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Interaction between juniper *Juniperus communis* L. and its fruit pest insects: Pest abundance, fruit characteristics and seed viability

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Abstract – The relationships between the fruit features of *Juniperus communis* and the presence of fruit pests were studied in Sierra Nevada, SE Spain. The abundance of two insect species – a pulp-sucking scale and a seed-predator wasp – was surveyed with respect both to fruit characteristics and to viability of seeds contained therein. Seed-predator pressure was not significantly related to any fruit characteristics; however, pulp suckers tended to be more abundant in plants with low pulp:seed ratios and high fruit-water content. In addition, fruits with high levels of pulp-sucker attack tended to have higher water content. A multi-factor ANOVA, considering the identity of the plant and the attack of the different pests as factors, showed that plant identity accounts for most of the variation in fruit characteristics. The viability of seeds tended to be lower in plants strongly attacked by both pests. Fruits attacked by seed predators showed significantly lower proportions of viable and unviable seeds than did unattacked fruits. Seed viability was also lower in those fruits heavily attacked by pulp suckers, but this pattern is strongly mediated by plant identity. Pest activity proved to be clearly associated with a direct decrease in juniper reproductive capacity. This loss involved a reduction of the viable-seed number, mainly related to the seed predator, as well as a reduction of fruit attractiveness to frugivorous dispersers, related to the pulp sucker. © Elsevier, Paris

Fruit characteristics / fruit pests / *Juniperus communis* / phytophagous insects / seed viability / SE Spain

1. INTRODUCTION

Fleshy fruits provide food for several kinds of frugivorous animals, which are beneficial to plants by dispersing their seeds [50]. However, fruits also attract pests, which, contrary to dispersers, harm plants by damaging fruits [9, 15]. Predispersal seed predators destroy seeds developing within fruits, directly decreasing plant offspring [39] and pest insects, by consuming fruit pulp, make fruit less attractive to vertebrate frugivores [24]. Fleshy-fruited plants, vertebrate dispersers and fruit pests are described as a complex ecological triad in which each component interacts simultaneously with the other two [1, 2, 10]. As a consequence of these pairwise interactions, the balance of disperser and pest effects on plant reproduction will determine whether or not the maintenance of fleshy fruit is a benefit for the plant. In an evolutionary sense, the fruit is the meeting point of selective pressures of both pest and disperser. Due to the dependence in the interaction, selective pressures of one type of frugivore (pest or disperser) upon fruit-dispersal traits can dilute evolutionary effects of the other type [12].

Junipers (*Juniperus* spp.) are gymnosperms whose reproductive cones (galbulae) develop a fleshy parenchyma surrounding seeds dispersed by frugivore vertebrates [17, 23, 40] and acting functionally as angiosperm fleshy fruits [13]. On the other hand, junipers present a varied cone-pest fauna which attack cone pulp or seeds before dispersal, thus affecting the reproductive process [6, 33, 37]. This fauna involves species which share with conifers a long evolutionary history (e.g. *Megastigmus* spp. seed chalcids [38, 46]) as well as genus specific for Cupressaceae [33]. Considering both the dispersal characteristics and the presence of the two main types of fruit pests (seed predators and pulp eaters), juniper fleshy cones represent a highly appropriate system for studying the plant-pest-disperser triad by differentiating two features of the reproductive capacity of the plant: fruit characteristics and seed viability. Toward this goal, I analysed the variation both in cone characteristics and in the viability of seeds contained in the cone of

Juniperus communis L. (Cupressaceae), in relation to pest abundance, interpreting this variation with respect to influence on seed dispersal.

2. METHODS

2.1. Study site and natural history of fruit pests

J. communis inhabits the high mountain of the Sierra Nevada (SE Spain), between 1 600 and 2 500 m a.s.l. In this area, *J. communis* is the main shrub, coexisting with other shrub species such as *Genista versicolor* Boissier and *Hormathophylla spinosa* (L.) Küpfer [27]. The general study zone is located at 2 300 m a.s.l., in the area called Campos de Otero. *J. communis* is dioecius, the female individuals bearing, every spring, axillary initial cones that take more than two years to develop fleshy galbulae (fruits hereafter). Three phases can be distinguished in the development from initial cone to ripe fruit (according to Roques [33] and Roques et al. [37]): 1) pollination and delayed fertilization of the cone, from spring of the first year to spring of the second year; 2) fruit growing phase (from a globular small green cone to a berry-like fruit with green colour and final size) during which the seeds begin to develop, from spring to autumn of the second year; and 3) fruit ripening and seed maturation, from the second autumn to the third autumn, the fruit colour changing in September to blue-grey. Cones are produced annually, and therefore it is possible to find initial cones and fruits of two different cohorts simultaneously in the same plant.

