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1                                   **Investigating preference-performance**  
2                                   **relationships in**  
3                                   **aboveground-belowground life**  
4                                   **cycles: a laboratory and field study with the**  
5                                   **vine weevil (*Otiorhynchus sulcatus*)**

6                                   **K.E. Clark<sup>1,2</sup>, S.E. Hartley<sup>2+</sup>, R.M. Brennan<sup>1</sup>, K. MacKenzie<sup>3</sup>**  
7                                   **and S.N. Johnson<sup>1,4\*</sup>**

8                                   <sup>1</sup>The James Hutton Institute (Dundee site), Invergowrie, Dundee, DD2 5DA,  
9                                   UK; <sup>2</sup>Department of Biology and Environmental Science, School of Life  
10                                   Sciences, University of Sussex, Falmer, Brighton, BN1 9QG, UK:  
11                                   <sup>3</sup>Biomathematics and Statistics Scotland, Invergowrie, Dundee, DD2 5DA,  
12                                   UK; <sup>4</sup>Hawkesbury Institute for the Environment, University of Western  
13                                   Sydney, Locked Bag 1797, Penrith South, NSW 2751, Australia

14                                   **Abstract**

15                                   The preference-performance hypothesis has principally considered insect herbi-  
16                                   vores with aboveground lifecycles, although the hypothesis could be equally relevant  
17                                   to insects with life stages occurring both aboveground and belowground. Moreover,  
18                                   most studies have focussed on either laboratory or field experiments, with little  
19                                   attempt to relate the two. In this study, the preference-performance hypothesis was  
20                                   examined in an aboveground-belowground context in the laboratory using the vine  
21                                   weevil (*Otiorhynchus sulcatus* F.) (Coleoptera: Curculionidae) and two cultivars of  
22                                   red raspberry (*Rubus idaeus*), Glen Rosa and Glen Ample. A two-year field study  
23                                   (2008–2009) was also undertaken to characterise the population dynamics of adult  
24                                   weevils on the two raspberry cultivars. Larval performance (abundance and mass)  
25                                   differed significantly between Glen Rosa and Glen Ample, with Glen Rosa resulting  
26                                   in 26% larger but 56% fewer larvae compared to Glen Ample. Larval abundances  
27                                   were significantly and positively correlated with root nitrogen and magnesium  
28                                   concentrations, but negatively correlated with root iron. However, concentrations of  
29                                   these minerals were not significantly different in the two cultivars. Adult weevils did  
30                                   not preferentially select either of the two cultivars for egg laying (laying 3.08 and 2.80  
31                                   eggs per day on Glen Ample and Glen Rosa, respectively), suggesting that there was  
32                                   no strong preference-performance relationship between adult vine weevils and their  
33                                   belowground offspring. Field populations of adult vine weevils were significantly  
34                                   higher on Glen Ample than Glen Rosa, which may reflect the higher larval survival  
35                                   on Glen Ample observed in laboratory experiments.

36                                   **Keywords:** host plant preferences, insect performance, insect–plant interactions,  
37                                   oviposition, red raspberry, *Rubus idaeus*

38                                   (Accepted 20 June 2011)

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\*Author for correspondence Fax: +61 (0)2 4570 1103 E-mail: Scott.Johnson@uws.edu.au

+Current address: York Environment and Sustainability Institute, Department of Biology, University of York, Wentworth Way,  
York YO10 5DD, UK

## Introduction

In insect-plant interactions, the selection of a host plant by a maternal insect can be a highly influential factor in parent-offspring relationships, where host plant suitability can affect both parental fecundity and offspring performance (Bernays & Chapman, 1994). The interaction between maternal choice of host plant and subsequent offspring performance is often addressed in relation to the preference-performance hypothesis (PPH), which has received renewed interest recently (Gripenberg *et al.*, 2010 and references therein). The PPH was first proposed by Jaenike (1978) and states that maternal insects will preferentially lay eggs on host plants that optimise the survival and performance of their offspring. The hypothesis particularly refers to insects whose larvae have limited or no ability to relocate and who are dependent on the maternal selection of host plant. In order to optimize offspring performance, the hypothesis predicts a strong association between the egg laying preferences of the mother and offspring performance (Mayhew, 2001).

