ECOSCIENCE

4 (1) : 48-56 (1997)

# Interactions between a high-mountain shrub, *Genista versicolor* (Fabaceae), and its seed predators[1]

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*Abstract:* For three years we studied the interaction between *Genista versicolor* (Fabaceae) and three seed-predator species, one moth (*Coleophora brunneosignata*; Coleophoridae) and two weevil species (*Exapion compactum* and *Exapion nov. sp.*; Apionidae), to assess the impact of the insects on seed production and the reciprocal effect of the plant reproductive strategies on the insect's survival. Plants experienced three predispersal mortality factors of ovules: early death of ovules, seed abortion and seed predation. Each fruit bore an average of 5.4 ovules, of which 4.0 ovules died early in their development and 0.1 aborted. Each fruit sets an average of 1.3 mature seeds. Seed predators invariably infested more than 65% of the fruits every year, killing 87% of the seeds ripened by the plants. More than 90% of the seeds predators were weevils. However, including the other two predispersal mortality factors, we found that the main loss was to ovule death (74% of the initial number of ovules), whereas seed predation destroyed 19% of the ovules. The effect of the plant on the seed-predator survival is somewhat different. Although weevils were parasitized by a wasp, the main mortality factor during the larval stage within the fruits was starvation. Of weevil larvae, 68% died before completing the life cycle because eggs were not laid on mature seed and were unable to enter a seed. As the plant capacity for filling seeds was not correlated with herbivory, the mortality of weevil larvae depended mostly on external predispersal events.

*Keywords:* predispersal seed predation, host-plant effect, *Genista versicolor*, high-mountain ecology, Spain.

*Résumé:* Nous avons étudié pendant trois ans les relations entre *Genista versicolor* (Fabaceae) et trois espèces prédatrices de graines, soit un papillon de nuit (*Coleophora brunneosignata*; Coleophoridae) et deux espèces de charançons (*Exapion compactum* et *Exapion nov. sp.*; Apionidae), pour évaluer l'impact de ces insectes sur la production de graines et l'effet réciproque des stratégies de reproduction de la plante sur la survie de l'insecte. Avant la dissémination des graines, les plantes ont subi l'action de trois facteurs agissant sur la mortalité des ovules, soit la mortalité hâtive d'ovules, ainsi que l'avortement et la prédation de graines. Chaque fruit portait en moyenne 5,4 ovules. De ce nombre, 4,0 ovules ont dégénéré aux premiers stades de leur développement et 0,1 ont avorté. Chaque fruit comportait en moyenne 1,3 graine mature. Les prédateurs de graines ont infesté plus de 65 % des fruits chaque année, faisant périr 87 % des graines parvenues à maturité. Les charançons représentaient plus de 90 % des prédateurs de graines. Toutefois, en considérant les deux autres facteurs de mortalité avant la dissémination, il appert que la perte a surtout été attribuable à la mortalité des ovules (74 % du nombre initial d'ovules), alors que la prédation de graines a contribué à la destruction des ovules dans une proportion de 19 %. L'influence de la plante sur la survie des prédateurs de graines est quelque peu différente. Bien que les charançons aient été parasités par une guêpe, le principal facteur de mortalité durant le stade larvaire à l'intérieur du fruit fut l'inanition. Au total, 68 % des larves de charançons sont mortes avant d'avoir complété leur cycle vital, car les oeufs n'avaient pas été pondus sur une graine mature et la larve n'a pu ainsi pénétrer à l'intérieur d'une graine. La capacité de la plante à former des graines matures n'étant pas corrélée à l'herbivorie, la mortalité des larves de charançons dépend donc surtout de facteurs externes précédant la dissémination.

*Mots-clés:* prédation des graines avant la dissémination, influence de la plante-hôte, *Genista versicolor*, écologie de hautes montagnes, Espagne.

## Introduction

Insects developing within fruits and living on the seeds can strongly alter a plant's reproductive success (Nilsson & Wästljung, 1987; Boe, McDaniel & Robbins, 1988; Windus & Snow, 1993). Several studies have documented that seed predators can destroy almost every seed produced by a plant, affecting its demography and limiting recruitment (Louda, 1982; Bertness, Wise & Ellison, 1987; Louda & Potvin, 1995). Also, these insects can impair the competitive abilities of their host-plants (Harper, 1977; Edwards, 1989). Lastly, seed predators can act as selective agents, affecting several plant traits such as seed masting, flowering phenology, seed size and seed abortion. (Augspurger, 1981; Brown & Venable, 1991; Marquis, 1992; Traveset, 1994).

Conversely, a fruit does not always represent a predictable environment for the insects, since they may experience a high mortality rate during the egg, larval, and pupal stages as well as in the adult phases (De Steven, 1981; Siemens & Johnson, 1992). Within-fruit mortality factors for insects feeding on seeds are numerous and diverse, including parasitism and predation (Traveset, 1990; 1991; Morris, 1991; Siemens, Ralston & Johnson, 1994), weather (Traveset, 1991), intra- and interspecific competition (Messina, 1991; Messina, Gardner & Morse, 1991; Ryoo & Chun, 1993) and plant phenotypic traits such as seed size, chemistry or pubescence (Nalepa & Grissell, 1993; Szentesi & Jermy, 1995), or a complex interaction of these (De Steven, 1981; Lamp & McCarty, 1982). Host-plant effects on insect life history and abundance have been reported for some seed-

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[1] Rec. 1996-03-26; acc. 1996-08-09.

predator species (De Steven, 1981; reviewed in Fox, Waddell & Mousseau, 1995), and these effects are important in understanding herbivore population dynamics. Plants can have significant effects on insect herbivores (Hunter & Price, 1992; Karban, 1992; Power, 1992; Fox & Tartar, 1994). For example, masting species can regulate populations of seed predator by alternating years of high and low fruit production (Crawley & Long, 1995). However, there is currently no consensus about whether seed-eating populations are resource- or predator-regulated (Karban, 1992), although, as Hunter & Price (1992) pointed out, it is more important to determine where and when either predators or resources will regulate herbivore populations.