In the Sierra Nevada, the fruits of *J. communis* are attacked mainly by two species of insects: a seed-predator chalcid, *Megastigmus bipunctatus* Swederus (Hymenoptera, Torymidae; *Megastigmus* hereafter), and a sessile sucking scale, *Carulaspis juniperi* Bouché (Homoptera, Diaspididae; *Carulaspis* hereafter). Other pests observed in juniper fruits in Sierra Nevada are *Pammene juniperana* Milliere (Lepidoptera, Tortricidae) and *Trisetacus quadrisetus* Thomas (Acarina, Eriophyiidae), but their appearance is extremely scarce (pers. obs.). From the end of June to mid-July, the adults of *Megastigmus* emerge from fruits in phase 3, mate, and females oviposit in fruits at the beginning of phase 2, before the seed coat hardens. The female usually lays one egg per seed, and the resulting larva develops with the seed, consuming it entirely. Larvae pupate the next summer, and emerging adults leave fruits by a typically circular exit hole [33, 47]. Unlike other *Megastigmus* species, *M. bipunctatus* rarely show a prolonged larval diapause in *J. communis* seeds [35]. *Carulaspis* infests either fruits or needles, attaching itself to the surface and covering itself with a white waxy scale. With respect to the fruit settlers, the mated females lay eggs in fruits at the beginning of phase 3, in May and June, hatching into first-instar crawlers (the dispersal stage), which settle on the fruits at the beginning of phase 2. Settled female crawlers become, after several moults, sessile adults which feed on the surface of fruits during the growing phase. The mated female scales overwinter, start laying eggs the next spring, and die in the fruits at the end of the summer of phase 3 [20]. Ripe fruits may show *Megastigmus* exit holes and/or *Carulaspis* white scales, covering homopteran carcasses. In a between-years comparison of pest abundance in different plants, *Megastigmus* abundance varies significantly [5]. On the contrary, *Carulaspis* tend to show little temporal variation in abundance and aggregated between-plants distribution, and most fruits show a low attack level [5]. Ripe fruits are consumed in autumn and early winter by frugivorous birds, mainly *Turdus torquatus* and *T. viscivorus*, which disperse the seeds through their faeces [17].

2.2. Quantification of pest attack on fruits

Quantifying pest attack, I differentiated two levels of attack variation: between different plants and between different fruits. At the plant level, the *Carulaspis* attack rate was defined as the proportion of fruits showing *Carulaspis*, and the *Megastigmus* predation rate was defined as the proportion of fruits containing attacked seeds. The percentage of *Megastigmus*-attacked fruits strongly correlate with the percentage of damaged seeds over the total seeds per plant (Spearman rank correlation coefficient Rho = 0.988, $P < 0.0001$, $n = 24$ plants) reflecting, therefore, the damage at plant-seed-set level. At the fruit level, the *Carulaspis* attack was divided into four semi-quantitative attack levels, depending on the number of scales per fruit: no attack = 0, low = 1–3, medium = 4–6 and high > 6 scales per fruit. The *Megastigmus* attack in fruits was determined by the number of depredated seeds per fruit (0, 1, 2 or 3).

2.3. Analysis of fruit characteristics in *J. communis*

In October 1992, I randomly collected 378 ripe fruits from 10 plants (30–40 fruits per plant). The plants were located in the same habitat, sharing similar general conditions of slope, irradiance and water availability. In a preliminary survey, the fruits of these plants showed a very low *Carulaspis* attack. For an arbitrary gradient to make comparisons between fruits with different *Carulaspis* attack levels, I also collected in October 1994 a total of 190 randomly chosen ripe fruits belonging to 4 different plants (40–50 fruit per plant) showing high *Carulaspis* attack. The entire sample was of 568 ripe fruits belonging to 14 plants. A total of 12 variables was initially considered in the study of fruit characteristics. Maximum fruit length

(length) and diameter (diameter) were measured after collection (with a precision of 0.01 mm) and the fruit shape was estimated with the length/diameter quotient (len/diam). Fruits were weighed after collection (WW.fruit: fruit wet weight, with a precision of 0.1 mg), and after drying 24 h at 70 °C to constant weight (DW.fruit: fruit dry weight). The pulp was separated from seeds, which were counted (n.seeds: number of seeds per fruit) and weighed individually. For each fruit, the mean of dry weight of the seeds (DW.me.seeds) was calculated. Pulp dry weight (DW.pulp) was calculated by subtracting the sum of dry weight of the seeds (DW.Σseeds) from fruit dry weight. Water content (water) was determined by substracting fruit dry weight from fruit wet weight. The fruit-water weight proportion (water%) was calculated by dividing the water content into fruit wet weight. Finally the pulp:seed ratio (pulp:seeds) was estimated by dividing DW.pulp into DW.Σseeds.

2.4. Analysis of seed viability in *J. communis*

The viability of seeds was analysed in the same fruits used to study the fruit characteristics. To increase the sample size, I added to this sample 189 ripe fruits belonging to 10 different plants (10–20 fruit per plant) randomly collected in October 1992 and 1994. The total sample size was thus of 757 ripe fruits belonging to 24 different plants. All the fruit seeds were opened. 'Viable' seeds were those considered to have a developed embryo and endosperm and which entirely filled the seed coat and 'unviable' seeds were those considered to have an undeveloped embryo and endosperm and which did not fill the seed coat. The ratios of viable and unviable seeds were calculated by dividing the number of viable and unviable seeds per fruit by the total number of seeds per fruit, respectively. These ratios were calculated for all plants as the mean of the fruits of each plant.

