

Seed growth suppression constrains the growth of seed parasites: premature acorn abscission reduces *Curculio elephas* larval size

RAÚL BONAL and ALBERTO MUÑOZ Departamento de Ciencias Ambientales, Facultad de Ciencias del Medio Ambiente, Universidad de Castilla-La Mancha, Toledo, Spain

Abstract. 1. The abscission of seeds infested by insects is common in many plants and has been proposed as a defensive mechanism, although its negative consequences for insects have rarely been assessed.

2. We assessed the consequences of seed abscission studying the interactions between the holm oak *Quercus ilex* and the chestnut weevil *Curculio elephas*, its main pre-dispersal seed predator. Female weevils oviposit into the acorns and the larvae must complete their development inside a single acorn feeding on the cotyledons. The growth of the infested acorns is suppressed because they are prematurely abscised.

3. Female weevils oviposit along the acorn growing period; hence, the size of the infested acorns increased with date. The growth of the larvae inside the smaller, early infested, acorns was constrained because food (i.e. cotyledons) was frequently depleted. Larval size increased with the date along with the size of the infested acorns, but it declined slightly in the latest dates as a result of the higher conspecific competition provoked by the larger number of larvae per acorn.

4. The present results demonstrate that premature seed abscission by *Q. ilex* had negative consequences for *C. elephas*, as a smaller acorn size reduced food availability and constrained larval size, a key insect life history trait. At the same time, it is suggested that the growth suppression of infested acorns may condition the oviposition phenology of these insects according to their body size. These results need to be considered in further research in the context of the evolutionary significance of premature seed abscission as a defensive mechanism.

Key words. Acorn, *Curculio*, granivorous insects, larval size, phenology, plant–insect interactions, pre-dispersal seed predation, *Quercus*, seed abscission, seed size.

Introduction

Plants have developed defensive mechanisms over evolutionary time to decrease the negative effects of herbivorous and granivorous insects by reducing insect growth, fecundity and/or survival (Williams & Whitham, 1986, review in Strauss & Zangerl, 2002). Some plant defences are induced, thus appearing only when the plant is attacked (Howe & Westley, 1988; Schultz, 1988). Although induced defences have been questioned in some cases (see Schultz, 1988), many studies have found that plants are able to perceive small damages in their tissues (Kessler & Baldwin,

2002; Schultz & Appel, 2004) and to respond by means of the activation of certain genes (Orozco-Cardenas & Ryan, 2003; Kessler *et al.*, 2004).

Plants may abscise parts of their body as a short-term response to both biotic and abiotic stimuli (Addicott, 1982). In plant–insect interactions, abscission of leaves, fruits or seeds infested by insects is considered a plant defence (Boucher & Sork, 1979; Strauss & Zangerl, 2002). The plant would lose some parts of its body devoted to produce energy (leaves) or propagules (seeds); however, it could be beneficial provided that this had a negative effect on insect fitness, because it would contribute to reduce insect numbers and thus their negative effects on plants in the long term. Leaf abscission, for instance, is considered a very effective defence against insects with low mobility, such as leaf miners and galls (Faeth *et al.*, 1981;

Correspondence: Raúl Bonal, Department of Entomology, The Natural History Museum, Cromwell Road SW7 5BD, London, U.K. E-mail: r.bonal@nhm.ac.uk

Stiling *et al.*, 1991; review in Connor & Taverner, 1997). In addition, abscission would prevent investing on plant structures that are being predated. The premature abscission of infested seeds is common in many plants, such as *Fagaceae* trees (e.g. oaks, nut trees etc). Boucher and Sork (1979) found that infested nuts stopped their growth and were prematurely abscised, and on average were smaller than uninfested nuts. This result led them to propose the defensive character of nut abscission based on two main arguments. First, seed abscission and growth suppression could save resources that would be otherwise wasted in non-viable infested nuts. Second, nut abscission could have negative consequences for the insects; however, no data have yet been provided to support this hypothesis.