*Genista versicolor* Boiss. (= *Genista baetica* Spach, Fabaceae), is an abundant stunted shrub endemic to the high-mountain of the Sierra Nevada in southeastern Spain (García Guardia, 1988). In this paper, we study the interaction between this woody legume and its seed predators, focusing on the effect of the insects on seed production and on the reciprocal effect of the plant reproductive pattern on insect survival. Our specific goals are: 1) to quantify seed losses due to seed predators; 2) to compare the importance of this seed mortality factor with others occurring during this phenological stage, such as seed abortion or pollination failure; 3) to assess insect mortality, determining the relative effects of parasitoids and resource limitation on insect survival probability during the larval stage.

## Methods

### SEED PREDATOR BIOLOGY

The seeds of *G. versicolor* are preyed upon by three species of insects: a microlepidopteran, *Coleophora brunneosignata* Toll (Coleophoridae; *Coleophora* hereafter) and two species of weevils, *Exapion compactum* Desbrochers and *Exapion nov. sp.* (Apionidae). Since we had to rely on a specialist in weevil taxonomy for distinguishing the two species of Apionidae, we have pooled both species in all analyses (*Exapion* hereafter). It was easy to differentiate between weevils and moths. *Coleophora* apparently develops within the seed until the third instar, leaving the pod as a larva through an exit hole made in the wall before pod ripening. In contrast, *Exapion* feeds on the seeds without penetrating them and completely develops within the pod, emerging as an adult when the two valves of the fully developed pod open to disperse the seeds.

Weevil larvae were parasitized by *Pteromalus sequester* Walker (Pteromalidae), a widely distributed wasp parasitizing the weevil larvae. This wasp develops completely within the fruit, emerging as an adult.

### STUDY SITE AND GENERAL METHODS

*G. versicolor* occupies a wide altitudinal gradient, from 1800 m above sea level, where it grows as an understory species in the subalpine forests of *Pinus sylvestris* L. or *Quercus pyrenaica* Willd., to 2600 m above sea level, above the treeline, where it accompanies other woody species such as *Juniperus communis* L., *Hormathophylla spinosa* (L.) Küpfer, and sometimes *Juniperus sabina* L. and *Berberis hispanica* L. The general study site is located in the Sierra Nevada (southeastern Spain) at 2300 m above sea level, above the treeline. We located two main populations at the same altitude, one on the north side of the mountain range (population "Umbría") and the other on the south side (population "Solana", hereafter), and separated by about 1 km in a straight line. In each of these populations, twenty plants were arbitrarily selected every year. We did not choose the same individuals each year because this plant species has an extremely low fruit set, and not all plants set fruit every year. We consistently selected all plants of the same size. Our aim was to collect 50 fruits per plant at the end of the fruiting period but before seed dispersal. However, as stated above, several plants produced less than 50 fruits and, therefore, for these we collected every fruit on the plant. In total, we gathered 1837 fruits in 1992, 940 fruits in 1993 and 1574 fruits in 1994.

In the laboratory, all fruits were opened and examined under a magnifying glass. For each fruit, we counted the number of initial ovules, the number of these that died very early in the development (early-dying ovules, hereafter), the number that aborted just before ripening (aborted seeds) and the number of mature seeds. It was easy to differentiate between the types of ovules within the fruit, since they differed morphologically. That is, the early-dying ovules (we do not know whether these were fertilized) invariably appeared as small white-brown hyaline forms hanging directly from the placenta while fertilized, but aborted seeds, appeared as green seeds almost the same size as mature seeds but wrinkled. Also the presence and identity of any seed predator was noted, and, in these cases, the number of seeds eaten or left intact after insect attack was counted. Seed predators were still present at the time of collection, completing their development in the laboratory. The contents of a single mature seed is apparently sufficient for the development of one individual of each species of seed predator studied, as we found no insect movements among mature seeds.

The intrafruit reproductive success in *G. versicolor* was estimated using several ratios. Firstly, by dividing the number of mature seeds by the number of initial ovules in each fruit, we obtained an estimate of the proportion of ovules naturally setting seeds; we have called this estimate the "seed set". Secondly, by dividing the number of intact seeds by the number of initial ovules in each fruit, we obtained an estimate of the final reproductive success of *G. versicolor* fruits; we have called this estimate "intact seed:ovule ratio". Finally, we define "attack rate" as the proportion of mature seeds killed by weevils in each infested fruit and "predation rate" as the proportion of the mature seeds per plant lost to the weevils. All fruits, even those without seed predators, were used for obtaining each parameter except "attack rate".

We thus quantified the reduction in plant reproductive potential caused by three mortality factors in the predispersal period: early loss (number of early-dying ovules), late abortion (number of aborted seeds) and seed predation (number of seeds eaten by insects). These reductions were regressed against the total loss of reproductive potential to determine the relative contribution of each stage to interplant variation in total predispersal losses, using a method analogous to key-factor analysis (Podoler & Rogers, 1975; Jordano, 1989; Traveset, 1994). The slopes of these regressions were used to assess the relative influence of each factor on variation in the magnitude of reduction of potential seed output among plants (see Jordano, 1989 for a similar analysis).

### SEED PREDATOR MORTALITY FACTORS

Egg mortality was not considered, since it was not possible to count the number of eggs laid per female in each infected fruit. Moth mortality rate was estimated during the three years of study by comparing the number of dead larvae in the pods against those that pupated outside the fruit. We were able to identify moths which were dead within the seeds (instars 1-3), since those seeds consistently showed external damage. For these reasons, our estimates of moth mortality refer to both those moths dying within the seed and those dying after leaving the seed but before emerging from the pod. Due to the low sample size, we did not differentiate between these two stages for analyses.