2.5. Statistical analysis

In the first analysis, I built a 12-variable correlation matrix with which to identify the fruit characteristics which gave redundant information. In this way, the most independent variables and those with the most biological relevance were selected, excluding from the following analysis strongly correlated variables (Spearman rank coefficient with a significance level of $P < 0.01$). The relationship between the *Megastigmus* predation rate in different plants and the fruit characteristics of these plants was analysed with Spearman rank correlations between the predation rate and each of the selected characteristics, using as sample units the mean value of fruit characteristics of each plant, in order to avoid pseudoreplication [14]. The same procedure was used with the *Carulaspis* attack rate. To compare the characteristics of fruits with different attack levels, both by *Megastigmus* and *Carulaspis*, I used a multi-factor ANOVA where the factors were plant identity, *Megastigmus* attack and *Carulaspis* attack. This analysis enabled a separation of the plant factor from the insect factor on the variables considered, and accounted for the possible effect of plant identity (genotype, site effect) in the relationship between pest and plant response. The relationships between viability rates and pest abundance per plant were analysed with two multiple regression analyses, using pest abundance as the independent variable, and viable and unviable seed ratios as dependent variables. I compared seed viability between fruits with different attack levels using the procedure described to compare fruit characteristics, but the number of plants was reduced to plants from which more than 25 fruits were collected (n = 17 plants), following the ANOVA requirements. For the two pools of data (related to fruit characteristics and seed viability), I studied the relationships between the abundance of *Carulaspis* and that of *Megastigmus* per plant with a Spearman rank correlation, and I analysed the co-occurrence degree of both pests in sampled fruit with a Chi-square test (χ^2). The category of '3 *Megastigmus* depredated seeds per fruit' was excluded from analysis, because the fruits belonging to this category were extremely scarce (1 and 2 fruits in the respective pools of data).

Most of the statistical analyses used in the present study were fixed to the standard significance level $P < 0.05$ [51]. However, when statistically analysing more than one related variable and to avoid the increase of probability of making a type-I error, I chose the sequential Bonferroni test for fitting the significance level [32]. In all cases, the type III sum of squares was used due to the unbalanced nature of the data. When necessary, variables were transformed for normality, homocedasticity and linearity, using the arcsine transformation for data expressed as frequencies, and the log-transformation for the remaining ones [51].

3. RESULTS

3.1. Fruit characteristics and pest presence

Six of the 12 initially considered variables showed strong correlations with others in the correlation matrix (*table I*). Thus, I selected the variables length, diameter, DW.fruit, n.seeds, water and pulp:seeds. The plants that were heavily attacked by the seed predator showed fruit characteristics similar to those of weakly attacked plants, the *Megastigmus* predation rate being significantly correlated with none of the selected fruit variables ($r_s < 0.43$, $P > 0.05$, $n = 14$ plants, in all the

Table I. Correlation matrix between the variables considered as fruit characteristics in *J. communis*. The Spearman rank coefficient is shown for each pair of variables (n = 14 plants, *: $P < 0.01$ after Bonferroni test).

	Diameter	Len/diam	WW.fruit	DW.fruit	DW.pulp	N.seeds	DW.Σseeds	DW.me.seeds	Water	Water%	Pulp:seeds
Length	–0.288	0.793*	–0.042	0.068	0.134	0.318	–0.178	–0.266	–0.200	–0.134	0.297
Diameter		–0.727*	0.741*	0.675*	0.455	0.155	0.534	0.490	0.604	0.235	–0.143
Len/diam			–0.481	–0.349	–0.112	0.142	–0.521	–0.600	–0.635	–0.385	0.407
WW.fruit				0.965*	0.763*	0.225	0.640	0.490	0.459	0.029	–0.073
DW.fruit					0.833*	0.256	0.565	0.393	0.310	–0.209	–0.055
DW.pulp						0.162	0.059	–0.086	–0.116	–0.288	0.560
N.seeds							0.157	–0.155	0.054	–0.019	–0.008
DW.Σseeds								0.895*	0.429	0.086	–0.776*
DW.me.seeds									0.521	0.266	–0.798*
Water										0.842*	–0.349
Water%											–0.323

Table II. Mean values (± 1 SE) of the different variables considered as characteristics in *J. communis* fruits, depending on the number of seeds predated by *Megastigmus* per fruit, and the attack level of *Carulaspis* (the number of fruits for each mean value is indicated, length and diameter in mm, DW.fruit and water in mg).

Megastigmus	0	1	2
N. of fruits	502	52	10
Length	6.55 ± 0.03	6.53 ± 0.09	6.70 ± 0.23
Diameter	6.58 ± 0.10	6.69 ± 0.10	6.55 ± 0.23
DW.fruit	80.79 ± 1.19	80.94 ± 3.70	82.57 ± 8.43
N.seeds	2.45 ± 0.03	2.61 ± 0.09	2.70 ± 0.20
Water	10.19 ± 0.27	9.20 ± 0.84	8.50 ± 0.19
Pulp:seeds	1.89 ± 0.04	1.90 ± 0.12	1.46 ± 0.28