Many studies examining maternal oviposition preferences and offspring performance support the PPH (e.g. Craig *et al.*, 1989; Heisswolf *et al.*, 2005; Staley *et al.*, 2009). Equally, though, linkages between egg laying preferences and offspring performance can be weak or go undetected (e.g. Rausher, 1979; Scheirs *et al.*, 2004; Digweed, 2006; Gripenberg *et al.*, 2007). The presence of weak PPH linkages has led to a range of alternate hypotheses examining why maternal insects do not select the optimal host plant. These include optimal foraging, where maternal insects select host plants with superior nutritional quality without accounting for the suitability for offspring performance (Scheirs *et al.*, 2000), and enemy free space (Thompson, 1988a,b), where preference-performance linkages are more strongly influenced by natural enemies (normally not incorporated in experiments).

To date, much of the research examining the PPH has incorporated insects with aboveground lifecycles. Equally, though, the hypothesis could be applied to maternal insects living aboveground that have soil-dwelling offspring with comparatively less capacity to relocate between plants (Johnson *et al.*, 2006). For example, the cabbage root fly (*Delia radicum*) preferentially lays eggs on plants with roots that had been pre-conditioned by existing larvae to be more suitable for their offspring (Baur *et al.*, 1996a,b). The same species, however, avoids laying eggs on plants that were in the vicinity of frass of its offsprings' competitors (Jones & Finch, 1987). The mechanisms and cues underpinning such linkages between aboveground maternal insects and belowground offspring are thought to be either plant- or soil-mediated (reviewed by Johnson *et al.*, 2006).

Here, we consider the PPH in an aboveground-belowground context in relation to two raspberry (*Rubus idaeus*) cultivars using the vine weevil (*Otiorhynchus sulcatus* F.) (Coleoptera: Curculionidae) as a model species. We selected Glen Ample and Glen Rosa as potentially good and poor hosts, respectively. Glen Rosa is generally more resistant to some insect pests (e.g. the large raspberry aphid, *Amphorophora idaei*: McMenemy *et al.*, 2009) and shows less vigorous growth than Glen Ample. Moreover, Glen Rosa is particularly susceptible to leaf rust, which may deter insect feeding (S.N. Jennings, personal communication) in the field. Vine weevils are parthenogenetic and unfertilised eggs develop into new females without the need for males. The vine weevil is a highly suitable study species for investigating

parent-offspring relationships in an aboveground-belowground context, as offspring are genetic clones of the adult. The adult weevil is highly polyphagous, feeding on over 150 different plant species (Smith, 1932; Warner & Negley, 1976). However, it is the root feeding larvae that cause most plant damage, decreasing plant vigour and growth and potentially causing death (Penman & Scott, 1976; La Lone & Clarke, 1981; Moorhouse *et al.*, 1992). Indeed, vine weevil larvae cause an estimated £8 million of damage to UK strawberry production every year (HDC, 2003).

The comparatively limited ability of the larvae to move belowground means they are restricted to the host plant choice of the maternal weevil. Adult weevils live aboveground where they lay eggs at soil surface and on plants (although the latter usually fall to the soil) which subsequently develop into root feeding larvae. The life cycle has four distinct stages: eggs, larvae, pupae and adults. Each stage may occur concurrently (Schread, 1972) and adults can, therefore, be feeding on plants aboveground, which are already exposed to root feeding larvae belowground.

The majority of studies investigating vine weevil preferences in relation to host plants have examined the relationship in terms of adult weevil oviposition and feeding behaviour (e.g. Shanks, 1980; Maier, 1981; Nielsen & Dunlap, 1981; Cram & Daubeny, 1982; Van Tol *et al.*, 2004). However, relatively few studies have considered the influence of host plants on larval performance. Strawberry (*Fragaria ananassa*) has been demonstrated to enhance both the establishment of vine weevil populations and larval survival in comparison with Norway spruce (*Picea abies*), white spruce (*Picea glauca*), yew (*Taxus baccata*) and rhododendron (*Rhododendron catiwbienense*) (Fisher, 2006). Additionally, larvae feeding on azalea (*Rhododendron kiusianum*) were smaller and had poorer survival on reaching adulthood compared to adults developing on strawberry (*Fragaria ananassa*) or *Taxus cuspidata* (Hanula, 1988). Such examples provide evidence that the developmental stage of vine weevil larvae can be affected by the host plant species. However, these laboratory studies were conducted in controlled environments, and so the relevance of any such infestations to field populations is unknown.

