorns, being seedling emergence rates the probability for a germinated acorn of producing a full grown seedling with stem and leaves. Acorn size was included in these models by classifying them into three size classes—small (≤ 3 g), medium (4–5 g) and large (≥ 6 g)—whose limits

were established to balance the number of acorns within each size class. We performed log-linear models categorizing acorns by size classes because these models are more robust than alternative generalized linear models that would include acorn size as continuous predictor.

The effects of infestation on seedling performance were tested by means of a two-way ANCOVA with seedling size (mass of root and stem) as the dependent variable, acorn size (fresh weight, either measured or estimated) as the covariate, infestation state (whether the acorn was infested or not) as a fixed factor and tree as a random factor to control for likely tree effects on seedling features (see Leiva and Fernández-Alés 1998; Díaz et al. 2003).

The relationship between acorn size and crop size at tree level was analyzed by regressing the mean number of acorns produced by unit of canopy area (mean number of grown acorns per trap, both sound and infested) against the mean acorn size of each tree. Mean acorn size was computed from a random sample of 20 acorns per tree, which were oven dried for 48 h at 80°C and then weighted to the nearest 0.01 g. Inspection of the change of mean acorn size with sample size revealed that such means did not change further when 10 or more acorns were measured and averaged, thus indicating low intra-individual variation in acorn size.

Results

The number of acorns highly varied among trees ($8,831 \pm 8,001$ acorns/tree, range: 630–37,850, $n = 32$). Infestation rates by *C. elephas* ranged from 0 % to 100% (mean 50.39; SD: 22.29; $n = 32$). A low proportion of acorns (7.65%; $n = 3,697$ grown acorns) were attacked by moth caterpillars *Cydia* spp. Trees with large crops had lower proportions of their acorns infested by *C. elephas* ($\beta = -0.43$; SE (β) = 0.16; $t_{30} = -2.59$; $P = 0.01$; see Fig. 1).

Fresh weight of acorns was strongly related to their linear dimensions ($R^2 = 0.92$; $P < 0.0001$; $n = 2,000$; multiple regression of acorn mass with length and maximum width), but the strength of these relationships was stronger after correcting from acorn shape ($W_{ac} = 5.63 \times 10^{-4} LW^2 - 7.13 \times 10^{-8} L^2W$; $R^2 = 0.97$; $P \ll 0.0001$; $n = 2,000$). The slope of this model did not differ from 1 ($t_{1998} = 0.076$; $P = 0.53$) and the Y-intercept did not differ from zero ($t_{1998} = 0.72$; $P < 0.72$).

Probability of embryo predation was negatively related to acorn size (Wald's statistic = 98.23; df = 1; $P < 0.0001$) and positively to the number of larvae inside it (Wald's statistic = 27.26; df = 1; $P < 0.0001$). Germination rates were significantly lower for weeviled acorns than for sound ones (36.73% vs. 79.33%, $n = 150$ for each group; $G^2_1 = 59.10$; $P < 0.0001$), whereas acorn size had no effect on germination rates ($G^2_2 = 4.14$; $P = 0.120$) or in the effect of infestation on germination (interaction size \times infestation: $G^2_2 = 0.41$; $P < 0.891$). A higher proportion of seedlings failed to emerge from germinated weeviled acorns as compared to sound ones (38.89% vs. 5.89%, $n = 58$ and $n = 119$, respectively; $G^2_1 = 26.69$; $P < 0.0001$). Again, acorn size had no significant direct or interactive effects on emergence rates ($G^2_2 = 2.11$; $P = 0.340$ and $G^2_2 = 0.85$; $P = 0.650$, respectively). Seedling mass was strongly correlated with acorn size ($F_{1, 75} = 12.42$; $P < 0.001$; covariate effect). Significant additive effects of infestation on seedling mass were also detected. Seedlings coming from infested acorns were smaller than seedlings coming from sound acorns of the same size ($F_{1,3} = 21.92$; $P = 0.010$ for the effect of infestation and $F_{7, 68} = 0.79$;