The larval and pupal mortality of the weevils, however, was analysed for 1992 and 1994 only, since in 1993 we found some larvae still developing within the fruits at the time of the study. We found two primary mortality factors for weevil larvae. The first one was wasp parasitism. It was easy to identify the parasitized weevil larvae by direct observation of wasp emergence from a pod and afterward by opening the pod to see the remains of weevil larvae. A second factor was mortality among larvae not living on seeds or living on non-matured seeds. We believe that this second mortality factor was starvation since larvae were not living on any resource. It was easy to differentiate between the two mortality factors. We also used a key-factor analysis for studying the contribution of each mortality factor to the among fruit differences in weevil survival.

We also analysed whether wasp parasitism was density dependent. For this, we regressed the parasitism rate, expressed as a $k$ value, against the log of weevil abundance (Lessell, 1985; Stiling, 1988), considering each plant to be a sampling unit. A positive significant relationship indicates density dependence. A negative significant correlation indicates inverse density dependence and a non-significant correlation indicates density independence between the two species (Stiling, 1988).

### STATISTICAL ANALYSIS

We have used both parametric analysis of variance (ANOVA) and contingency analysis for spatio-temporal comparisons. To avoid pseudoreplication, individual plants have been used as sampling units. We have used type III sum of squares, due to the unbalanced nature of the data. We arcsin-transformed data expressed as frequencies and log-transformed the remaining ones (Zar, 1984). When more than one variable response has been analysed by the same statistical model, we have chosen the sequential Bonferroni test for fitting the significance level, because this test increases the power to detect more than one false null hypothesis and does not require independence in the variables (Rice, 1989).

## Results

### SEED PRODUCTION IN *GENISTA VERSICOLOR* FRUITS

Fruits of *G. versicolor* were an average of 12.2 ± 0.1 mm long and 3.7 ± 0.1 mm wide ($n$ = 1837 fruits), each one bearing about 5.4 ovules (Table I). This figure varied significantly among years ($F = 16.89$, df = 2,90, $p = 0.0001$), but not between populations ($F = 0.03$, df = 1,93, $p = 0.858$). Approximately 4.0 ovules per fruit were lost early in the development and 0.1 aborted just before ripening. These two mortality factors were also similar between populations but varied again among years ($F = 7.48$, df = 2,90, $p = 0.001$ for early-dying ovules and $F = 14.45$, df = 2,90, $p = 0.0001$ for aborted seeds). Therefore, the average number of ovules setting seeds per fruit was 1.3, without among-year and between-population statistical differences ($p > 0.05$ in all cases, one-way ANOVA with sequential Bonferroni test). The seed set was around 25%, without any significant differences either among years or populations ($p > 0.2$ for all cases, one-way ANOVA; Table I).

TABLE I. Summary of the value for each reproductive parameter quantified for *Genista versicolor* fruits. Data (mean ± 1 SE [range]) are shown in a per fruit basis ($N$ = 1837 fruits in 1992, 940 fruits in 1993 and 1574 fruits in 1994), and all fruits, even those without insect attack, have been used for obtaining the parameters. "Seed set" is the proportion of ovules naturally setting seeds per fruit. "Predation rate" is the proportion of mature seeds lost to insects per fruit. "Intact seed:ovule ratio" is the proportion of ovules setting intact seeds per fruit

| | 1992 | 1993 | 1994 |
|---|---|---|---|
| INITIAL OVULES/FRUIT | | | |
| Solana | 5.79 ± 0.05 [1-12] | 5.19 ± 0.05 [2-9] | 5.41 ± 0.05 [2-9] |
| Umbría | 5.77 ± 0.04 [1-11] | 4.94 ± 0.05 [2-8] | 5.56 ± 0.06 [2-9] |
| EARLY-DYING OVULES/FRUIT | | | |
| Solana | 4.29 ± 0.06 [0-10] | 3.85 ± 0.05 [1-8] | 3.87 ± 0.06 [0-7] |
| Umbría | 4.25 ± 0.05 [0-10] | 3.69 ± 0.08 [1-7] | 4.11 ± 0.06 [1-8] |
| ABORTED OVULES/FRUIT | | | |
| Solana | 0.13 ± 0.01 [0-3] | 0.13 ± 0.02 [0-2] | 0.05 ± 0.01 [0-2] |
| Umbría | 0.19 ± 0.01 [0-3] | 0.12 ± 0.02 [0-1] | 0.03 ± 0.01 [0-1] |
| MATURE SEEDS/FRUIT | | | |
| Solana | 1.37 ± 0.03 [0-6] | 1.21 ± 0.03 [0-5] | 1.49 ± 0.05 [0-6] |
| Umbría | 1.33 ± 0.03 [0-6] | 1.14 ± 0.04 [0-4] | 1.42 ± 0.05 [0-5] |
| SEED SET (%) | | | |
| Solana | 24.7 ± 1.0 [0-100] | 24.0 ± 1.0 [0-75] | 28.2 ± 1.0 [0-100] |
| Umbría | 24.1 ± 1.0 [0-100] | 23.6 ± 1.0 [0-75] | 25.5 ± 1.0 [0-80] |
| DEPREDATED SEEDS/FRUIT | | | |
| Solana | 1.21 ± 0.03 [0-5] | 1.05 ± 0.03 [0-4] | 0.82 ± 0.04 [0-4] |
| Umbría | 0.98 ± 0.03 [0-5] | 1.06 ± 0.04 [0-4] | 0.91 ± 0.05 [0-5] |
| PREDATION RATE (%) | | | |
| Solana | 89.2 ± 1.0 [0-100] | 87.1 ± 1.6 [0-100] | 48.1 ± 1.7 [0-100] |
| Umbría | 73.9 ± 1.4 [0-100] | 93.1 ± 1.5 [0-100] | 60.1 ± 1.7 [0-100] |
| INTACT SEEDS/FRUIT | | | |
| Solana | 0.16 ± 0.02 [0-4] | 0.15 ± 0.02 [0-3] | 0.73 ± 0.03 [0-5] |
| Umbría | 0.35 ± 0.02 [0-3] | 0.08 ± 0.02 [0-2] | 0.51 ± 0.02 [0-4] |
| INTACT SEED:OVULE RATIO (%) | | | |
| Solana | 2.9 ± 0.3 [0-67] | 3.3 ± 0.4 [0-75] | 15.10 ± 0.6 [0-100] |
| Umbría | 6.5 ± 0.4 [0-100] | 1.8 ± 0.4 [0-50] | 9.29 ± 0.4 [0-80] |