Carulaspis	No attack	Low	Medium	High
N. of fruits	258	181	64	65
Length	6.58 ± 0.04	6.69 ± 0.05	6.38 ± 0.10	6.17 ± 0.09
Diameter	6.57 ± 0.05	6.62 ± 0.05	6.57 ± 0.10	6.57 ± 0.07
DW.fruit	81.01 ± 1.75	84.51 ± 1.93	74.42 ± 3.26	74.33 ± 2.47
N.seeds	2.48 ± 0.04	2.50 ± 0.05	2.32 ± 0.09	2.49 ± 0.07
Water	9.42 ± 0.29	9.89 ± 0.35	11.80 ± 1.59	11.24 ± 0.40
Pulp:seeds	2.03 ± 0.06	1.89 ± 0.07	1.68 ± 0.08	1.53 ± 0.08

correlations). On the other hand, the *Carulaspis* attack rate was significantly higher in the plants with mean values higher in water ($r_s = 0.682$, $P = 0.013$, n = 14 plants) and lower in pulp:seeds ($r_s = -0.575$, $P = 0.038$, n = 14 plants). However, these correlations lost their statistical significance level after the Bonferroni test ($P > 0.05$). Fruits with different numbers of depredated seeds showed similar values for all of the fruit characteristics (*table II*). On the other hand, fruits heavily attacked by *Carulaspis* had a shorter length, a lighter weight and a lower pulp:seeds ratio but a higher water content than those left unattacked or suffering weak attack (*table II*). The multi-factor ANOVAs for each of the fruit characteristics showed a significant effect of plant identity upon all the selected variables (*table III*). The same analysis showed that *Carulaspis* attack affected the variation in length, diameter, DW.fruit, and especially in water, but all the significance levels were $P < 0.05$ after the Bonferroni test. There was no significant relationship either between the attack rates of *Megastigmus* and *Carulaspis* in the studied plants ($r_s = -0.167$, $P > 0.05$, n = 14 plants) or the co-occurrence of the two pests in the sampled fruits ($\chi^2 = 9.98$, $P > 0.05$, df = 6).

Table III. Summary of multi-factor ANOVA with respect to the different variables considered as fruit characteristics in *J. communis*. The factors considered as independent variables in the analysis were plant identity, attack level of *Carulaspis* and number of seeds depredated by *Megastigmus* (F: F-rate value; df: degrees of freedom; *P*: significance level; *: $P < 0.05$ after Bonferroni test; between parentheses, the value of the adjusted variance percentage R^2 is indicated).

	Plant	*Carulaspis*	*Megastigmus*	Model
df	13	3	2	545
Length	F = 24.28 *P* < 0.0001 *	F = 2.63 *P* = 0.050	F = 0.29 *P* = 0.74	F = 6.73 (0.15) *P* < 0.0001 *
Diameter	F = 9.11 *P* < 0.0001 *	F = 3.26 *P* = 0.021	F = 0.64 *P* = 0.52	F = 20.43 (0.38) *P* < 0.0001 *
DW.fruit	F = 7.37 *P* < 0.0001 *	F = 3.31 *P* = 0.019	F = 0.50 *P* = 0.60	F = 6.06 (0.14) *P* < 0.0001 *
N.seeds	F = 3.09 *P* = 0.0002 *	F = 1.81 *P* = 0.14	F = 0.94 *P* = 0.39	F = 2.73 (0.05) *P* = 0.0002 *
Water	F = 10.40 *P* < 0.0001 *	F = 4.03 *P* = 0.0075	F = 1.32 *P* = 0.27	F = 8.36 (0.19) *P* < 0.0001 *
Pulp:seeds	F = 13.27 *P* < 0.0001 *	F = 1.42 *P* = 0.24	F = 1.11 *P* = 0.33	F = 11.47 (0.25) *P* < 0.0001*

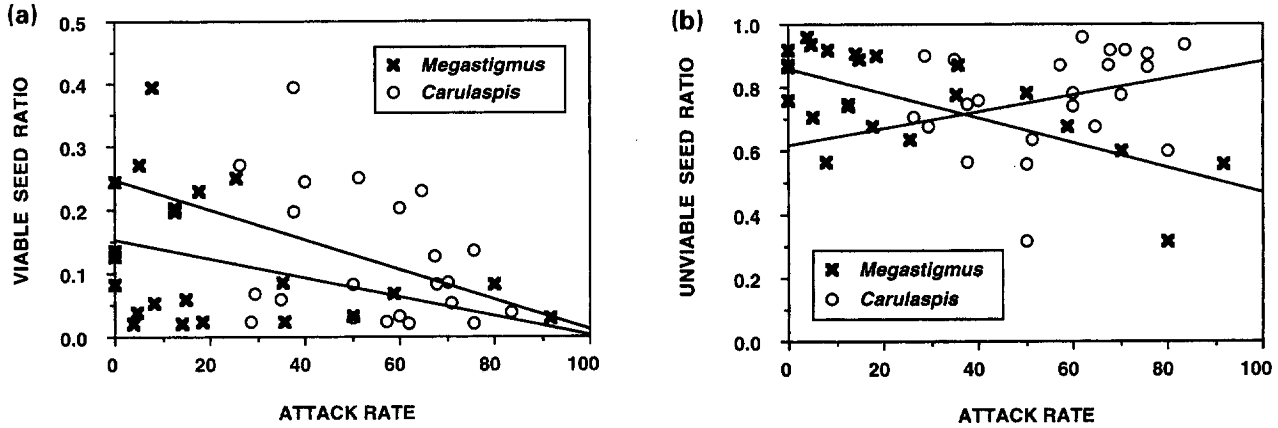

Figure 1. Representation of viable (a) and unviable (b) seed-ratio values depending on the *Megastigmus* and *Carulaspis* attack rates, respectively, expressed in percentage of attacked fruits ($n = 24$ plants).