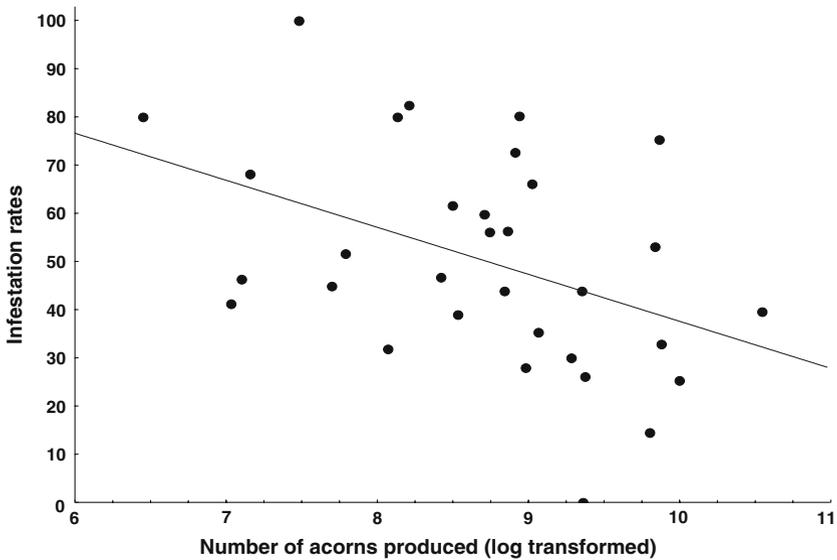


Fig. 1 Relationship between the acorn crop (total number of grown acorns produced by each holm oak tree, log-transformed) and infestation rates by weevils (proportion of grown acorns attacked)

$P = 0.590$ for the covariate \times factors interaction; see Fig. 2). These results did not vary among trees ($F_{3, 75} = 1.01$; $P = 0.370$ for the tree effect and $F_{3, 75} = 1.14$; $P = 0.330$ for the infestation \times tree interaction). Testing for tree effects supposed the removal of 44 seedlings of two trees from the analysis, as seedlings coming from infested acorns of these trees failed to germinate and/or emerge.

Mean acorn mass (fresh weight) ranged between 1.39 g and 8.02 g (mean: 4.41; SD: 1.40; $n = 32$ trees). There was a negative relationship between the number and the size of the acorns produced across trees. The mean number of acorns per trap were negatively related to mean acorn mass among trees ($\beta = -0.50$; SE (β) = 0.16; $t_{29} = -3.10$; $P < 0.01$; Fig. 3A). Trees with larger acorns suffered higher rates of multi-infestation in their seeds, being the mean number of larvae per acorn (log transformed) positively related to mean acorn mass ($\beta = 0.46$; SE (β) = 0.16; $t_{28} = 2.78$; $P < 0.01$; see Fig. 3B). This higher predation pressure at the acorn level compensated for the advantages of a large acorn size, as the percentage of acorns whose embryo was predated was unrelated to mean acorn mass between trees ($\beta = -0.08$; SE (β) = 0.18; $t_{28} = -0.39$; $P = 0.690$). Nevertheless, the absolute mean amount of cotyledon left uneaten increased significantly with mean acorn mass across trees ($\beta = 0.79$; SE (β) = 0.12; $t_{25} = 6.51$; $P < 0.0001$; see Fig. 3C).

Discussion

Our results provide evidence of satiation at the plant level. Holm oaks that produced more acorns satiated weevils more effectively, experiencing lower infestation rates than less productive trees (see also Miller and Schlarbaum 2005 for *Quercus rubra*). In addition, we also found evidences of satiation at the seed level. Weeviled holm oak acorns can produce viable seedlings, unlike seeds which are always killed by

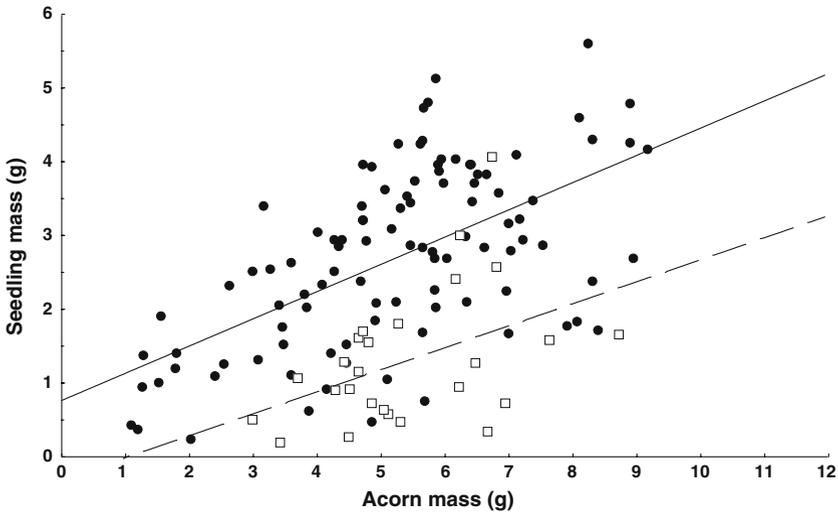


Fig. 2 Relationship between acorn mass (grams) and the mass (grams) of the 1-year old seedlings coming from them for both sound (filled circles, continuous line) and weeviled (open squares, broken line) acorns grown in a common garden experiment. Weeviled acorn mass corresponds to their weight prior to infestation and is computed from their linear dimensions (width and length)