A study was performed with the Holm oak *Quercus ilex* and its main predispersal acorn predator, the chestnut weevil *Curculio elephas* (Gyllenhal; Coleoptera: Curculionidae), to find out whether acorn abscission had negative consequences for this insect. Infested acorns are prematurely abscised and their growth is suppressed (Oliver & Chapin, 1984; Siscart *et al.*, 1999; Yu *et al.*, 2003; Pulido & Díaz, 2005; Bonal *et al.*, 2007). Larvae must complete their development feeding inside a single acorn. Larval size is a widely acknowledged key life history trait of insects (e.g. Engelmann, 1984; Fox *et al.*, 1996 or Fox & Savalli, 1998), and in the case of *C. elephas* it has been shown to be strongly related to several key fitness variables such as larval diapause survival, adult size or female potential fecundity (Desouhant *et al.*, 2000). Hence, acorn growth suppression could limit the food available for larval development, thus constraining larval size and reducing the fitness prospects of these insects. Nonetheless, growth suppression of abscised acorns might also reduce acorn survival likelihood, as embryo survival chances are higher the larger the infested acorn (Siscart *et al.*, 1999; Bonal *et al.*, 2007). The specific objectives of the study were: (i) to monitor acorn drop phenology, (ii) to quantify the effect of early abscission on acorn size, (iii) to analyse whether acorn size may constrain larval size, and (iv) to examine the likelihood of embryo survival in abscised acorns.

Methods

Study area

The study was carried out at Cabañeros National Park (Ciudad Real province, central Spain; 39°24'N, 3°35'W). The vegetation of the Park is Mediterranean and the holm oak, *Q. ilex* is the most common tree species. The study area has a surface of 7 ha and was settled at a savannah-like grassland with scattered oaks (density 13.28 trees/ha) resulting from past clearing of shrubs (Pulido *et al.*, 2001).

Study organisms

The Holm oak *Q. ilex* is an evergreen oak widespread in the Iberian Peninsula (Blanco *et al.*, 1997). The more frequent predispersal seed predators are the larvae of Coleoptera (*Curculio*

spp.) and Lepidoptera (*Cydia* spp.) (Pulido & Díaz, 2005; Bonal *et al.*, 2007). In the Iberian populations of holm oaks, *C. elephas* (chestnut weevil) is the main pre-dispersal acorn predator. In our study area, the proportion of the acorn crop infested by this insect is very high (mean 50.39%; SD: 22.29; $n = 32$ trees; Bonal *et al.*, 2007).

Curculio elephas is a specialist predator of chestnuts and acorns (Desouhant *et al.*, 2000; Hughes & Vogler, 2004). The adults emerge after pupation from late summer to mid-autumn (Menu, 1993) and climb into the tree foliage, where females perforate a tiny hole through the seed coat with their snout and oviposit into the acorn using their oviscap (Desouhant *et al.*, 2000). Usually a single egg is laid per acorn (Desouhant *et al.*, 2000) but different females may lay into the same acorn (Desouhant *et al.*, 2000); hence, several non-sibling larvae may be found growing together (Bonal, 2005). No cannibalism takes place between the larvae, cotyledons being the only food source available until development is finished and the larvae leave the acorn to burrow underground for diapause (Menu & Debouzie, 1993). Weevil larvae start feeding at the opposite pole to the distal end where the embryo is; thus, a large acorn size increases the probabilities of embryo survival, as the larva may finish its development before reaching and predated the embryo (Siscart *et al.*, 1999; Bonal *et al.*, 2007). On the other hand, for any acorn size, the likelihood of embryo survival decreases as the number of larvae increases (Bonal *et al.*, 2007).

Sampling methods

Holm oaks (32 trees) were randomly chosen from the 93 present in our study area. Acorns were collected using seed traps that were placed under the oak canopies. Seed traps were randomly located (according to Skalski, 1987). Traps consisted of plastic buckets with an opening of 0.12 m² and a depth of 50 cm, hung from the lower branches to avoid predation by large ungulates. The opening was not covered with a wire mesh because, as a result of the large size of some holm oak acorns, the mesh may impede the entrance of some of them. It was assessed whether acorns were removed from the traps. To do so, 200 acorns were marked with a tiny incision in the proximal portion, and placed in pairs within 100 seed traps at the beginning, and none of them were removed during the course of the study. The number of traps per tree was proportional to its canopy surface, in all of them it was covered between 1.5–2% of the canopy (see Pulido & Díaz, 2005 for a similar procedure).