Like foliar feeding insects, root feeding vine weevil larvae are likely to be influenced by the nutritional status of their host plant, where minerals have been shown to have beneficial, detrimental or neutral influences on insect herbivores (Awmack & Leather, 2002). Nitrogen (N) and phosphorus (P) are often deemed the most limiting factors in insect development (Mattson, 1980; White, 1993; Elser *et al.*, 2000; Huberty & Denno, 2006) due to their low concentrations in plants compared to insects. However, other minerals have been shown to significantly affect insect performance but are often overlooked. These include calcium (Ca) (Scutareanu & Loxdale, 2006), potassium (K) (Stamp, 1994), magnesium (Mg) (McKinnon *et al.*, 1999), Zinc (Zn) (Alyokhin *et al.*, 2005) and iron (Fe) (Thangavelu & Bania, 1990).

The objective of this study was to investigate vine weevil oviposition behaviour and performance, both aboveground and belowground, on two contrasting raspberry cultivars. The specific aims of this study were: (i) to determine how the two cultivars affected different larval abundance and body mass, and establish whether these traits were related with each other in terms of competition (e.g. high survival giving rise to competition and small body size); (ii) to determine whether either, or both, larval performance traits influenced

166 oviposition behaviour by adults; and (iii) to assess whether  
167 these differences were reflected in the field over a two-year  
168 period.

169 It was hypothesised that: (i) vine weevil larvae feeding on  
170 Glen Ample would show improved performance (in terms of  
171 either abundance or body mass, or both) compared to larvae  
172 on Glen Rosa; (ii) adult vine weevils would preferentially lay  
173 more eggs on the cultivar that resulted in greatest larval  
174 performance, but would not lay excessively to avoid offspring  
175 competition; and (iii) field populations of adult vine weevils  
176 would be higher on the cultivar that increased larval per-  
177 formance and that was preferentially selected by ovipositing  
178 adults.

## 179 Methods and materials

### 180 *Plants and insects*

181 Raspberry plants (*cvs.* Glen Ample and Glen Rosa) were  
182 grown in plastic pots (12.5 cm diameter) containing a 2:1  
183 mixture of insecticide-free compost (peat-sand-perlite mix  
184 containing 17N:10P:15K; William Sinclair Horticulture Ltd,  
185 Lincoln, UK) and sand (Silver sand, J. Arthur Bowers, Lincoln,  
186 UK). Plants were grown in a greenhouse at optimum condi-  
187 tions (15–20°C, supplemented with artificial light). All  
188 experiments were conducted in controlled temperature en-  
189 vironments at 21°C ± 2°C and 16:8 L:D photoperiod.

190 Ovipositing adult weevils were used from cultures main-  
191 tained at 17°C ± 2°C and 16:8 L:D photoperiod fed on a mix-  
192 ture of strawberry cultivars. Melanised vine weevil eggs used  
193 in experiments were collected from the cultures ensuring egg  
194 viability (Smith, 1932).

### 195 *Larval performance*

196 Ten plants (*ca.* 13 cm high) of each cultivar were treated  
197 with 30 vine weevil eggs (inserted into a small indentation in  
198 the soil 1 cm from the plant stem). After five weeks, plants  
199 were harvested. Roots were carefully teased apart to recover  
200 larvae. Individual larvae were counted and weighed on a  
201 microbalance (accuracy ± 0.01 mg). Root biometrics (root mass  
202 and maximum root length) were measured after washing and  
203 roots were then snap frozen in liquid nitrogen and stored at –  
204 18°C for subsequent chemical analyses.

