

# Oviposition and feeding behaviour by the vine weevil *Otiorhynchus sulcatus* on red raspberry: effects of cultivars and plant nutritional status

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- Abstract**
- 1 The vine weevil *Otiorhynchus sulcatus* is a major pest of horticultural crops worldwide, with root-feeding larvae causing most damage. Adult oviposition aboveground may therefore influence levels of damage as the larvae are relatively immobile after oviposition.
  - 2 The present study investigated feeding and oviposition behaviour on red raspberry *Rubus idaeus* using intact plants, ensuring that choices reflected the realistic differences in cultivar appearance and chemical composition. Previous studies investigating vine weevil feeding and oviposition on other crops have used excised plant material, which may inadvertently influence behaviour.
  - 3 Adult weevils significantly preferred to feed on particular cultivars in the choice experiment (e.g. Tulameen), although they consumed significantly more foliage (0.22–1.03 cm<sup>2</sup>/day) on different raspberry cultivars (e.g. Glen Moy, Glen Rosa and a wild accession) in no-choice situations.
  - 4 In choice experiments, weevils tended to avoid laying eggs on some cultivars (e.g. Glen Moy and the wild accession). The number of eggs laid (1.91–4.32 eggs per day) did not, however, differ significantly between the cultivars in a no-choice situation. Foliar nitrogen and magnesium concentrations were positively, although weakly, correlated with the total number of eggs laid.
  - 5 The present study highlights the importance of considering both choice and no-choice tests when assessing crop susceptibility to attack because weevils may avoid feeding on certain cultivars (e.g. Glen Moy) when given a choice, although this would cause significant damage to such cultivars if they were grown in monoculture (i.e. when there is no alternative).

**Keywords** Host-plant preferences, plant–insect interactions, preference–performance hypothesis, *Rubus idaeus*.

## Introduction

The vine weevil *Otiorhynchus sulcatus* F. (Coleoptera: Curculionidae) originates from Europe, although it is a significant

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pest in both horticultural and nursery crops worldwide (Moorhouse *et al.*, 1992). The adult insect is particularly polyphagous and has been recorded feeding on over 150 different plant species (Smith, 1932; Warner & Negley, 1976). Adult weevils feed aboveground, causing characteristic notching on leaf margins, and lay eggs both on the plant foliage and the soil surface (Moorhouse *et al.*, 1992). Eggs laid on the plant either desiccate, or fall to the ground where they hatch and give rise to larvae. Root-feeding larvae are also polyphagous and cause considerable damage by reducing plant vigour and growth, potentially resulting in plant death (Penman & Scott, 1976; La Lone & Clarke, 1981; Moorhouse *et al.*,

1992). Although the larvae are predominantly responsible for most of the plant damage, their limited mobility belowground means that they are reliant on the host plant choice of the maternal weevil. Determining egg-laying behaviour by adult weevils on host plants could therefore be very important for limiting the damage caused by this pest.

Several studies have investigated vine weevil oviposition in relation to a wide range of host plants (Shanks, 1980; Nielsen & Dunlap, 1981; Hanula, 1988; Van Tol *et al.*, 2004; Fisher, 2006). Certain species have been found to be unsuitable hosts (e.g. *Campanula isophylla* and *Euphorbia pulcherrima* (for larval development) and *Thuja occidentalis* (egg laying and adult mortality) (Moorhouse *et al.*, 1993). However, the majority of this research has used a diverse selection of plant species rather than considering whether weevils are able to detect subtle differences between cultivars or varieties of the same species. In particular, only a minority have addressed whether vine weevils can distinguish between horticultural cultivars (Cram & Pearson, 1965; Cram & Daubeney, 1982; Cowles, 2004), despite the economic consequences of vine weevil herbivory in such high value crops (Alford, 2007). Additionally, in most studies, vine weevil behaviour has been investigated with excised leaves rather than whole plants. Leaf damage has been shown to influence insect-feeding preferences (Risch, 1985; Dalin & Bjorkman, 2003). For example, mechanically-damaged leaves of early-season *Euonymus fortunei* were preferred by vine weevils compared with undamaged leaves, mediated by changes in volatile emissions (Van Tol *et al.*, 2002). Mechanically-damaged plants may therefore inadvertently influence the preferences of vine weevils to different extents on different cultivars.