3.2. Seed viability and pest presence

Mean values of viable and unviable seed ratio (± 1 SE) in fruits of *J. communis* were 0.14 ± 0.01 and 0.78 ± 0.01, respectively ($n = 757$ fruits). The viable seed ratio was very low in plants heavily attacked both by *Megastigmus* and by *Carulaspis* (*figure 1*a). Both pest attack rates were negatively related to the viable seed ratio (*table IV*). On the other hand, plants with high values of unviable seed ratio showed high levels of *Carulaspis* attack but a low predation by *Megastigmus* (*figure 1*b). The *Carulaspis* attack rate showed a positive β-coefficient in the multiple regression model with unviable seed ratio as a dependent variable (*table IV*). On the contrary, the same model showed a negative β-coefficient value for *Megastigmus* predation rate, but it was the only significant coefficient after the Bonferroni test (*table IV*). The viable seed ratio was higher in unattacked fruits than in fruits heavily attacked by both *Megastigmus* and *Carulaspis* (*figure 2*). Fruits attacked by *Megastigmus* showed a significantly lower unviable seed ratio than did unattacked ones; however, this value was higher in fruits strongly attacked by *Carulaspis* than in weakly attacked and unattacked ones (*figure 2*). *Megastigmus* attack was a significant factor in the two multi-factor ANOVA, with respect to viable seed ratio and unviable seed ratio, respec-

Table IV. Summary of multiple regression analysis with *Megastigmus* and *Carulaspis* attack rates as independent variables, and viable and unviable seed ratios as dependent ones ($n = 24$ plants; B: partial regression coefficient ± 1 SE; β: partial regression coefficient standard value; *t*: *t*-test value; R^2: explained variance percentage; R^2 adj: R^2 adjusted; F: F-rate value with degrees of freedom; *P*: significance level; *: $P < 0.05$ Bonferroni test).

	B ± 1SE	β	*t*	*P*
Viable seed ratio				
Intercept	0.67			
Megastigmus attack rate	–0.23 ± 0.09	–0.43	2.41	0.024
Carulaspis attack rate	–0.34 ± 0.16	–0.40	2.21	0.038
$R^2 = 0.33$	R^2 adj. = 0.27		$F_{(2,21)} = 5.23$	0.014
Unviable seed ratio				
Intercept	0.96			
Megastigmus attack rate	–0.38 ± 0.09	–0.66	4.32	0.0002 *
Carulaspis attack rate	0.26 ± 0.15	0.27	1.78	0.089
$R^2 = 0.52$	R^2 adj. = 0.47		$F_{(2,21)} = 11.15$	0.0003 *

tively (*table V*). Both analyses showed a significant effect of plant identity upon the variation of viable and unviable seed ratios (*table V*). There was no significant relationship between the attack rates of *Megastigmus* and *Carulaspis* ($r_s = -0.026$, $P > 0.05$, $n = 24$ plants) nor for co-occurrence of either pests in

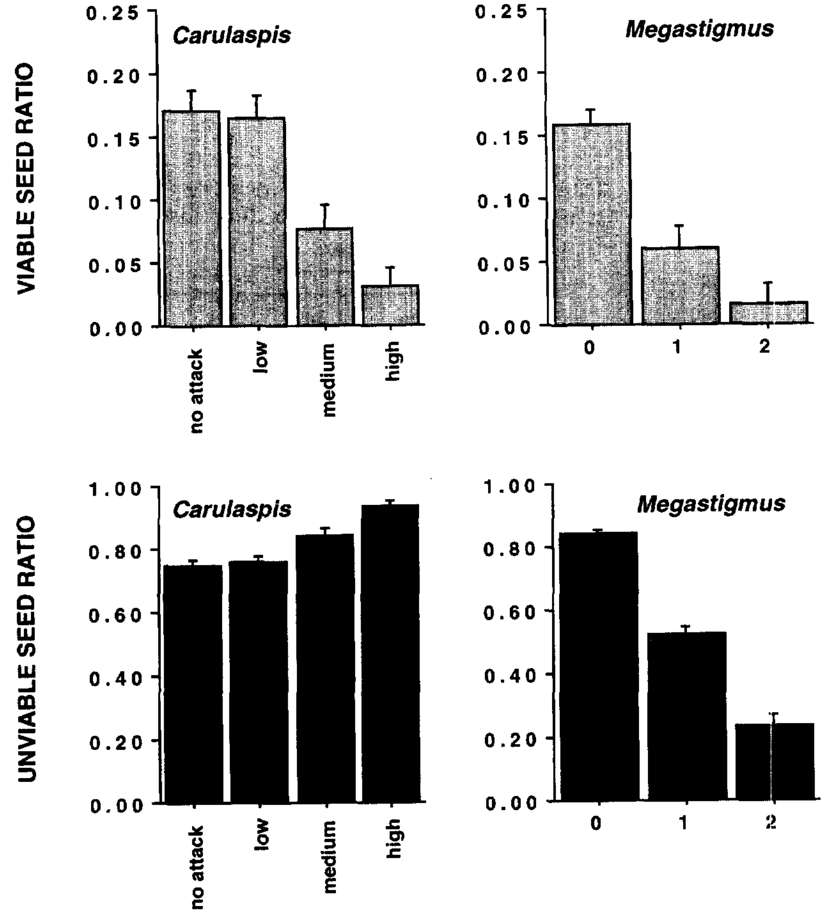

Figure 2. Representation of mean values for viable and unviable seed ratios (+ 1 SE) on *J. communis* fruits, depending on the *Carulaspis* attack level (n. of fruits: no attack = 325, low = 258, medium = 96, high = 76) and the number of seeds depredated by *Megastigmus* per fruit (n. of fruits: 0 seeds per fruit = 638, 1 seed per fruit = 96, 2 seeds per fruit = 21).