205 Frozen root samples were milled to a fine powder for all  
206 chemical analyses. The %N and %C concentrations of 2-mg  
207 samples were determined by a combination of the Dumas  
208 and Pregl methods and were carried out using an Exeter  
209 Analytical CE440 Elemental Analyser. The percentage of C  
210 and N in the sample was calculated by comparison with  
211 known standards.

212 Measurement of other mineral elements was carried out  
213 as described in Johnson *et al.* (2009). In brief, root samples  
214 (0.05 g) were acid digested for 20 min at 180°C in 3 ml of 15.8 M  
215 HNO<sub>3</sub> (Anistar grade, VWR International, Poole, UK) fol-  
216 lowed by oxidation with 1 ml of H<sub>2</sub>O<sub>2</sub> for 20 min at 180°C  
217 in closed vessels within a MARS-Xpress microwave oven  
218 (CEM, Buckingham, UK). Digested samples were diluted  
219 to 50 ml using de-ionised water. Total mineral contents of  
220 calcium (Ca), phosphorus (P), magnesium (Mg), zinc (Zn),  
221 iron (Fe) and potassium (K) in the digested leaf samples  
222 were determined by inductively-coupled plasma mass spec-  
223 trometry (Elan DRC-e, Perkin-Elmer, Beaconsfield, Bucks,  
224 UK).

### *Paired oviposition experiment with two raspberry cultivars* 225

226 For the paired choice experiment, 20 Glen Ample (*ca.* 226  
227 9 cm high with 14 leaflets) plants were selected and paired  
228 up with 20 Glen Rosa (*ca.* 8 cm high with 14 leaflets) plants  
229 according to size. Each plant pair was placed into a mesh cage  
230 (45 × 45 × 30 cm, height × length × width). The bases of the cage  
231 comprised a wooden base with two opposed holes (12.5 cm  
232 diameter) into which potted plants could be inserted. This  
233 ensured that plants were at least 15 cm apart from one another  
234 and were discrete units separated by non-soil substrate  
235 that would be unsuitable for oviposition. A fine mesh circular  
236 collar was placed around the stem of all plants and then  
237 covered with washed gravel (Coarse grit, J. Arthur Bowers,  
238 Lincoln, U.K.) (~ 2–6 mm) to allow the retrieval of vine  
239 weevil eggs at the end of the experiment (see Johnson *et al.*,  
240 2010b).

241 One ovipositing weevil (*ca.* 1–2 months old) was intro-  
242 duced into each cage. Plants were harvested three weeks after  
243 the addition of the weevils. Weevils were recovered from the  
244 cages and plant biometrics were recorded (plant height, plant  
245 mass, number of leaves, leaf area and root mass). Eggs were  
246 recovered from the gravel by immersing it in a saturated KCl  
247 solution and gently stirred so that the eggs floated to the  
248 surface (see Johnson *et al.*, 2010b).

249 Leaf consumption was calculated using a LI-3100C area  
250 meter (LI-COR Inc. Lincoln, Nebraska, USA) and digitally  
251 scanned leaf areas. Digital images were analysed to determine  
252 eaten leaf areas (see Johnson *et al.*, 2010b). Previous work has  
253 established that leaf area was directly correlated with leaf mass  
254 in raspberry (Coyle *et al.*, 2011).

### *Field experiment* 255

256 The experiment was conducted in six separate and adjacent  
257 polytunnels at SCRI, Dundee, UK (56°27'N, 3°04'W). Protected  
258 cropping systems now provide >80% of UK soft fruit sold  
259 through supermarkets (McMenemy *et al.*, 2009) and thus  
260 reflect the most realistic field environment for vine weevils  
261 feeding on raspberry. Each tunnel (22 × 8 × 3.3 m, length ×  
262 width × height) was covered with Luminance THB polythene  
263 film (BPI, London, UK) and contained three raised beds of *ca.*  
264 24 plants covered with polythene mulch. Three tunnels had  
265 been planted with Glen Ample and three with Glen Rosa in  
266 April 2005. In all three years of the experiment, the tunnels  
267 were left uncovered from October until June, according to  
268 commercial practice.