Larval size is positively related to acorn size, but it is negatively related to the number of larvae per acorn (Desouhant *et al.*, 2000). Thus, the study was carried out over all the acorn drop season, as both the size of abscised infested acorns and the number of larvae per acorn could change according to the date. On the one hand, *C. elephas* lay into acorns that are still growing, and on the other hand, the risk of superparasitism increases with the date, because the number of females increases progressively (Fernández *et al.*, 2002) while the number of uninfested acorns decreases (Bonal, 2005). Seed traps were sampled periodically; first infested acorns were collected on 10 September 2002 and from that date onwards traps were checked every 10 days until acorn

rain ceased in late December. In each revision, traps were emptied and their content taken to the laboratory.

Classification of infested acorns

Acorns with a weevil exit hole or suspected of containing larvae were kept apart and measured to the nearest 0.01 mm (length and width) using a digital calliper. Those from which the larvae had not exited yet were easily identified, as the oviposition puncture made by the female through the seed coat can be easily recognized. This recognition method had a 100% success, as no larvae emerged from the acorns classified as not infested ($n = 1960$). Infested acorns, from which no larvae had emerged yet, were frequently collected in the seed traps ($n = 1466$; 62.94% of all the infested acorns) and were used to calculate the number of larvae per acorn. These acorns were individually placed outdoors in plastic vials opened above and covered with a fine mesh (0.5–1 mm) to prevent predation by rodents or birds. In a pilot study, it had been verified that the larvae could not climb the walls and escape by observing that all the larvae were still in the plastic vials several days after leaving the acorn. When the legless larvae exited, all of them were counted. Acorns were checked daily to detect any new larvae, which were immediately weighted to the nearest 0.1 mg using a precision balance. Two weeks after the last larvae had exited, all infested acorns were opened to verify their correct classification and to register whether the embryo had been predated or the cotyledons had been completely eaten or not. Dead larvae were also recorded to recalculate the number of larvae per acorn if necessary; however, in accordance with other studies (Desouhant *et al.*, 2000) larval mortality inside the acorn was very low (less than 1% in the present study).

So as to analyse the effect of acorn abscission on acorn size the mass of the infested acorns was estimated. The fresh mass of the infested acorns was not used directly because it obviously depends on the amount of cotyledon consumed by the larvae. Instead, a formula was used to estimate accurately the fresh mass of the infested acorns from their length and width (see Bonal *et al.*, 2007). The formula is given by the expression $W_{ac} = 5.63 \cdot 10^{-4} \cdot L \cdot W^2 - 7.13 \cdot 10^{-8} \cdot L^2 \cdot W$, where W_{ac} is acorn mass before being infested, and L and W are acorn length and width, respectively. To know the extent to which the size of infested acorns had been reduced with respect to their potential size, the masses estimated with the formula were compared with the actual mean mass of the sound acorns from the corresponding tree. At each oak, the mean sound acorn mass from a random sample of 20 sound acorns was considered as the maximum potential size that the infested acorns could have reached. This method is accurate as acorn size is very repeatable within each tree (Leiva & Fernández-Alés, 1998; Bonal *et al.*, 2007). In fact, the variance did not change further with sample size when 10 or more sound acorns of the same tree were weighted and averaged.

Data analyses

We analysed whether the size of the infested acorns, the mean number of larvae per acorn and the mean larval weight changed

with the date. In the different analyses, we assessed the relationships between the dependent and independent variables to find the model (linear or non-linear) which best fitted the data. In the analyses, logistic regressions were used using individual acorns to assess whether the likelihood of a complete consumption of the cotyledons was related to acorn size and the number of larvae per acorn.

Results

Infested acorns were dropped prematurely. Figure 1 shows that infested acorn rain was earlier than sound acorn rain. The relationship between the size of the infested acorns and the date was logarithmic ($F_{1,1540} = 308.72$; $\beta = 0.41$; $P < 0.0001$; Fig. 2). Those dropped in the earliest dates had reached, on average, half of their potential size. The size of infested acorns increased quickly at the beginning until it stabilized on 20 October 2002 at the maximum potential size.

The mean number of larvae per acorn registered in each sampling increased linearly with date ($F_{1,7} = 18.39$; $R = 0.85$; $P < 0.01$; Fig. 3a). The logistic regression performed with data from individual acorns showed that the probability of a complete consumption of the cotyledons by the larvae was negatively related to acorn size (Wald's statistic = 151.20; d.f. = 1; $P < 0.0001$) and positively to the number of larvae inside the acorn (Wald's statistic = 6.42; d.f. = 1; $P < 0.01$). The proportion of infested acorns whose cotyledons had been completely eaten was higher the earlier the date ($F_{1,10} = 28.05$; $\beta = -0.85$; $P < 0.001$).