Table V. Summary of multi-factor ANOVA with respect to the viable seed ratio and unviable seed ratio, respectively. The factors considered as independent variables in the analysis were plant identity, attack level of *Carulaspis* and number of seeds predated by *Megastigmus* (see *table III* for notation).

	Plant	*Carulaspis*	*Megastigmus*	Model
df	17	3	2	682
Viable seed ratio	F = 8.50 $P < 0.0001$ *	F = 1.51 $P = 0.21$	F = 13.68 $P < 0.0001$ *	F = 8.67 (0.19) $P < 0.0001$*
Unviable seed ratio	F = 8.62 $P < 0.0001$ *	F = 1.69 $P = 0.17$	F = 55.25 $P < 0.0001$ *	F = 15.35 (0.32) $P < 0.0001$*

the sampled fruits ($\chi^2 = 5.57$, $P > 0.05$, df = 6). Neither larvae nor adults of *Megastigmus* in prolonged diapause were found inside the seeds analysed.

4. DISCUSSION

In the present study, no relationship was found between seed predation and fruit characteristics, and fruits with depredated seeds developed normally. These results differ from those of studies dealing with other species of *Megastigmus*, where attack was associated with cone sizes smaller than average [22, 30, 31]. Jordano [16] and Krischik et al. [21] also related the presence of seed predators with fleshy fruit characteristics such as pulp quantity and fruit colour, respectively. Conversely, the cones of *Cupressus sempervirens* attacked by *M. wachtli* showed a size similar to those of unattacked cones [7]. The independence between the seed-predator attack and the fruit characteristics observed here might be related to the lack of physiological relationships between pulp and seeds, the maternal tissues developing independently of embryogenesis [48]. On the other hand, *Megastigmus* predation seriously decreased the number of viable *J. communis* seeds, a factor which can strongly influence the potential regeneration of junipers [6, 37]. The clear negative relationship between unviable seed rate and seed predation could show that adult chalcids emerged mainly from fruits with few unviable seeds, as a result of an oviposition selection of female wasp based on seed viability [11, 19], or because initial larvae die in unviable seeds, and consequently imagos emerge only from potentially viable seeds [39]. Although the females of *Megastigmus* show host-selection behaviour depending on visual and olfatory cues [34, 36, 46], the fact that *Megastigmus* attack is associated with a lower proportion of both viable and unviable seeds per fruit suggests that *M. bipunctatus* is capable of developing in both type of seeds, rather than selecting only viable seeds for oviposition. In this sense, *M. spermotrophus* larvae reportedly develop entirely within unpollinated, unfertilized seeds of *Pseudotsuga menziensii*, their development being supported by a cessation of the endosperm degeneration due to either a mechanical action of female ovipositor or compounds emitted by larvae during feeding [29, 31].

Carulaspis tended to be more abundant in plants with a lower pulp:seed ratio and fruits with a higher water content. Thus, the scale attack could hold predictive value of fruit-quality variation, when pulp:seed ratio and water content are considered to be variables determining fruit attractiveness for dispersers [18]. In addition, *Carulaspis* presence appeared to be associated with seed viability, and heavy scale attack indicated low seed viability, especially at plant level. The correlations between pulp eaters and fruit traits have been demonstrated in several fleshy-fruited plants [16, 39]; however, pulp-eater attack was independent of fruit diameter in *Juniperus phoenicea* [44]. Moreover, it is well known that sap-feeding insects can affect fruit and seed production, decreasing plant reproductive capacity [25, 26, 43], and several studies suggest that pest insects feeding on cone parenchyma cause cone dehydration, indirectly promoting seed abortion in *Juniperus* and *Cupressus* [6, 7, 37]. The association between *Carulaspis* presence and fruit features presented here appears strongly mediated by individual plant and by the contagious distribution of scale attack at the plant level, the latter fact probably due to the low dispersal ability and sessile life-habit of scales [8]. Two compatible hypotheses, taking into account the importance of plant identity in the variation of fruit features, could explain the relationship between *Carulaspis* and juniper fruit traits. Firstly, strong *Carulapis* attack on fruit usually accompanies a heavy attack on juniper needles (pers. obs.) and this scale can seriously damage host-plant vegetative tissues [41]; consequently, between-plant variation in fruit traits and seed viability can be the phenotypic changes due to stress when herbivore pressure is strong [4]. Secondly, plant reproductive-trait variation may be a consequence of stressful environmental conditions, such as drought or low nutrient availability, which makes plants more susceptible to herbivore attack [3, 49].

From the perspective of the plant-pest-disperser triad, pest attack on juniper fruits serves as an indicator of low seed viability and low fruit quality, irrespective of the cause-effect direction of the interaction between pest presence and plant reproductive traits. There is no direct interaction between pest insects and juniper dispersers, because insects end their life-cycles and leave the fruits before seed dispersal. There is no evidence of prolonged diapause of *M. bipunctatus* in *J. communis* and thus no possibility of being dispersed while inside the seed by birds [28]. Therefore, the lack of temporal concurrence results in a low influence of vertebrate dispersers on insect populations [42]. On the contrary, pests indirectly affect the outcome of plant-disperser interaction when their attack promotes fruit rejection by vertebrates, as has been described in several studies [16, 39, 45], and as, in fact, has happened in the case of *J. communis* [5].