granivores (e. g. Cipollini and Stiles 1991). This absence of an “all or none” rule confers an advantage to large acorns, as the likelihood for a larva to finish its development before reaching the embryo increased with seed size. To our knowledge, this is the first study that quantifies this relationship between infested acorn size and survival likelihood. In addition, multi-infestation reduced the chances of embryo survival: for a given acorn size, the probability of embryo survival decreased as the number of larvae increased.

Embryos were predated in many cases, so that a high proportion of weeviled acorns failed to germinate. Moreover, our results also showed that weeviled acorns that germinated had reduced chances of producing a full grown seedling as compared to sound ones. This could be due to a reduction of cotyledon tissue below a threshold needed for seedling emergence. On the other side, acorn vulnerability to pathogen infections could be increased because of the hole in the seed coat drilled by the larvae to leave the acorn (Oliver and Chapin 1984). Lack of significant interactive effects of acorn size on the reduced likelihoods of germination and emergence of weeviled acorns supported the second alternative.

Seedlings arising from weeviled acorns were smaller than those of sound ones. Seedling growth depends on the amount of reserves provided by the seed (Westoby et al. 1992, Moles and Westoby 2004) and, therefore, cotyledon consumption decreased seedling size (see also Oliver and Chapin 1984; Branco et al. 2002). However, these studies have not considered the effects of acorn size on seedling performance. We found that seedlings coming from large weeviled acorns were still larger, as they retained a larger absolute amount of cotyledon uneaten. The effect of infestation was additive, as both large and small infested acorns suffered a similar loss of potential seedling mass. This is a key point to understand the role of cotyledons as either resources for seedling growth or as means to satiate predispersal seed predators (Mack 1998; Dalling and Harms 1999). The linear relationships