The temporal changes of the mean larval weight recorded in each sampling followed an inverse U-shape pattern; mean larval weight increased along the date but in the latest dates it started to decline again (Fig. 3b). The function that better explained the variance was the quadratic ($y = -0.51 + 0.003x + 6.4 \cdot 10^{-6}x^2$; $F_{2,5} = 7.20$; $R = 0.86$; $P < 0.03$). Finally, the viability of infested acorns increased along the season, as the proportion of acorns whose embryos were predated was higher the earlier the date ($F_{1,10} = 30.76$; $\beta = 0.86$; $P < 0.001$).

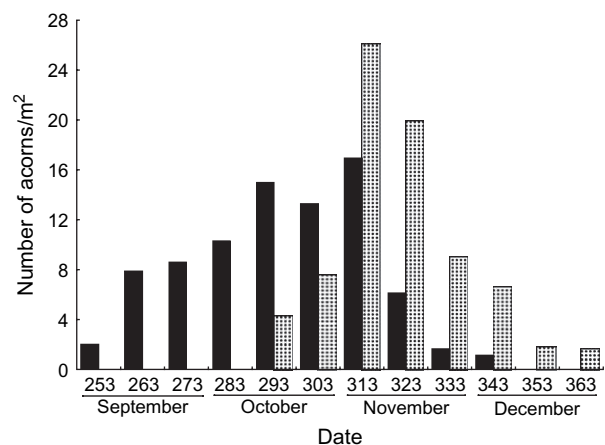


Fig. 1. Number of weeviled acorns (black bars) and sound acorns (dashed bars) collected in the seed traps along the date. Julian dates (day 1 = 1 January) are used.

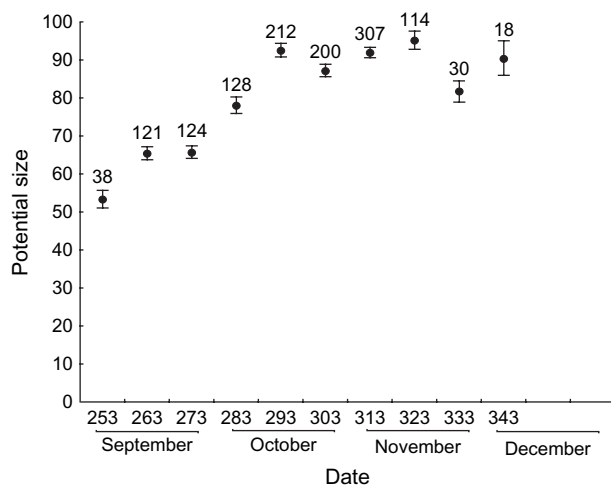


Fig. 2. Relationship between the potential size of weeviled acorns and the date. Mean values \pm SE of size are given as a percentage with respect to the maximum potential size that the weeviled acorns might have reached if their growth had not been suppressed. The size of the weeviled acorns was computed from their linear dimensions (width and length). Their potential size was considered to be the mean weight of the sound acorns of the tree from which each weeviled acorn was collected. Julian dates (day 1 = 1 January) are used. Figures over the bars indicate sample sizes.

Discussion

The present study demonstrates that holm oak acorns infested by weevils are prematurely abscised. Previous studies with other oaks had shown that infested acorns are prematurely abscised too (Yu *et al.*, 2003). In general, for Fagaceae (e.g. oaks, beeches, nut trees), the premature abscission of infested seeds had been suggested as a plant defence that might have negative consequences for insect fitness (Boucher & Sork, 1979; Yu *et al.*, 2003), although no evidence of it had been provided so far. The present data show that acorn abscission has negative consequences for insect fitness as it constrains larval size, which largely conditions *C. elephas* larval survival, adult size and female potential fecundity (Desouhant *et al.*, 2000). Moreover, larvae do not get any benefit from being prematurely dropped from the tree; in fact, larvae spend an average of 20 days inside the acorn after it has fallen on the ground, and in that period larval mortality increases to a great extent as a result of incidental predation by large post-dispersal acorn consumers such as red deer or wild boar (Bonal & Muñoz, 2007).