Host plant quality for insect herbivores is influenced by a range of nutritional aspects including nitrogen (N), carbon (C) and elemental minerals that can have positive, negative or neutral influences on insect herbivores (Awmack & Leather, 2002). The higher N and phosphorus (P) content in insects compared with plants results in a constant struggle to gain adequate nutrition and, thus, N and P are often considered to be the most limiting factors in insect development (Mattson, 1980; White, 1993; Elser *et al.*, 2000; Huberty & Denno, 2006). However, mineral nutrients that are often overlooked can also have significant influences on insect performance. For example, potassium (K) had a negative influence on the performance of the tobacco hornworm (*Manduca sexta*) (Stamp, 1994), whereas magnesium (Mg) was found to positively influence gall density and gall success for the eastern spruce gall adelgid (*Adelges abietis*) (McKinnon *et al.*, 1999). Other minerals have also been found to affect insect herbivores, including calcium (Ca) (Scutareanu & Loxdale, 2006), zinc (Zn) (Alyokhin *et al.*, 2005) and iron (Fe) (Thangavelu & Bania, 1990).

The present study aimed to investigate whether adult weevil feeding and oviposition behaviour would be influenced by the chemical composition and growth characteristics of nine different red raspberry *Rubus idaeus* L. cultivars. The cultivars were chosen to represent a range of geographical origin and genetic diversity (Table 1). The germplasm included both commercially cultivated varieties and a wild Scottish accession of *R. idaeus*. Manipulation of plant physiology and chemistry was kept to a minimum by using whole plants for the

experiments rather than excised leaves. No-choice situations were used to test whether weevil egg laying and feeding would be affected by the chemical composition and plant characteristics of the raspberry cultivars. Choice situations were used to determine whether vine weevils would oviposit or feed on particular cultivars. In particular, the present study aimed to: (i) test whether vine weevil adults fed and oviposited on particular raspberry cultivars when given a choice between all nine cultivars; (ii) determine whether feeding behaviour and the number of eggs laid varied between cultivars in the absence of other cultivars; and (iii) assess whether differences in nutritional status between cultivars were correlated with feeding and/or oviposition behaviour.

## Materials and methods

### *Plants and insects*

Six-week-old plants of nine raspberry cultivars (Table 1) were grown in plastic pots (diameter, 12cm) containing a 2 : 1 mixture of insecticide-free compost (peat-sand-perlite mix containing 17 N : 10 P : 15 K; William Sinclair Horticulture Ltd, U.K.) and sand (Silver sand; J. Arthur Bowers, U.K.). Plants were grown in a greenhouse at optimum conditions (LD 16 : 8 h photoperiod at 15–20 °C). All experiments were conducted in controlled temperature environments under an LD 16 : 8 h photoperiod at 21 ± 2 °C. Ovipositing adult weevils were obtained from a culture maintained under an LD 16 : 8 h photoperiod at 17 ± 2 °C at Scottish Crop Research Institute (SCRI). Adults in the culture were originally collected as general adults from a field site (56°27' N, 3°04' W) with a mixture of raspberry, strawberry and blackcurrant (Johnson *et al.*, 2011). Weevils were thus all of a similar age (approximately 8 weeks old) when used in the experiments. Weevils were fed on a mixture of strawberry (*Fragaria × ananassa*) cultivars to limit any effects of previous feeding on their behaviour.

### *Experimental set-up*

**Choice experiment.** One plant of each raspberry cultivar was randomly placed into one of 16 mesh cages (length 62 cm, width 62 cm, height 45 cm) (i.e. each cage contained nine plants, with one plant of each cultivar in each cage) (Fig. 1). Plants were grouped according to size to minimize any influence that plant biometrics may have on the vine weevil. A fine mesh circular collar with washed gravel (Coarse grit; J. Arthur Bowers) (approximately 2–6 mm) was placed around the stem of each plant to enable the recovery of weevil eggs at the end of the experiment (Johnson *et al.*, 2010b). One ovipositing adult weevil was introduced into each cage.