### SEED PREDATOR ABUNDANCE

Seed predators infested 69.2% of fruits collected in 1992 ($n$ = 1837 fruits), 78.3% in 1993 ($n$ = 940 fruits) and 68.1% in 1994 ($n$ = 1574 fruits). Most of the insects we found living in *G. versicolor* seeds were weevils. Of the seed predators, 98.9% of the Solana population and 99.7% of the Umbría population during 1992 were *Exapion*, and we found no statistical difference between populations in these proportions ($\chi^2 = 2.55$, $p > 0.1$, $n = 1272$; Chi-square with continuity correction). Similarly, 99.5% in Solana and 99.6% in Umbría were apionids in 1993 ($\chi^2 = 4.37$, $p > 0.11$, $n = 736$). The percentage of weevils in 1994 was 91.7% in Solana and 94.0% in Umbría ($\chi^2 = 7.49$, $p > 0.05$, $n = 975$). We found both types of seed predators, weevils and moths, living together into 2.3% of the fruits collected in 1994.

The number of moths per fruit was 1.67 ± 0.24 (range = 1-3 larvae) in 1992, and 1.0 in the remaining years ($n = 61$ infested fruits). Similarly, the number of weevil larvae per fruit ranged between one and five, with an average (± 1 SE) of 1.25 ± 0.01 in 1992 (range = 1-4 insects), 1.70 ± 0.01 in 1993 (range = 1-3 insects) and 1.37 ± 0.02 in 1994 (range = 1-5 insects; see Figure 1). Weevils preferentially oviposited on larger fruits (Wald $\chi^2 = 2.62$, df = 1,1171, $p = 0.0001$, Loglikelihood Logistic regression). In addition, there were significantly more weevil larvae in fruit with more seeds than in fruit with fewer seeds during the three years of the study (1992: $\chi^2 = 941.3$, $p = 0.00001$; 1993: $\chi^2 = 519$, $p = 0.00001$; 1994: $\chi^2 = 611.2$, $p = 0.001$; Figure 2).

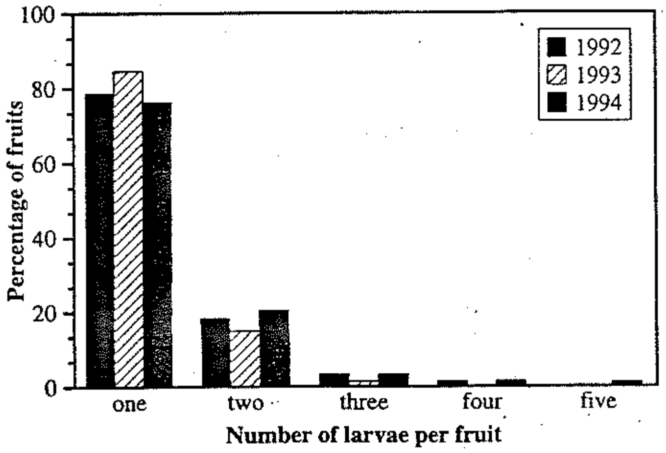

FIGURE 1. Frequency distributions of the initial number of weevil larvae per infested fruit each year. All larvae were counted, dead or alive. There was no statistical difference between the distribution frequencies ($p > 0.1$ for every pair-wise comparision, Kolmogorov-Smirnov test).

### EFFECT OF PREDISPERSAL SEED PREDATION ON *GENISTA VERSICOLOR* REPRODUCTIVE SUCCESS

Of the insect infested fruit, attack rate was always close to 100%, irrespective of whether the fruit harboured *Exapion*, *Coleophora* or both larvae (Table II). However, in fruit infested by *Exapion*, the attack rate increased when the number of larvae living in the fruit also increased, both in 1992, as well as 1994 ($r^2 = 0.85$, $t = 4.13$, $p = 0.05$ for 1992; $r^2 = 0.94$, $t = 8.17$, $p = 0.004$ for 1994; linear regression analysis; Figure 3), although in 1993 there was no positive correlation between attack rate and number of larvae per fruit ($p > 0.1$, linear regression analysis). Within fruits, apionids did not selectively eat larger seeds ($t = 0.416$, df = 38, $p = 0.68$, paired $t$-test; depredated seed length = 1.68 ± 0.03 mm $n = 93$; unpreyed seed length = 1.73 ± 0.03 mm, $n = 67$).

As a consequence of the high proportion of infested fruits and the high attack rate within each infested fruit, *G. versicolor* lost an average of about one mature seed per fruit to seed predators, with a predation rate of 87% of the total mature seeds (Table I). Again, among-year differences existed in the predation rate ($F = 28.78$, df = 2,90, $p = 0.0001$; one-way ANOVA, Table I). This predispersal seed predation caused the number of seeds dispersed to be very low (Table I). Thus, intact seed:ovule ratio ranged from 2.5% to 15.1% (Figure 4), with 79% of the fruits during