The negative consequences for larval size suggest that the abscission of the infested seeds could be a plant defence, as it can reduce insect fitness and thus it might contribute to control insect numbers too. However, the mechanism underlying acorn abscission in oaks remains unknown. It is not probably just a necessary physical consequence of larval feeding as, when infested acorns are abscised, the mechanical damage by the larvae is still negligible because the larvae are in the first stages of development (less than 5 mm long; R. Bonal pers. obs.). However, it has been demonstrated that plants have fine mechanisms to detect insects, and there are genes involved in the defensive response (Kessler &

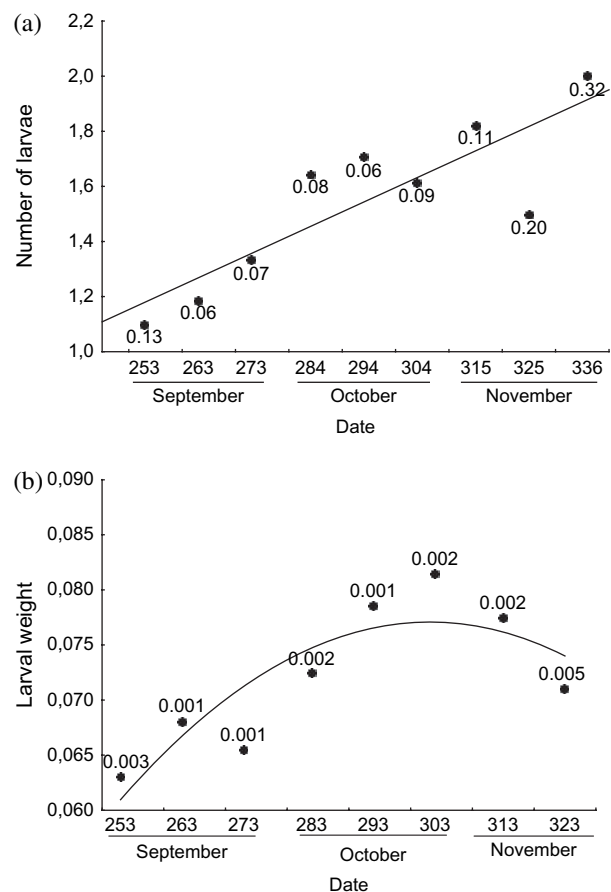


Fig. 3. (a) Relationship between the number of larvae per acorn and the date. Each point represents the mean number of larvae in each 10-day period and the figures show the Mean SE. Julian dates (day 1 = 1 January) are shown, (b) Relationship between mean larval weight and the date. Each point represents the mean larval weight (grams) in each 10-day period and the figures show the Mean SE. Julian dates (day 1 = 1 January) are shown.

Baldwin, 2002; Kessler *et al.*, 2004; Schultz & Appel, 2004). In the case of seed and fruit abscission, the abscission mechanism involves the production of chemical compounds by the plant that provoke the breakdown of the cell wall matrix at discrete sites (Roberts *et al.*, 2000), such as the stems supporting the seeds.

The fact that the seeds stop their growth once they have been infested can condition oviposition phenology. Weevil females are expected to oviposit when the acorns have reached a certain size. In fact, larvae growing inside larger, later infested acorns grew to a larger size compared with those developing inside the early infested smaller acorns, which very frequently completely consumed the cotyledons and suffered food deprivation. However, females should not oviposit too late either because in the latest dates acorns have stopped growing and, at the same time, the risk of superparasitism (i.e. different females laying inside the same acorn) is higher, because the number of adults by the trees increases (Fernández Carrillo *et al.*, 2002) and the availability of uninfested acorns decreases. Superparasitism provokes

an increase in the number of larvae per acorn thus increasing conspecific competition for food, which has a negative effect on larval size. Hence, there seems to be an optimum window of time for oviposition after the acorns reach a certain size but before competition between the larvae is too great.

Acorn growth phenology would also determine the very onset of oviposition. In early September, *C. elephas* larvae frequently suffer food shortage and, earlier than that, the acorns are probably too small to allow a minimum larval growth. This opens an interesting perspective on how body size could condition the phenological order in multispecific communities of different-sized insects of this type. For example, in multi-specific *Curculio* weevil populations, the smaller larvae of the small-sized species are capable of developing inside smaller acorns which are infested and stop growing earlier. A smaller body size allows an earlier oviposition phenology as well (R. Bonal and J. Espelta unpublished data).