Plants were harvested 3 weeks after the introduction of the weevil. Some larvae may have potentially hatched from the initial eggs laid at the start of the 3-week period. This will have been the case across all of the plants and thus should not have influenced the results. In addition, the conditions in the gravel meant that the eggs are more likely to have desiccated than hatch. Weevils were removed from cages and plant biometrics were recorded (plant height, plant mass, number of leaves,

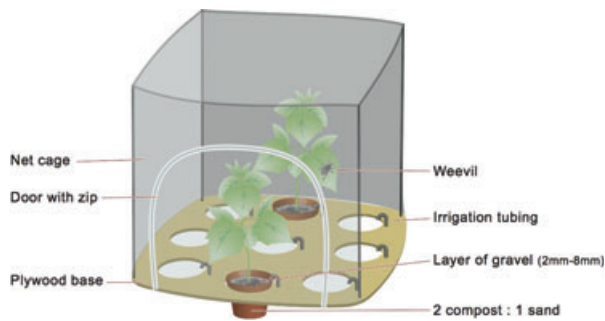
**Table 1** Background of raspberry genotypes used in the experiments

Raspberry cultivar	Origin	Parentage	Summer season <sup>a</sup>	Commercial availability	Spines on canes	Cane vigour <sup>b</sup>	Fruit size <sup>c</sup> (g)
Glen Ample	Scotland	SCRI 7326E1 × SCRI 7412H16	Mid season	Commercial	None	Vigorous	4.6
Glen Clova	Scotland	11/510 × SCRI S29/122	Early	Previously commercial	Spines	Vigorous	3.6
Glen Magna	Scotland	Meeker × SCRI 7719B11	Late	Amateur market	Spines (at base of cane)	Very vigorous	5.1
Glen Moy	Scotland	SCRI 688/12 × SCRI 6815/113	Early	Previously commercial	None	Low	3.5
Glen Rosa	Scotland	7326E1 × 7412H16	Mid season	Amateur market	None	Moderate	4.2
Malling Jewel	England	Prussen × EM23/50	Mid season	Previously commercial	Spines	Vigorous	3.8
Octavia	England	Glen Ample × Malling Hestia	Late	Commercial	Spines	Vigorous	4.9
Tulameen	Canada	Nootka × Glen Prosen	Mid season	Commercial	Spines	Vigorous in tunnel	4.0
Wild	Scotland	Scotland – 56°35'53" N, 4°18'09" W	—	—	Spines	—	—

<sup>a</sup>Early season: early June to middle of August, mid season: third week in July to middle of August, late season: early August onwards.

<sup>b</sup>Cane vigour primarily defined by plant height.

<sup>c</sup>Fruit size measured from open field plots at Scottish Crop Research Institute (SCRI).



**Figure 1** Schematic of mesh cage used for choice experiment with nine raspberry cultivars.

maximum root length, root mass and leaf area). Eggs were recovered from the plants by immersing the gravel in a saturated KCl solution and gently agitating so that the eggs floated to the surface (Johnson *et al.*, 2010b).

Total leaf consumption per plant was calculated using a LI-3100C area meter (LI-COR Inc., Lincoln, Nebraska) and digitally scanned leaf areas. Digital images were analyzed to determine eaten leaf areas (Johnson *et al.*, 2010b). Soil water measurements were made using a profile probe and moisture meter (Delta-T Devices, U.K.).

**No-choice experiment.** Eight plants of each of the nine cultivars were placed into individual mesh cages (height 52 cm, diameter 12.5 cm), constituting 72 cages in total. Plants were then treated and harvested as described in the choice experiment.

After digitally scanning all leaves, leaves that had been sampled by weevils were snap frozen in liquid nitrogen for subsequent chemical analysis (see below). Control plants (containing no weevils) were included in both choice and no-choice tests to establish that herbivory was not affecting those chemical traits measured in the study.