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REFERENCES

[1] Borowicz V.A., Do vertebrates reject decaying fruits? An experimental test with *Cornus amomum* fruits, Oikos 53 (1988) 74–78.

[2] Bulchholz R., Levey D.J., The evolutionary triad of microbes, fruits, and seed dispersers: an experiment in fruit choice by cedar waxwings, *Bombycilla cedrorum*, Oikos 59 (1990) 200–204.

[3] Crawley M.J., Herbivory: the dynamics of plant-animal interactions, Blackwell Scientific Publications, Oxford, 1983, 437 p.

[4] Gange A.C., Brown V.K., Insect herbivory affects size variability in plant populations, Oikos 56 (1989) 351–356.

[5] García D., Efecto de las plagas del fruto en la interacción mutualista entre plantas y aves dispersantes: El caso del enebro (*Juniperus communis* L.) en Sierra Nevada, Ms Dissertation, Granada Univ., Granada, 1997, 88 p.

[6] Guido M., Roques A., Impact of the phytophagous insect and mite complex associated with cones of Junipers (*Juniperus phoenicea* L. and *J. cedrus* Webb and Berth.) in the Canary Islands, Ecol. Medit. 22 (1996) 1–10.

[7] Guido M., Battisti A., Roques A., A contribution to the study of cone and seed pest of the evergreen cypress (*Cupressus sempervirens* L.) in Italy, Redia 78 (1995) 211–227.

[8] Hanks L.M., Denno R.F., Natural enemies and plant water relations influence the distribution of an armoured scale insect, Ecology 74 (1993) 1081–1091.

[9] Herrera C.M., Defense of ripe fruit from pests: its significance in relation to plant-disperser interactions, Am. Nat. 120 (1982) 219–241.

[10] Herrera C.M., Avian interference of insect frugivory: an exploration into the plant-bird-fruit pest evolutionary triad, Oikos 42 (1984) 203–210.

[11] Herrera C.M., Selective pressures on fruit seediness: differential predation of fly larvae on the fruits of *Berberis hispanica*, Oikos 42 (1984) 166–176.

[12] Herrera C.M., Vertebrate-dispersed plants: why they don't behave the way they should, in: Estrada A., Fleming T.H. (Eds.), Frugivores and seed dispersal, Junk Publishers, Dordrecht, 1986, pp. 5–18.

[13] Herrera C.M., Interspecific variation in fruit shape: allometry, phylogeny, and adaptation to dispersal agents, Ecology 73 (1992) 1832–1841.

[14] Hulbert S.H., Pseudoreplication and the design of ecological field experiments, Ecol. Monogr. 54 (1984) 187–211.

[15] Janzen D.H., Why fruit rot, seeds mold, and meat spoils, Am. Nat. 111 (1977) 691–713.

[16] Jordano P., Avian fruit removal: effects of fruit variation, crop size, and insect damage, Ecology 68 (1987) 1711–1723.

[17] Jordano P., Geographical ecology and variation of plant-seed disperser interactions: southern Spanish junipers and frugivorous thrushes, in: Fleming T.H., Estrada A. (Eds.), Frugivory and Seed Dispersal: Ecological and Evolutionary Aspects, Vegetatio 107/108, 1993, pp. 85–104.

[18] Jordano P., Angiosperm fleshy fruits and seed dispersers: a comparative analysis of adaptation and constraints in plant-animal interactions, Am. Nat. 145 (1995) 163–191.

[19] Knight R.S., Coping with seed parasitism: a possible response by *Protasparagus aethiopicus*, Oikos 48 (1987) 15–22.

[20] Kosztarab M., Kozar F., Scale insects of central Europe, Academiai Kiadó, Budapest, 1989.

[21] Krischik V., McCloud E.S., Davidson J.A., Selective avoidance by vertebrate frugivores of green holly berries infested with a cecidomyiid fly (Diptera: Cecidomyiidae), Am. Midl. Nat. 121 (1989) 350–354.

[22] Lessman D., Ein Beitrag zur Verbreitung und Lebenswise von *Megastigmus spermotrophus* Wachtl. und *M. bipunctatus* Swederus (Hymenoptera: Chalcidoidea), Z. Angew. Ent. 75 (1974) 1–42.

[23] Livingston R.B., Influence of birds, stones and soil on the establishment of pasture juniper *Juniperus communis*, and red cedar, *J. virginiana* in New England pastures, Ecology 53 (1972) 1141–1147.

[24] Manzur M.I., Courtney S.P., Influence of insect damage in fruits of hawthorn on bird foraging and seed dispersal, Oikos 43 (1984) 265–270.

[25] Meyer G.A., A comparison of the impact of leaf- and sap-feeding insects on growth and allocation of goldenrod, Ecology 74 (1993) 1101–1116.

[26] Meyer G.A., Root R.B., Effects of herbivorous insects and soil fertility on reproduction of goldenrod, Ecology 74 (1993) 1117–1128.

[27] Molero J., Pérez F., Valle F., Parque Natural de Sierra Nevada, Ed. Rueda, Madrid, 1992, 520 p.