269 During April–May 2007, plants in each row (three rows per  
270 tunnel) were separated into plots of four and enclosed using a  
271 corrugated plastic (Correx<sup>®</sup>; DS Smith Plastics, Warwickshire,  
272 UK) barrier (3.25 × 1.25 × 0.60 m, length × width × height) that  
273 was dug *ca.* 10 cm into the soil (i.e. each row contained six  
274 plots). Weevil eggs collected from culture were applied  
275 to plants at regular intervals so that each row received 576  
276 eggs in total (equivalent to *ca.* 24 eggs per plant). Inoculations  
277 were split over four separate occasions during August  
278 and September 2007 to facilitate inoculation of the 10,368  
279 *O. sulcatus* eggs. Eggs were applied equally to the bases of the  
280 four plants in each plot.

281 Vine weevil adults were surveyed every 14 days (± 2 days)  
282 at night (22:00–01:00) from mid-May until mid-October in  
283 2008 and 2009, starting with the initial population in 2008.  
284 Weevils were dislodged on to white beating trays (110 cm ×  
285 86 cm) (Watkins and Doncaster, Cranbrook, UK) held either

286 side of the plants by shaking the two middle plants in each plot  
 287 five times. Weevils were placed in labelled containers for  
 288 counting on the following day after which they were returned  
 289 to the base of the plants where they had been captured.

290

### Data analysis

291 Larval mass was analysed by analysis of variance, with a  
 292 plant as a block factor. Larval survival was analysed with a  
 293 generalised linear model with a Binomial error structure and  
 294 logit link function. The number of larvae recovered from each  
 295 plant was analysed with a two-sample *t*-test. Relationships  
 296 between root mineral element concentrations and larval  
 297 performance were analysed using Pearson's product moment  
 298 correlation. Mann-Whitney or *t*-tests (as indicated in text) were  
 299 used to determine whether the two cultivars were significantly  
 300 different in terms of specific minerals. Egg laying and feeding  
 301 behaviour of adult weevils in relation to the paired cultivar  
 302 experiment were analysed using paired *t*-tests with trans-  
 303 formed data (log and log+1, see figure legends) to address  
 304 non-normally distributed data. Egg laying in relation to  
 305 feeding behaviour was examined using Spearman's rank  
 306 correlations. All of the above analyses were conducted in  
 307 Genstat version 11 (Payne *et al.*, 2007).

308 Differences between the numbers of weevils caught on the  
 309 two cultivars (Glen Ample and Glen Rosa) in the field were  
 310 analysed using a generalised linear mixed model with Poisson  
 311 error structure and log link function. Cultivar and year were  
 312 included as fixed terms in the model. Tunnel and survey  
 313 number were both included as random terms. The analysis  
 314 was conducted using the 'lme4' package in 'R' programme  
 315 (version 2.12.1, R Foundation for Statistical Computing).

316

## Results

317

### Larval performance

318 Vine weevil larvae were significantly more abundant on  
 319 Glen Ample than on Glen Rosa ( $t_{18}=2.50$ ,  $P=0.022$ ) (fig. 1),  
 320 with larval survival in terms of the original inoculation with  
 321 eggs considerably higher ( $P=0.052$ ) on Glen Ample (18%)  
 322 than on Glen Rosa (8%). While survival rates were compara-  
 323 tively low compared to strawberry (Cowles, 2004), they were  
 324 similar to levels reported in other woody perennial plants  
 325 (Johnson *et al.*, 2011). In contrast, larval mass was significantly  
 326 higher on Glen Rosa than on Glen Ample ( $F_{1,65}=1.14$ ,  
 327  $P=0.001$ ) (fig. 1).