#### Plant chemical analysis

Frozen leaf samples were milled to a fine powder for all further chemical analyses. The N and C concentrations of 2 mg samples were determined by a combination of the Dumas and Pregl methods and were carried out using an CE440 Elemental Analyser (Exeter Analytical, U.K.). The percentage of C and N in the sample was calculated by comparison with known standards.

Measurement of mineral elements was carried out by acid digesting leaf samples (0.05 g) for 20 min at 180 °C in 3 mL of 15.8 M HNO<sub>3</sub> (Aristar grade; VWR International, U.K.) followed by oxidation with 1 mL of H<sub>2</sub>O<sub>2</sub> for 20 min at 180 °C in closed vessels within a MARS-Xpress microwave oven (CEM, U.K.). Digested samples were diluted to 50 mL using de-ionized water. Total mineral contents of Ca, P, Mg, Zn, Fe and K in the digested leaf samples were determined by inductively-coupled plasma mass spectrometry (Elan DRC-e, Perkin-Elmer, U.K.).

#### Statistical analysis

For the choice tests, egg laying was analyzed using a generalized linear model with Poisson error structure and logarithm link function with cultivar and cage number as fixed effects. All plant biometrics and chemistry were initially included in the model, with stepwise removal of the nonsignificant terms until all explanatory variables were statistically significant. The quantity and number of plants eaten by the weevil was very low in the choice experiment; thus, rather than modelling leaf area directly, the model considered the probability of a weevil eating a particular cultivar out of the choice of nine cultivars. Each plant cultivar was scored as having been eaten or not, and the data were then analyzed using a generalized model with a binomial error structure and logit link function, from which the probability of each cultivar being eaten was predicted. Cage

number was again included in these models. Once the effect of cultivar, plant biometrics and chemistry had been assessed for choice tests, the analyses were repeated with generalized linear mixed models, which permits cage to be included as a random term (although this does not allow plant biometric and plant chemistry terms to be simultaneously included in the model). Cages where feeding was not detected or eggs were not recovered were removed from the analysis, resulting in 13 and ten replicates for feeding and egg models, respectively.

In the no-choice experiment, egg laying was analyzed with a generalized linear model with normal distribution and identity link function. Cultivar was included as a fixed effect. All plant biometrics and chemistry were initially included in the model, with stepwise removal of nonsignificant terms. Leaf consumption in no-choice tests was analyzed with analysis of variance, including all plant biometrics and chemistry as covariates. In a few of the cages, the adult weevils were not recovered and these replicates were excluded from the analyses; thus, the number of replicates per cultivar varied between six and eight. Any significant effects of plant biometrics and chemistry on egg-laying and feeding behaviour were further investigated using Pearson's product moment correlations. All statistical analyses were conducted in GENSTAT, version 12 (VSN International, U.K.).