[28] Nalepa C.A., Piper W.H., Bird dispersal of the larval stage of a seed predator, Oecologia 100 (1994) 200–202.

[29] Niwa C.G., Overhulser D.L., Oviposition and development of *Megastigmus spermotrophus* in unfertilized Douglas-fir seed, J. Econ. Entomol. 85 (1992) 2323–2328.

[30] Rappaport N., Roques A., Resource use and clonal differences in attack rate by the Douglas-fir seed chalcid, *Megastigmus spermotrophus* Wachtl (Hymenoptera: Torymidae), in France, Can. Ent. 123 (1991) 1219–1228.

[31] Rappaport N., Mori S., Roques A., Estimating effect of *Megastigmus spermotrophus* (Hymenoptera: Torymidae) on Douglas-fir seed production: the new paradigm, J. Econ. Entomol. 86 (1993) 845–849.

[32] Rice W.R., Analyzing tables of statistical test, Evolution 43 (1989) 223–225.

[33] Roques A., Les insectes ravageurs des cônes et graines des conifères en France, Inra Versailles, 1983, 138 p.

[34] Roques A., Interaction between visual and olfactory signals in cone recognition by insect pests, in: Labeyrie V., Fabres G., Lachaise D. (Eds.), Proc. 6th Int. Symp. Insect-Plant Relationship, Pau 1986, Dr W. Junk Publishers, Dortrecht, 1987, pp. 153–160.

[35] Roques A., New results and some thinkings about significance and induction of prolonged diapause in cone insects with particular references to the larch cone fly (*Lassioma melania*) and to the Douglas-fir seed chalcid (*Megastigmus spermotrophus*), in: Miller G.E. (Ed.), Proc. 3rd Cone and Seed Insects Working Party Conference (IUFRO S2.07-01), Victoria 1988, For. Can. Pacific For. Cent., Victoria, Canada, 1989, pp. 64–81.

[36] Roques A., Raimbault J.P., Response of *Megastigmus spermotrophus* to colour traps baited with volatile constituents of *Pseudotsuga menziensii* seed cones, in: Battisti A., Turgeon J.J. (Eds.), Proc. 5th Cone and Seed Insects Working Party Conference (IUFRO S7.03-01), September 1996, Monte Bondone, Italy, Inst. Agr. Entomol., Padova, Italy, 1997, pp. 101–108.

[37] Roques A., Raimbault J.P., Goussard F., La colonisation des cônes et des galbules des genévriers méditerranéens par les insectes et acariens et son influence sur les possibilités de régéneration naturelle de ces essences, Ecol. Medit. 10 (1984) 147–169.

[38] Roux G., Roques A., Biochemical genetic differentiation among seed chalcid species of genus *Megastigmus* (Hymenoptera: Torymidae), Experientia 52 (1996) 522–530.

[39] Sallabanks R., Courtney S.P., Frugivory, seed predation, and insect-vertebrate interactions, Annu. Rev. Entomol. 37 (1992) 377–400.

[40] Schupp E.W., Gomez J.M., Jimenez J.E., Fuentes M., Dispersal of *Juniperus occidentalis* (Western juniper) seeds by frugivorous mammals on Juniper Mountain, Southeastern Oregon, Great Bassin Nat. 57 (1997) 74–78.

[41] Soria S., Cadahia D., Muñoz A., El género *Carulaspis* Mac. Gillivray, 1921 (Homoptera, Diaspididae) en los jardines del Patrimonio Nacional, Bol. San. Veg. Plagas 19 (1993) 273–284.

[42] Traveset A., Weak interactions between avian and insect frugivores: the case of *Pistacia terebinthus* L. (Anacardiaceae), in: Fleming T.H., Estrada A. (Eds.), Frugivory and Seed Dispersal: Ecological and Evolutionary Aspects, Vegetatio 107/108, 1993, pp. 191–203.

[43] Traveset A., The effect of *Agonoscena targionii* (Licht.)(Homoptera: Psyllodea) on seed production by *Pistacia terebinthus* L., Oecologia 98 (1994) 72–75.

[44] Traveset A., Sans A., Insect frugivory in *Juniperus phoenicea* (L.)(Cupressaceae) in Cabrera island (Balearic Archipelago), Boll. Soc. Hist. Nat. Balears 37 (1994) 143–150.

[45] Traveset A., Willson M.F., Gaither Jr J.C., Avoidance by birds of insect-infested fruits of *Vaccinium ovalifolium*, Oikos 73 (1995) 381–386.

[46] Turgeon J.J., Roques A., de Groot P., Insect fauna of coniferous seed cones: diversity, host plant interactions and management, Annu. Rev. Entomol. 39 (1994) 179–212.

[47] Vikberg V., Observations on some Finnish species of *Megastigmus dalman* (Hym., Torymidae), including the biology of *Megastigmus bipunctatus* (Swederus), Annu. Ent. Fenn. 32 (1966) 309–315.

[48] Westoby M., How diversified seed germination behavior is selected, Am. Nat. 118 (1981) 882–885.

[49] White T.C.R., The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants, Oecologia 63 (1984) 90–105.

[50] Willson M.F., The ecology of seed dispersal, in: Fenner M. (Ed.), Seeds: the ecology of regeneration in plant communities, C.A.B. International, London, 1992, pp. 61–86.

[51] Zar J.H., Biostatistical analysis, 3rd ed., Prentice Hall, New Jersey, 1996, 662 p.