Regarding the tree, premature seed abscission has also been proposed as a way of saving resources from being spent on unviable seeds. However, the present study shows that infested seeds would increase their viability if not abscised, as the larger the acorn the more likely is embryo survival. To disentangle this disparity, the physical possibility of keeping on investing in an infested acorn for a prolonged period should be explored. In addition, there would be a parent-offspring conflict of interests, because it may be better for the tree to save resources originally devoted to infested seeds with low viability (Bonal *et al.*, 2007) in the current seeding season, provided that those resources could be invested in seeds with a higher viability in future seeding seasons.

In conclusion, this study is the first to report negative effects of seed abscission on seed endoparasitic insects such as *C. elephas* larvae. Seed growth suppression provoked by premature abscission constrained larval size, a key insect life history trait. In addition, seed growth suppression may condition the timing of oviposition according to insect body size. These results open new perspectives to be considered in further research in the context of the evolutionary significance of premature seed abscission as a defensive mechanism.

Acknowledgements

Comments of M. Diaz, J. M. Aparicio and two anonymous referees improved previous versions of this manuscript. L. Arroyo, B. Nicolau and A. Nicolau helped with the field work. J. Jimenez allowed and provided facilities for field work at Cabañeros National Park. L. Muñoz helped us with the mathematical functions to calculate acorn volumes. This study was supported by the projects REN2003-07048/GLO of Ministerio de Ciencia y Tecnología, PAC-02-008 of Junta de Comunidades de Castilla-La Mancha and 096/2002 of Ministerio de Medio Ambiente. R.B. and A.M. are supported by a fellowship from the Junta de Comunidades de Castilla La Mancha.

References

Addicott, F.T. (1982) *Abscission*. PhD thesis, University of California Press, Berkeley, California.

- Blanco, E., Casado, M.A., Costa, M., Escribano, R., García, M., Génova, M. *et al.* (1997) *Los Bosques Ibéricos*. Una Interpretación Geobotánica. Planeta. Madrid, Spain.
- Bonal, R. (2005) *Fitness consequences of the interactions between Quercus ilex and its specialist predispersal seed predator, Curculio elephas*. PhD thesis, Universidad Autónoma de Madrid, Spain.
- Bonal, R. & Muñoz, A. (2007) Multitrophic effects of unguulate intraguild predation on acorn weevils. *Oecologia*, **152**, 533–540.
- Bonal, R., Muñoz, A. & Díaz, M. (2007) Satiation of predispersal seed predators: the importance of considering both plant and seed levels. *Evolutionary Ecology*, **21**, 367–380.
- Boucher, D.H. & Sork, V.L. (1979) Early drop of nuts in response to insect infestation. *Oikos*, **33**, 440–443.
- Connor, E.F. & Taverner, M.P. (1997) The evolution and adaptive significance of the leaf-mining habit. *Oikos*, **79**, 6–25.
- Desouhant, E., Debouzie, D., Ploye, H. & Menu, F. (2000) Clutch size manipulations in the chestnut weevil, *Curculio elephas*: fitness of oviposition strategies. *Oecologia*, **122**, 493–499.
- Engelmann, F. (1984) Reproduction in insects. *Ecological Entomology* (ed. by C. B. Huffaker and R. L. Rabb), pp. 113–147. Wiley, New York.
- Faeth, S.H., Connor, E.F. & Simberloff, D. (1981) Early leaf abscission: a neglected source of mortality for folivores. *American Naturalist*, **117**, 409–415.
- Fernández Carrillo, J.L., Fernández Carrillo, E. & Alonso-Zarazaga, M.A. (2002) *Las especies del género Curculio Coleoptera, Curculionidae del Parque Nacional de Cabañeros*. Comunicación al X Congreso Ibérico de Entomología. Sociedad Española de Entomología, Zamora, Spain.
- Fox, C.W., Martin, J.D., Thakar, M.S. & Mousseau, T.A. (1996) Clutch size manipulations in two seed beetles: consequences for progeny fitness. *Oecologia*, **108**, 88–94.
- Fox, C.W. & Savalli, U.M. (1998) Inheritance of environmental variation in body size: superparasitism of seeds affects progeny and grandprogeny body size via a nongenetic maternal effect. *Evolution*, **52**, 172–182.
- Howe, H.F. & Westley, L.C. (1988) *Ecological Relationships of Plants and Animals*. Oxford University Press, Oxford, U.K.
- Hughes, J. & Vogler, A.P. (2004) Ecomorphological adaptation of acorn weevils to their oviposition site. *Evolution*, **58**, 1971–1983.
- Kessler, A. & Baldwin, I.T. (2002) Plant responses to insect herbivory: the emerging molecular analysis. *Annual Review of Plant Biology*, **53**, 299–328.
- Kessler, A., Halitschke, R. & Baldwin, I.T. (2004) Silencing the jasmonate cascade: induced plant defenses and insect populations. *Science*, **305**, 665–668.
- Leiva, M.J. & Fernández-Alés, R. (1998) Variability in seedling and water status during drought within a *Quercus ilex* subsp. *ballota* population, and its relation to seedling morphology. *Forest Ecology and Management*, **111**, 147–156.
- Menu, F. (1993) Strategies of emergence in the chestnut weevil *Curculio elephas* Coleoptera: Curculionidae. *Oecologia*, **96**, 383–390.
- Menu, F. & Debouzie, D. (1993) Coin-flipping plasticity and prolonged diapause in insects: example of the chestnut weevil *Curculio elephas* Coleoptera: Curculionidae. *Oecologia*, **93**, 367–373.
- Oliver, A.D. & Chapin, J.B. (1984) *Curculio fulvus* Coleoptera, Curculionidae and its effects on acorns of live oaks, *Quercus virginiana* Miller. *Environmental Entomology*, **13**, 1507–1510.
- Orozco-Cardenas, M.L. & Ryan, C.A. (2003) Polygalacturonase beta-subunit antisense gene expression in tomato plants leads to a progressive enhanced wound response and necrosis in leaves and abscission of developing flowers. *Plant Physiology*, **133**, 693–701.
- Pulido, F.J. & Díaz, M. (2005) Regeneration of a Mediterranean oak: a whole-cycle approach. *Ecoscience*, **12**, 92–102.
- Pulido, F.J., Díaz, M. & Hidalgo, S.J. (2001) Size-structure and regeneration of holm oak *Quercus ilex* forests and dehesas: effects