328 Overall, the number of larvae recovered per plant was  
 329 positively correlated with root N concentrations (fig. 2 and  
 330 table 1). Root C and root N concentrations were not signifi-  
 331 cantly different between the two cultivars (C:  $t_{16}=0.90$ ,  
 332  $P=0.384$ ; N:  $t_{16}=0.22$ ,  $P=0.831$ ), nor did larval performance  
 333 show any relationship with root C concentrations. The  
 334 concentration of Mg in the roots was positively correlated  
 335 with the number of larvae recovered per plant (table 1) but  
 336 was not significantly different between Glen Ample and Glen  
 337 Rosa ( $t_{17}=0.65$ ,  $P=0.527$ ). The number of larvae recovered was  
 338 additionally negatively correlated with the concentration of Fe  
 339 in the roots (table 1), but there was no difference in Fe root  
 340 concentrations between Glen Ample and Glen Rosa (Mann-  
 341 Whitney *U* test  $U=25.0$ ,  $P=0.113$ ). Larval abundance was not  
 342 correlated with any other root mineral concentrations and  
 343 larval masses showed no relationships with root mineral con-  
 344 tent (table 1). Root biometrics (root mass and maximum root

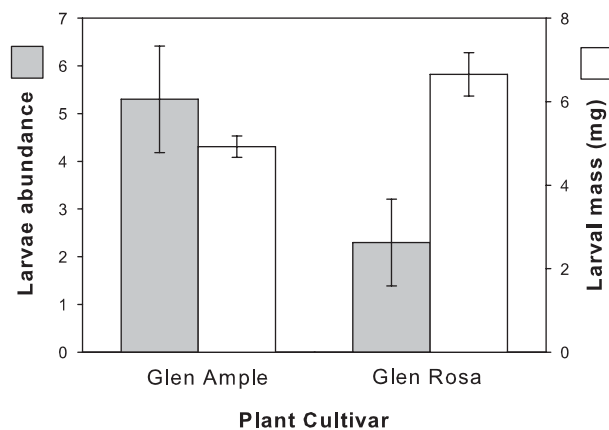


Fig. 1. Differences in larval abundance (■) and average larval mass (□). Mean values ± SE shown. Larval abundance and mass transformed prior to analysis (log + 1 and log, respectively).

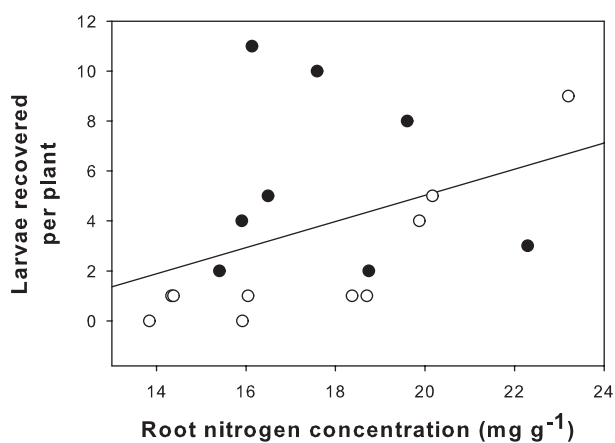


Fig. 2. Relationship between root nitrogen concentrations and number of weevils per plant, Glen Rosa (○) and Glen Ample (●). Pearson's product moment correlation analyses shown are for Glen Ample and Glen Rosa data collectively, linear regression line fitted to data is:  $y=0.524x-5.45$ .

length) were not significantly correlated with either the  
 number of larvae recovered per plant or larval mass (results  
 not shown).

### Paired oviposition experiment on two raspberry cultivars

Adult weevils laid eggs on plants and the surrounding  
 gravel only, with none being laid elsewhere in the cage.  
 Weevils laid similar numbers of eggs on Glen Ample  
 (64.6 ± 4.8, mean ± SE) and Glen Rosa (58.9 ± 6.1, mean ± SE)  
 when allowed to choose between the plants ( $t_{19}=0.92$ ,  
 $P=0.369$ ,  $n=20$ ). Oviposition was not related with any of  
 the plant characteristics quantified (data not shown) and  
 nor was it related to adult feeding in terms of leaf area eaten  
 ( $r_s=0.067$ ,  $df=38$ ,  $P=0.681$ ) or proportion of plant eaten  
 ( $r_s=0.012$ ,  $df=38$ ,  $P=0.943$ ). Adult weevil feeding preferences  
 between Glen Ample and Glen Rosa were not detected in  
 terms of either the leaf area consumed ( $t_{19}=0.71$ ,  $P=0.488$ ) or  
 proportion of plant eaten ( $t_{19}=0.58$ ,  $P=0.566$ ).