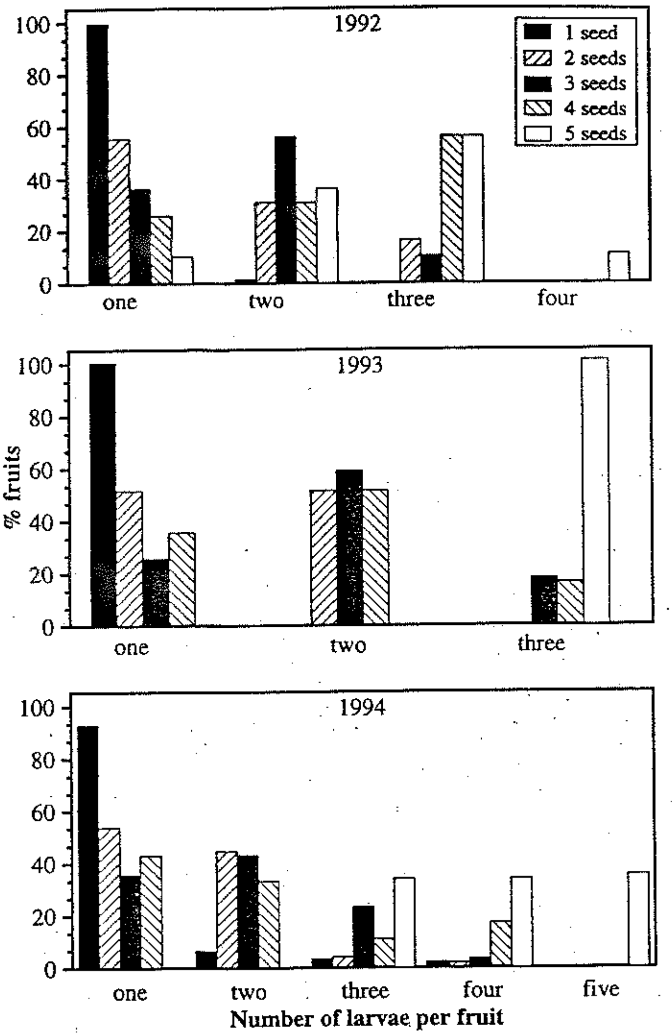

FIGURE 2. Variation of the number of *Exapion* larvae per fruit in relation to the number of mature seeds per fruit. All larvae were counted, dead or alive.

TABLE II. Attack rate, estimated as the proportion of mature seeds killed by insects in each infested fruit, for the predispersal seed predators of *Genista versicolor*, expressed as percentage of mature seeds eaten in each infested fruit. The values of Mann-Whitney (Z) test for 1992 and 1993 and Kruskal-Wallis (H) test for 1994 ($p > 0.2$ in all cases) are also shown

| | 1992 | | 1993 | | 1994 | |
|---|---|---|---|---|---|---|
| Species | *n* | mean ± SE | *n* | mean ± SE | *n* | mean ± SE |
| *Exapion* | 1260 | 94.6 ± 0.4 | 729 | 98.3 ± 0.3 | 840 | 84.5 ± 1.0 |
| *Coleophora* | 9 | 100 ± 0.0 | 6 | 100 ± 0.0 | 46 | 90.9 ± 3.0 |
| Both insects | | | | | 18 | 93.5 ± 3.0 |
| *Z/H* | -1.08 | | -0.48 | | 3.20 | |

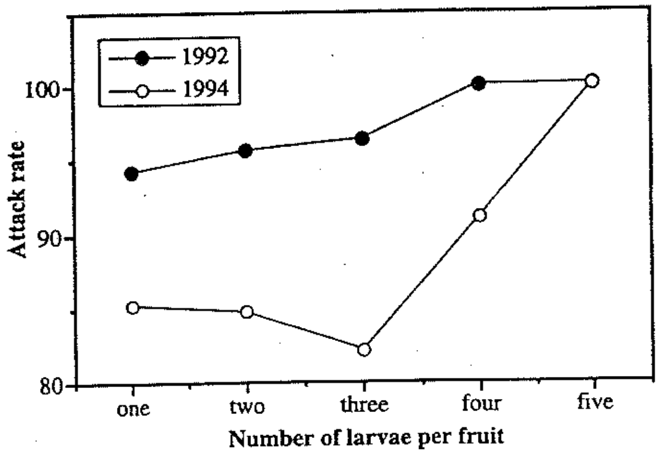

FIGURE 3. Relationship between the number of *Exapion* larvae per fruit and the attack rate, estimated as the number of seeds eaten by the insects in these infested fruits.

1992, 89% during 1993 and 55% in 1994 dispersing no seeds at the very end of this phenological phase. Similarly, this reproductive parameter varied among years ($F = 22.60$, df = 2,90, $p = 0.0001$) but not between populations ($p > 0.2$; one-way ANOVA).

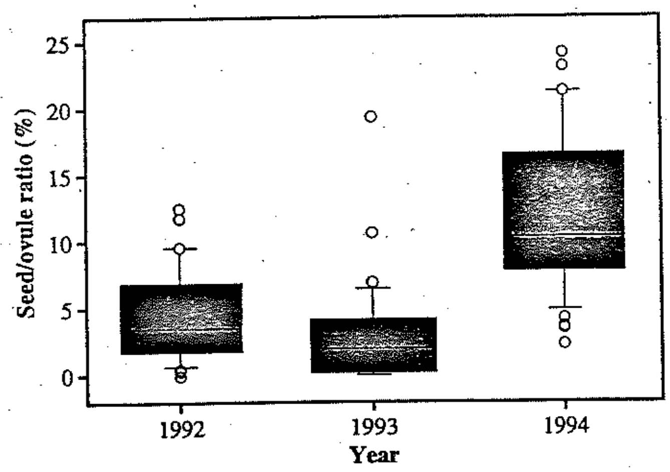

FIGURE 4. Box-plots of the proportion, expressed in percentage, of ovule dispersing seeds per *Genista versicolor* fruit (Intact seed:ovule ratio). Data have been pooled according to populations.

As a result of all the losses accumulated over the predispersal phases, *G. versicolor* lost more than 90% of its reproductive potential prior to dispersal, 18% due to predispersal seed predation (Figure 5). No mortality factor produced a regression slope larger than one in the key-factor analysis, although early-dying ovules consistently had the largest values of the regression slopes and the lowest values of CVs (Table III).

### SEED PREDATOR MORTALITY

The percentage of *Coleophora* larvae dying within the fruit was 33% in 1992 and 1993 ($n$ = 15 and 3 larvae, respectively) and 39% in 1994 ($n$ = 28 larvae). We did not observe any moth larva dying from parasitism.