## Results

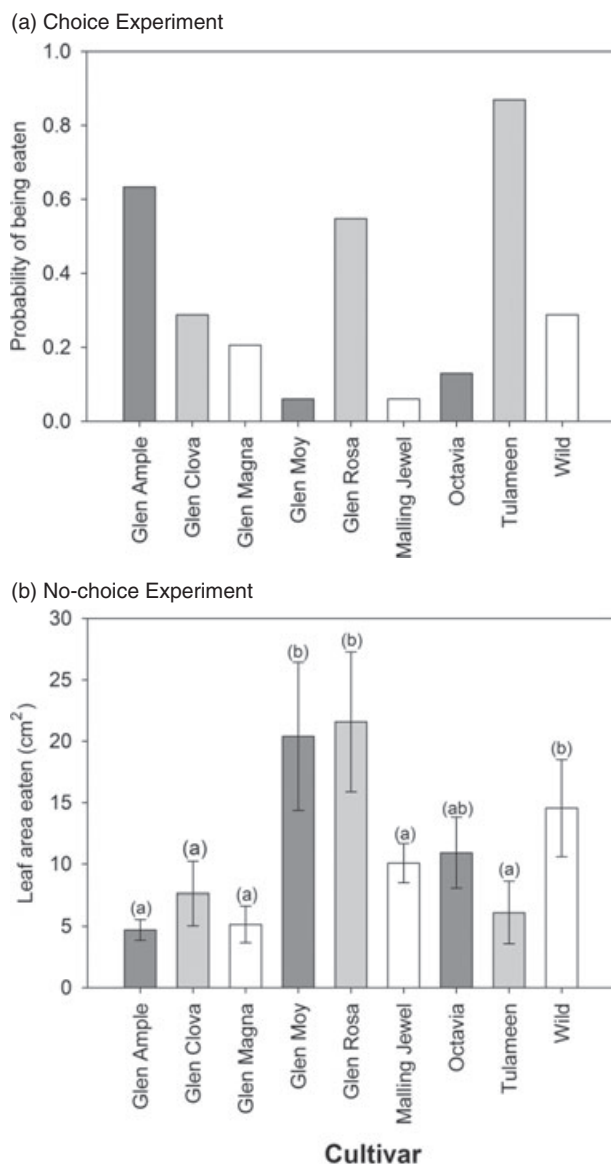
### Feeding behaviour

When given a choice, the probability of a weevil eating was significantly higher on some raspberry cultivars than others ( $F_{9,107} = 4.14$ ,  $P < 0.001$ ), which was confirmed with the mixed model ( $F_{8,106} = 3.24$ ,  $P = 0.002$ ). The probability of a particular cultivar being eaten was most notably higher for Glen Ample, Glen Rosa and Tulameen (Fig. 2a). In addition, raspberry cultivars significantly influenced the quantity of leaf area eaten when the weevils were given no choice ( $F_{8,55} = 5.26$ ,  $P < 0.001$ ) (Fig. 2b). None of the plant biometrics or chemistry traits were influential in determining the probability of a weevil eating a particular raspberry cultivar in either choice or no-choice tests (results not shown).

There were statistically significant differences in the amount of foliage consumed in choice and no-choice tests ( $F_{1,174} = 4.34$ ,  $P = 0.039$ ), with weevils consuming approximately 45% more foliage in no-choice situations compared with choice tests.

### Egg-laying behaviour

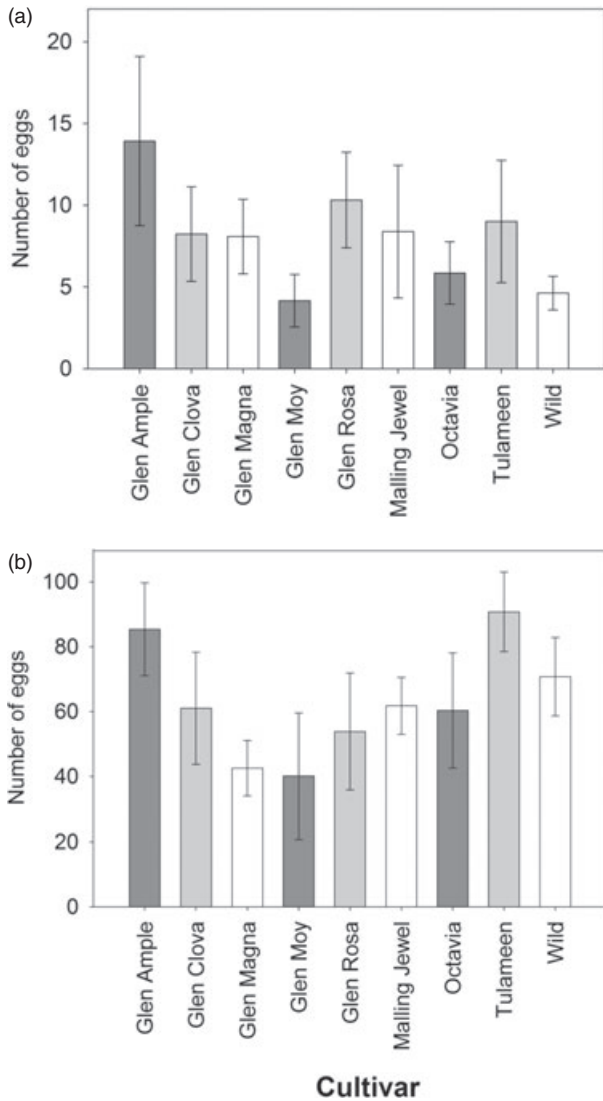
Adult vine weevils showed significant preferences in terms of egg laying on different cultivars in the choice test ( $F_{8,70} = 2.52$ ,  $P = 0.018$ ) (Fig. 3a), although the mixed model (which could only include cultivar) narrowly missed statistical significance at the 95% confidence interval ( $F_{8,70} = 1.94$ ,  $P = 0.068$ ). Total egg laying on different cultivars was not statistically significant in no-choice experiments ( $F_{8,53} = 1.26$ ,  $P = 0.092$ ) (Fig. 3b). In the no-choice experiment, none of the plant biometrics affected egg laying (data not shown), although there was a statistically significant relationship with foliar N ( $F_{1,53} = 7.67$ ,