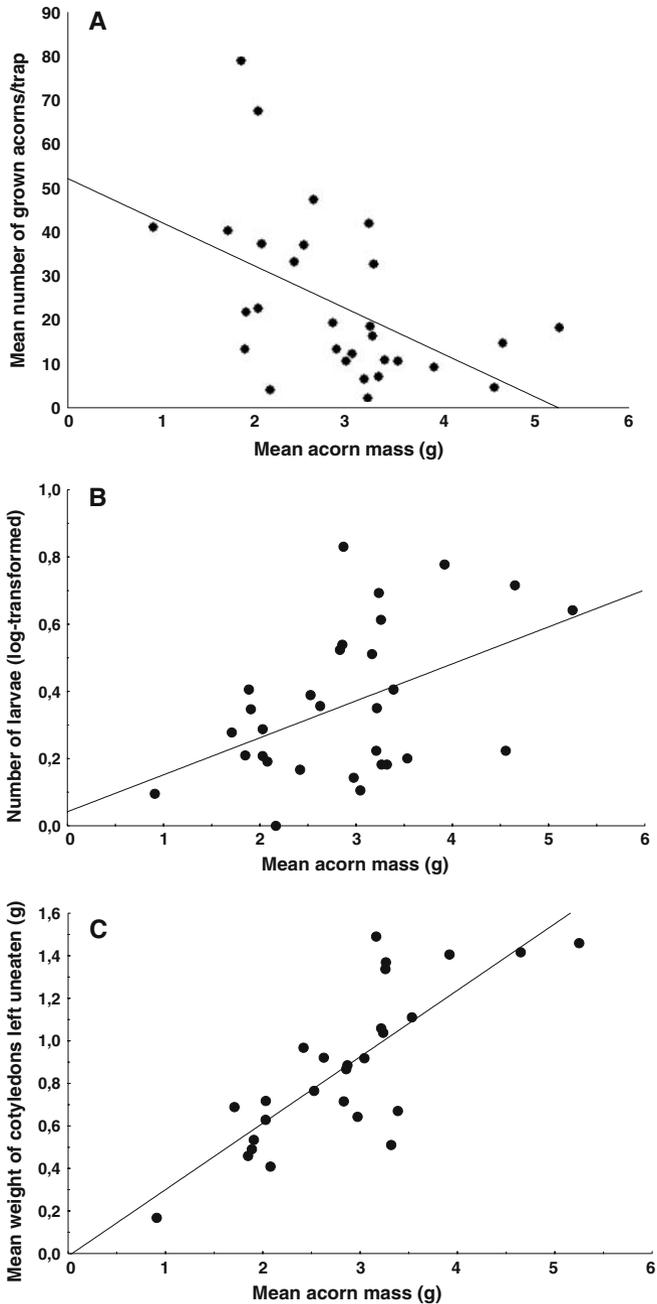


Fig. 3 (A) Relationship between the mean dry mass of the acorns of each tree (grams) and the mean number of grown acorns collected per seed trap. (B) Relationship between the mean dry mass of the acorns (grams) and the mean number of larvae per acorn (log-transformed) across trees. (C) Relationship between the mean dry mass of the acorns of each tree (grams) and the mean dry mass of cotyledons (grams) left uneaten by weevil larvae. Only acorns whose embryo was not predated (i.e. partially consumed acorns) were considered

between acorn size and seedling size and purely additive effects of weevil infestation point to the former function in holm oaks. By contrast, asymptotic relationships would have indicated that part of the cotyledons were in excess for seedling growth. This is the case of other plants (Mack 1998), in which one of the roles of the cotyledons seems to be the satiation of seed predators (Mack 1998; Dalling and Harms 1999).

Both large seed crops and large acorns were effective ways for satiating weevils. However, the negative relationship found between the number and the size of the acorns precluded the combination of both types of satiation by the same tree. This inverse relationship could suggest a trade-off arising from a resource allocation conflict (see Smith and Fretwell 1974; Sakai and Harada 2001). Nonetheless, data on acorn size and number from the same individual trees in different years are needed to demonstrate it, preferably encompassing years of high and low acorn production. Trees producing larger acorns had a larger proportion of their crop attacked by weevils, but they should have been more effective satiating at the seed level. By contrast, the mean number of larvae per acorn increased with mean acorn size, apparently due to increased risk of multi-infestation as acorn number decreased (Bonal 2005). As a consequence, embryo predation likelihood did not differ significantly between oaks. Hence, small-seeded trees produced not only larger numbers of sound acorns, but also larger total numbers of infested but potentially viable acorns than large-seeded ones. In this context, granivore satiation could be considered to imply an indirect selective pressure against large-seeded trees (see Janzen 1969).

The disadvantages of large acorns for satiating granivore insects would be increased by higher predation rates on them by ungulates and rodents (Gómez 2004b). However, producing large acorns could have, on the other side, some positive effects. They are more likely dispersed by rodents (Muñoz 2005) and birds and large seedlings have higher survival prospects (Gómez 2004b). All this configures a complex scenario in which different selective pressures act in opposite directions (see Gómez 2004b for a theoretical model on this subject). These divergent pressures might favor the large differences in acorn size observed between trees.

The results of the present study are worth to be discussed in the context of how they could be affected by the spatial distribution of the trees and the mobility of the insects. Many predispersal granivorous insects, like *C. elephas*, usually have small home ranges, even encompassing only one individual plant (Coutin 1960; Eikenbary and Raney 1973), and dispersal usually takes place within the same tree under which they have emerged (Debouzie et al. 1996). However, if dispersal abilities were higher or trees were close by, satiation at the level of individual plants could differ from that found at our savannah-like system. Higher flows of weevils between trees could make less likely multi-infestation. In this situation, trees producing large acorns could be favored by improved satiation at the seed level, unless female weevils moving between trees were able to locate them and select positively large acorns.

Summarizing, our results evidence that studies on satiation of granivorous insects should take into account not only satiation by means of large crops, but also by means of large seeds. Moreover, the present study highlights the necessity of considering both levels when satiation is studied for individual trees, as the compatibility of both satiation strategies were conditioned by inverse relationships between seed size and crop size. Finally, effective satiation by larger acorns was precluded by

larger multi-infestation rates associated to smaller seed crops. Long-term monitoring of seed crops and seed size for individual oaks will help to assess whether there is a seed size-number trade-off and, if it existed, to what extent it could condition the fitness consequences of both satiation strategies.

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