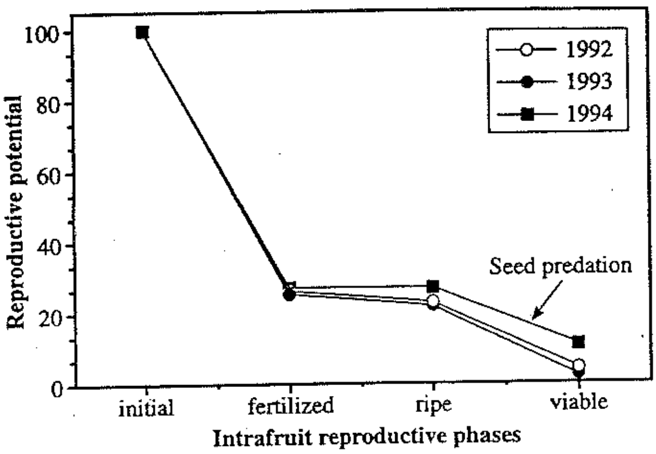

FIGURE 5. Cumulative loss of reproductive potential during the predispersal phase in *Genista versicolor*. The effect of seed predation is shown.

Weevil mortality occurred only during the larval stage, with every larva that pupated surviving to adult. Of the weevil larvae, 6.2% ($n$ = 1580 larvae) were parasitized by *Pteromalus sequester* in 1992. The parasitism rate was similar between populations ($p > 0.1$ in all cases, Chi-square). Moreover, parasitism was not density dependent in this year ($p > 0.05$, Chi-square). In addition, it appears that parasitoids did not choose fruits with more larvae for oviposition, since we did not find a significative relationship between probability of parasitism and number of weevil larvae per fruit ($p > 0.5$, Chi-square). In that year, in addition to the mortality due to parasitism, 23.7 ± 1.2% of weevil larvae ($n$ = 1467 larvae) died before completing their life cycle within the pods. This figure varied markedly between populations ($\chi^2 = 81.1$, $p = 0.0001$), with 43.5% of the larvae dying in the Umbría population, but only 19.9% dying in the Solana population. Larval mortality was not related to either fruit size or initial

TABLE III. Main factors contributing to predispersal within-fruit losses of potential seed production in *Genista versicolor*. Figures for the key-factor analysis indicate the mean proportion loss due to each mortality factor related to the initial number of ovules per fruit, the slope of the simple regression of each factor on total loss of ovules and the corresponding correlation coefficient. Data were log-transformed prior to analysis. $N = 40$ plants every year. The significance level of the correlation coefficients has been fixed according to the sequential Bonferroni test to $p < 0.05$ (Rice, 1989)

| Mortality factors | Mean proportion loss | C.V. | Key factor | |
|---|---|---|---|---|
| | | | Slope | $r$ |
| 1992 | | | | |
| Early loss | 0.7388 | 8.49 | 0.650 | $0.539^{*}$ |
| Late abortion | 0.0328 | 57.37 | 0.016 | $0.151^{ns}$ |
| Seed predation | 0.1883 | 28.59 | 0.158 | $0.05^{ns}$ |
| 1993 | | | | |
| Early loss | 0.7506 | 6.94 | 0.868 | $0.316^{ns}$ |
| Late abortion | 0.0248 | 77.61 | 0.523 | $0.093^{ns}$ |
| Seed predation | 0.2006 | 26.10 | 0.207 | $0.207^{ns}$ |
| 1994 | | | | |
| Early loss | 0.7420 | 8.61 | 0.897 | $0.507^{****}$ |
| Late abortion | 0.0050 | 158.46 | 0.370 | $0.003^{ns}$ |
| Seed predation | 0.1290 | 45.88 | 0.600 | $0.443^{****}$ |

$^{ns}$: non significant
$^{*}p < 0.05$
$^{****}p < 0.0001$

number of ovules per fruit ($p > 0.1$ in both cases). However, the probability that a weevil larva would die was significantly related to the number of larvae or number of mature seeds per fruit, without interaction between those factors (Table IV). In fact, larval mortality decreased when the number of mature seeds per fruit increased (Figure 6).

TABLE IV. Summary of the two-way analysis of variance on arcsin of % of weevil larvae mortality within individual fruit; df, degrees of freedom; SS, type III sum of square; *F*-test, *F*-ratio value; *P*, significance level. Only fruits with at least one dying weevil larva were used

| Sources | df | SS | *F*-test | *P* |
|---|---|---|---|---|
| 1992 | | | | |
| *N* larvae/fruit | 3 | 1.124 | 41.542 | 0.0001 |
| *N* seeds/fruit | 6 | 0.310 | 5.734 | 0.0001 |
| *N* larvae × *N* seeds | 4 | 0.042 | 1.166 | 0.3255 |
| Residuals | 381 | 3.436 | | |
| 1994 | | | | |
| *N* larvae/fruit | 3 | 0.432 | 7.895 | 0.0001 |
| *N* seeds/fruit | 4 | 0.762 | 10.436 | 0.0001 |
| *N* larvae × *N* seeds | 8 | 1.215 | 8.317 | 0.0001 |
| Residuals | 100 | 1.826 | | |

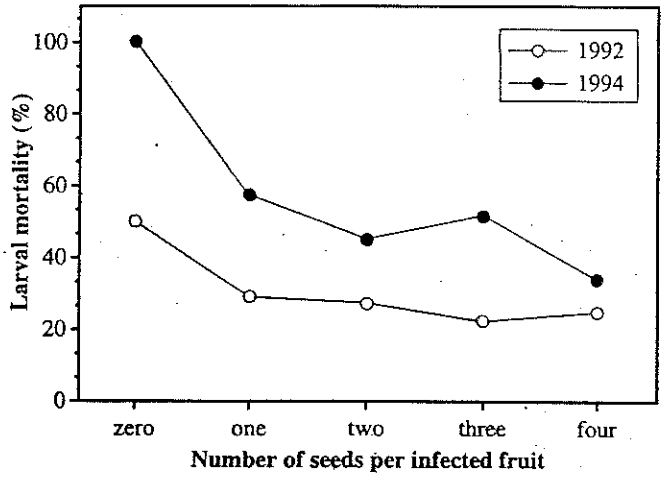

FIGURE 6. Relationship between the number of mature seed per pod and the probability of larval mortality.