Table 1. Summary of correlations for larval mass and abundance in relation to root nutritional quality. Significant relationships highlighted in bold where  $P < 0.05$ . Correlations were calculated using Pearson's product moment correlations or Spearman's rank correlations as appropriate. Larval mass,  $n = 17$ ; larval abundance  $n = 19$ .

| Weevil Response | Correlations |              |          |          |          |          |          |          |              |              |          |          |                      |              |          |          |
|-----------------|--------------|--------------|----------|----------|----------|----------|----------|----------|--------------|--------------|----------|----------|----------------------|--------------|----------|----------|
|                 | N            |              | C        |          | Ca       |          | P        |          | Mg           |              | Zn       |          | Fe                   |              | K        |          |
|                 | <i>r</i>     | <i>p</i>     | <i>r</i> | <i>p</i> | <i>r</i> | <i>p</i> | <i>r</i> | <i>p</i> | <i>r</i>     | <i>p</i>     | <i>r</i> | <i>p</i> | <i>r<sub>s</sub></i> | <i>p</i>     | <i>r</i> | <i>p</i> |
| Mass            | -0.300       | 0.259        | -0.204   | 0.449    | -0.122   | 0.640    | 0.129    | 0.621    | -0.037       | 0.888        | -0.051   | 0.845    | 0.061                | 0.815        | -0.386   | 0.126    |
| Abundance       | <b>0.501</b> | <b>0.034</b> | -0.079   | 0.755    | 0.367    | 0.126    | 0.273    | 0.265    | <b>0.635</b> | <b>0.004</b> | -0.259   | 0.294    | - <b>0.566</b>       | <b>0.009</b> | 0.162    | 0.506    |

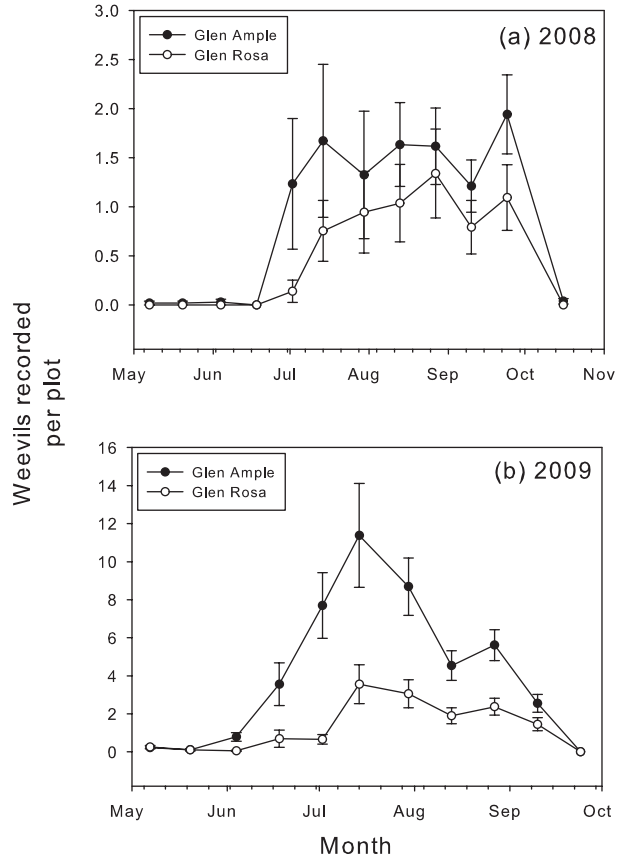


Fig. 3. Mean number of weevils captured per plot on Glen Ample and Glen Rosa in (a) 2008 and (b) 2009. Mean values  $\pm$  SE shown.