- of agroforestry use on their long term sustainability. *Forest Ecology and Management*, **146**, 1–13.
- Roberts, J.A., Whitelaw, C.A., Gonzalez-Carranza Z.H. & McManus, M.T. (2000) Cell separation in plants – models, mechanisms and manipulation. *Annals of Botany*, **86**, 223–235.
- Schultz, J.C. (1988) Plant responses induced by herbivores. *Trends in Ecology and Evolution*, **3**, 45–49.
- Schultz, J.C. & Appel, H.M. (2004) Cross-kingdom cross-talk: hormones shared by plants and their insect herbivores. *Ecology*, **85**, 70–77.
- Siscart, D., Diego, V. & Lloret, F. (1999) Acorn ecology. *The Ecology of Mediterranean Evergreen Forests* (ed. by F. Rodà, C. Gracia, J. Retana and J. Bellot), pp. 75–87. Springer-Verlag, Heidelberg, Germany.
- Skalski, J.R. (1987) Selecting a random sample of points in circular field plots. *Ecology*, **68**, 749.
- Stiling, P., Simberloff, D. & Brodbeck, B.V. (1991) Variation in rates of leaf abscission between plants may affect the distribution patterns of sessile insects. *Oecologia*, **88**, 367–370.
- Strauss, S.Y. & Zangerl, A.R. (2002) Plant-insect interactions in terrestrial ecosystems. *Plant-Animal Interactions, an Evolutionary Approach* (ed. by C. M. Herrera and O. Pellmyr), pp. 77–106. Blackwell Science, Ltd. Oxford, U.K.
- Williams, A.G. & Whitham, T.G. (1986) Premature leaf abscission: an induced plant defense against all aphids. *Ecology*, **61**, 1619–1627.
- Yu, X.D., Zhou, H.Z. & Luo, T.H. (2003) Spatial and temporal variations in insect-infested acorn fall in a *Quercus liaotungensis* forest in North China. *Ecological Research*, **18**, 155–164.

Accepted 3 July 2007

First published online 27 November 2007