The parasitism rate of weevils sharply decreased in 1994 to 0.24% ($n$ = 1238 larvae), being again similar between populations ($p > 0.1$ in all cases, Chi-square) and density independent ($p > 0.05$, Chi-square). In that year, in addition to parasitism, 67.7 ± 0.02% of weevil larvae ($n$ = 246 larvae) in the Umbría population died before completing the cycle within the fruits, whereas the remaining larvae, living always on a mature seed, survived to the pupa stage. Of the unsuccessful larvae, 48.10% died because they were laid directly on the inner side of the wall rather than on seeds and thus larvae were unable to find any mature seed within the fruit (Starvation type I), and the remaining 50.89% died from hatching on a seed dying early in the development (Starvation type II). The probability that a weevil larva would die from starvation was significantly related to the number of larvae or number of mature seeds per fruit, with a significant interaction between those factors (Table IV). As in 1992, the probability of larval mortality decreased in 1994 when the number of mature seeds per fruit increased (Figure 6). The probability of an aborted seed being attacked by weevil larvae did not depend on the number of aborted seeds per fruit ($p > 0.1$, logistic regression). On the contrary, that probability significantly increased with the number of initial ovules per fruit ($\chi^2 = 11.95$, $p = 0.0005$; logistic regression), and when the number of mature seeds still intact per fruit decreased ($\chi^2 = 9.45$, $p = 0.02$; logistic regression). Thus, weevil larvae lived on aborted seeds in 2.72% of fruits with no intact seed and in 9.3% of fruits with just one intact seed. However, we did not find larvae living on aborted seeds in fruits with two, three or four intact seeds. In 1994, we found some larvae living within fruits with no mature seed; every larva was dead.

As shown in Table V, the two starvation mortality factors (type I and II) obtained steeper slopes in the key-factor analysis, whereas wasp parasitism was not important in either quantitative magnitude or as a key factor.

TABLE V. Main factors contributing to pre-dispersal, within-fruit losses in potential larval production in *Exapion spp.* Figures for the key-factor analysis indicate the slope of the regression of each factor on total loss of larvae and the corresponding correlation coefficient. Data were log-transformed prior to analysis. $N = 5$ plants. The significance level of the correlation coefficients has been fixed according to the sequential Bonferroni test to $p < 0.05$ (Rice, 1989).

| Mortality factors | Mean proportion loss | C.V. | Key factor | |
|---|---|---|---|---|
| | | | Slope | *r* |
| 1994 | | | | |
| Starvation type I | 0.349 | 24.45 | 1.05 | 0.47 |
| Starvation type II | 0.329 | 25.57 | 0.60 | 0.78* |
| Parasitism | 0.002 | 223.61 | -0.05 | 0.01 |

*$p < 0.05$.

### BENEFIT TO THE FRUIT FROM LARVAL MORTALITY

In 1992, neither wasp parasitism ($p > 0.55$, Mann-Whitney *U*-test) nor the weevil mortality due to starvation ($p > 0.05$, Mann-Whitney *U*-test) caused fruits with any dead larvae to disperse more seeds than fruits with all larvae developing to the pupa stage. The number of seeds dispersed by the former type of fruits was 1.53 ± 0.04, whereas the number of intact seeds in the latter was 1.45 ± 0.02 ($Z = -1.97$, $p = 0.05$, Mann-Whitney *U*-test). However, in 1994 we did find a significant difference between the two types of fruits ($Z = -3.41$, $p = 0.0007$); fruits in which every larva survived dispersed only 0.24 ± 0.09 seeds whereas fruits in which some larvae died during the development dispersed 0.66 ± 0.07 seeds.

## Discussion

Seed predators seriously decreased the reproductive output of *G. versicolor*. The weevils infested around 70% of the fruits produced by this plant species during the three years of study, killing more than 90% of the mature, fully developed seeds and causing more than 50% of fruits not to disperse any seeds. When a pod was infested by seed predators, few, if any, seeds remained. These percentages are far higher than those found for other members of the Fabaceae (Green & Palmbald, 1975; Moore, 1978; Boe, McDaniel & Robbins, 1989), although some *Astragalus* species, such as *A. canadensis, A. cibarius* and *A. utahensis*, can lose 44-60% of their fruits to seed-predators (Platt, Hill & Clark, 1974; Green & Palmbald, 1975; Boe, McDaniel & Robbins, 1989). Thus, our data suggest that seed predation may act as a major determinant of reproductive success in *G. versicolor*. However, when the entire predispersal phase is analysed, the effect of seed predators dramatically decreases, owing to the existence of two other mortality factors acting during the within-fruit stage of seed production and also decreasing the reproductive success of this plant species, the early mortality of the ovules and the abortion of the developing seeds. In fact, although we found a significant relationship during 1994 between seed-predation intensity and seed production, most of the reproductive potential that *G. versicolor* consistently lost during the three years of study (up to 75% of ovules) was due to early ovule mortality. This early mortality of ovules was not due to predation by early instars (1-3) of moth larvae, since even at this time they currently produce noticeable damage on seed surface.

This early mortality may result either from nutrient or pollination limitation. Many plant species living in the high mountain, where pollinators are scarce (Arroyo, Primack & Armesto, 1982; Warren, Harper & Booth, 1988), are pollination-limited (Galen, 1985; Campbell, 1991; Berry & Calvo, 1991; Stenström & Molau, 1992). The low fruit set in *G. versicolor* at high altitudes of the Sierra Nevada, where less than 5% of the flowers set fruits (pers. observ.), is consistent with the hypothesis of pollination limitation, since plants normally drop unpollinated flowers. However, in the Mediterranean high mountain, not just pollinators but water is a limiting resource during summer. For this reason, it is problematic to identify whether limited resources or pollinators caused the early mortality of ovules in *G. versicolor*.