Field experiment

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In 2008, 817 weevils were captured across 12 sampling dates, whilst in 2009 2753 weevils were caught across 11 sampling dates. Weevils were significantly less abundant in 2008 (fig. 3a) than 2009 (fig. 3b) ( $Z = 3.50, P < 0.001$ ). Moreover, weevils were significantly more abundant on Glen Ample than Glen Rosa (fig. 3) ( $Z = 3.36, P < 0.001$ ). The difference between the two cultivars was particularly apparent in 2009 (fig. 3b), which was reflected in the statistically significant interaction between cultivar and year ( $Z = -7.15, P < 0.001$ )

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Discussion

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Vine weevil larval performance (abundance and masses) differed significantly between Glen Rosa and Glen Ample, with Glen Rosa having fewer, but heavier, larvae than Glen Ample. Larger offspring are often deemed to show superior performance in comparison to smaller offspring (Stearns, 1992), which would suggest that larvae developing on Glen Rosa would be at an advantage. However, whilst the larvae on Glen Ample were smaller in terms of mass than those on Glen Rosa, they were more abundant. The specific reasons for these differences between Glen Rosa and Glen Ample were not established in this study, but Glen Rosa may be better at deterring first instar larvae (e.g. using chemical or physical mechanisms, see Johnson & Gregory, 2006; Johnson *et al.*,

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2010a) leading to a higher early mortality. This in turn would lead to a decrease in competition, which could result in fewer but larger larvae. Differences in larval performance were not observed on different cultivars of strawberry (Cowles, 2004), although such differences are commonly observed between different plant species (Fisher, 2006).

Overall, larval abundance was found to be positively correlated with root N concentrations, which is consistent with the reliance of young insect larvae on an N rich source (White, 1993). Potentially, root N concentration could play an important role in the performance of vine weevil larvae on host plants. Additionally, larval abundance was positively correlated with root Mg concentrations, but negatively correlated with root Fe concentrations. Foliar concentrations of Mg have been associated with both increases (e.g. Thangavelu & Bania, 1990) and decreases (Clancy & King, 1993) in insect performance, yet the exact role that Mg plays in insect nutrition remains unclear. Fe content in rice plants was found to detrimentally impact the growth and development of the white backed planthopper (*Segatella furcifera*) (Hovarth), causing lower nymphal survival and prolonged nymphal development (Rath, 2004). Consequently, root mineral concentrations may be influential in determining the development of vine weevil larvae.

In our study, the presence of a trade off in larval performance parameters between the two raspberry cultivars may have complicated the decision of the adult weevil. The results showed no evidence of any link between adult weevil oviposition and the performance of vine weevil larvae belowground. The inability of maternal adult insects to select a host plant for oviposition which maximises the survival and development of subsequent offspring has been considered several times in relation to the preference-performance hypothesis (Jaenike, 1978; Denno *et al.*, 1990; Price, 1991; Scheirs & De Bruyn, 2002). A subtle decision between increased abundance or larval masses may simply prove too complex for the highly polyphagous vine weevil. The neural restraints hypothesis (Levins & Macarthur, 1969; Bernays, 2001) states that insects have limited capabilities to process information. Consequently, generalist insects are believed to make poorer decisions regarding their choice of host plants, in comparison to specialist insects, due to difficulties in assessing multiple host plant options. Offspring competition may also explain why adults laid similar quantities of eggs on both cultivars. For instance, if Glen Ample were a more suitable host in terms of larval survival, the consequent increased competition (possibly explaining smaller body size, see above) may have caused adults to lay initially on Glen Ample but then switch to Glen Rosa to avoid excessive offspring competition. For pragmatic reasons, our study did not measure the sequence of egg laying, but this is at least a tenable argument.

Typically, the preference-performance hypothesis is studied in a controlled environment devoid of factors that may influence the relationship between mother and offspring, for instance the presence of enemies (Thompson, 1988a,b). In this study, the preference-performance hypothesis was not investigated directly in the field (due to difficulties in the collection of both eggs and larvae); however, the build up of a vine weevil population on the two cultivars was monitored for two consecutive years. Larval abundances were significantly higher on Glen Ample than Glen Rosa in the laboratory, which corresponded with the significant difference in adult population sizes recorded on the two cultivars in the field.

This suggests that, while there wasn't a strong preference-performance linkage, there is indirect evidence that larval survival is more strongly related to adult abundance than larval body size.

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