Another possibility is that a plant selectively aborts infested ovules to kill weevil larvae. However, we think that this hypothesis is highly unlikely, since in 1994 we found 684 early-dying ovules but only 106 weevil larvae living on them. In any case, this mortality factor had the largest mean proportion of loss and the steepest slopes in the key factor analysis and thus, the seed predators only slightly affected overall seed production. In addition, there was a temporal consistency in these results over the three years studied. Several other authors have also noted the failure of seed predators to affect the overall female fitness of the host plants when other seed mortality factors were analysed (De Steven, 1983; Moran & Hoffman, 1989; Szentesi & Jermy 1995). For example, Jordano, Fernández Haeger & Rodríguez (1990) found that although *Astragalus lusitanicus* seeds were eaten by the larva of the butterfly *Tomares ballus* (Lycaenidae), seed losses due to pollination failure and seed abortion were the main factors accounting for the low fecundity of the plant.

Insect species completing their development in only one seed normally select larger seeds (Nalepa & Grissell, 1993). Consequently, in addition to seed number, seed predators can affect other plant traits such as seed size (Cipollini & Stiles, 1991; Gómez & Zamora, 1994; Szentesi & Jermy, 1995). However, although each *Exapion* larva developed in only one *G. versicolor* seed, they did not selectively eat the bigger seeds, suggesting that neither seed size is affected by weevil behaviour.

In brief, our results suggest that, in the populations studied, the effect of a seed predator is not decisive for *G. versicolor* reproduction. The loss of unfertilized ovules and undeveloped seeds was more important for this legume than the loss of seeds preyed upon by weevils.

### EFFECT OF HOST-PLANT ECOLOGY ON WEEVIL SURVIVAL

The effect of the plant on seed-predator survival is somewhat different. Mortality of the insects could come from above and below trophic levels. Firstly, *Exapion* larvae were parasitized by *Pteromalus sequester*. Parasitism is a highly important mortality factor for some species of seed-eating weevils (Boe, McDaniel & Robbins, 1989; Morris, 1991; Traveset, 1991; Gómez & Zamora, 1994), as many species of beetles living on legumes suffer parasitism rates higher than 40% (Mitchel, 1977; Boe, McDaniel & Robbins, 1989). However, in our study the proportion of weevils killed by wasps was consistently less than 7%, with a high interannual variability in the parasitism rate. In addition, there was density-independence between parasites and weevils each year, the parasite not choosing the pods with more weevil larvae. Moreover, although several *Coleophora* species are known to be parasitized by wasps (Randall, 1982; Ellison, 1991), we were unable to find any parasitoid of *C. brunneosignata*. As Randall (1982) showed for *C. alticolella*, the parasitism rate decreases with altitude. Thus, the high altitude of our study area may explain why no parasitoids lived on our moths, although probably also because the low abundance of *Coleophora*. Thus, it appears that parasitism is not a strong mortality factor for either curculionids or moths living on *G. versicolor* seeds in the study area.

The main mortality factor of *Exapion* during the larval stage seems to be starvation. There was a large percentage of weevil larvae dying before emerging as adults both in 1992 and 1994. In 1994, we were able to pinpoint the time at which the larvae died because they were laid on non-mature seeds or not on any seed at all. A proximate cause of weevil mortality might be the intraspecific competition among larvae developing within the same pod, since mortality probability depended on the number of larvae per pod as well as the number of seeds per fruit. Similar patterns were shown by Ryoo & Chun (1993) for *Callosobruchus chinensis* (Bruchidae), who reported intraspecific competition affecting several demographic and reproductive traits in beetles. However, since unsuccessful *Exapion* larvae died before getting a mature seed, there was no possibility for competition within *G. versicolor* fruits because these larvae would have died even with no other larvae living in the same fruit. In addition, some larvae living within fruits with some intact seeds also died because they were unable to get a seed. The proximate mechanism explaining the death of weevil larvae is just the lack of enough seeds for the development of every beetle together with the inability of the weevil larvae to move within the fruit to nearby intact seeds.

Many insects oviposit in food patches which present limited resources to developing offspring, such that patch quality and size play a major role in determining the number of eggs laid per patch (Siemens & Johnson, 1992). The probability of larval survival highly depends on the female capacity of selecting good patchs for ovipositing the eggs. However, *Exapion* females seem to oviposit during *G. versicolor* flowering, laying the eggs directly in the flowers. Thus, the females do not control whether the flowers will set fruit (*G. versicolor* normally has a dramatically low fruit:flower ratio) or how many seeds will be produced within the fruit. This can explain why there were normally one or two larvae per *G. versicolor* pod, even though the number of ovules (and potential seeds) per pod was nearly five every year; they would try to minimize egg loss by starvation. Furthermore, it appears that female weevils can detect the quantity of filled seeds per fruit, since in fruits with more mature seeds there were more larvae than in few-seeded fruits (Figure 2).

Our data point to a host-plant effect on *Exapion* populations, which is currently suffering high mortality for a scarcity of mature seeds within *G. versicolor* fruits. Thus, in the interaction between *G. versicolor* and its seed predators, as Crawley (1983) concluded for most plant-herbivore systems, the plant affects weevil-population dynamics more than vice versa. As the plant availability for filling seeds was apparently not related to the herbivory, weevil mortality depended on external predispersal events.

## Acknowledgements

We are most grateful to R. Zamora, P. Jordano, D. Bazely and one anonymous reviewer for their helpful suggestions and invaluable ideas and comments and to D. Nesbitt for linguistic advice. Insect identifications were kindly provided by M. J. Verdú (Pteromalidae), M. A. Zarazaga (Curculionidae) and Antonio Vives (Coleophoridae). J. M. G. was supported by a PFPI grant by the Junta de Andalucía (Andalusian Goverment), and D. G. by a PFPU grant by the Ministerio de Educación y Ciencia (Spanish Government). This study was partially supported by a grant from DGICYT no. PB90-0852.

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