**Figure 2** (a) Probability of a raspberry cultivar being eaten by a weevil in the choice experiment ( $n = 13$ ). (b) Mean leaf area eaten in relation to raspberry cultivar in no-choice experiment (mean  $\pm$  SE;  $n = 6-8$ ). Differences between cultivars analyzed using a generalized linear model with normal errors and identity link function. Bars accompanied by the same lowercase letter are not significantly different at the 5% significance level.

$P = 0.008$ ) and Mg ( $F_{1,53} = 5.61$ ,  $P = 0.022$ ). Concentrations of nutrients in plants with and without weevils were statistically indistinguishable ( $P < 0.20$  in all cases), and so weevils were not considered to have altered overall plant chemistry during the experimental timeframe. There was a positive, although weak, correlation between the number of eggs laid and concentrations of N ( $r = 0.310$ ,  $P = 0.013$ ) (Fig. 4a) and Mg ( $r = 0.251$ ,  $P = 0.045$ ) (Fig. 4b). There were significant differences in N ( $F_{8,55} = 5.85$ ,  $P < 0.001$ ) and Mg ( $F_{8,55} = 3.89$ ,  $P = 0.001$ ) concentrations between cultivars in the no-choice experiment, although these did not directly correspond with egg-laying





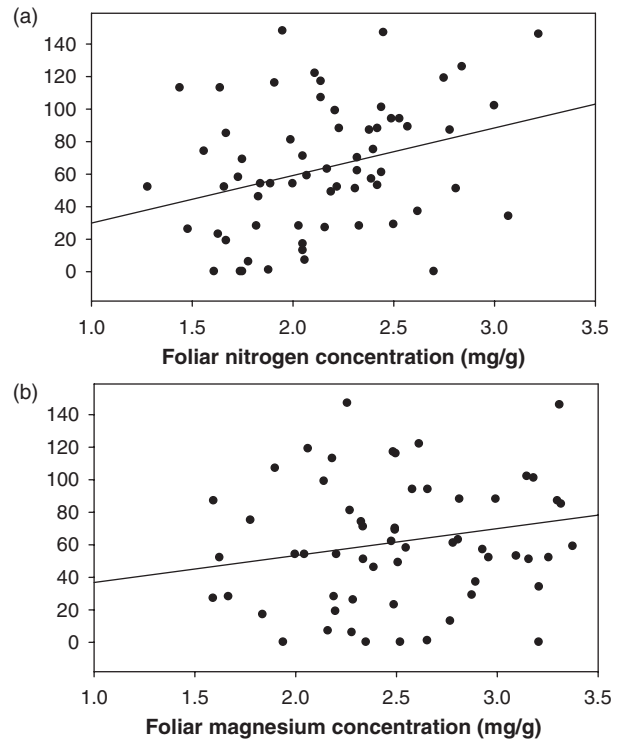
**Figure 3** Egg-laying behaviour of vine weevil in relation to nine raspberry cultivars. (a) Choice experiment: number of eggs laid in relation to nine raspberry cultivars (mean  $\pm$  SE;  $n = 10$ ). (b) No-choice experiment: number of eggs laid in relation to nine raspberry cultivars (mean  $\pm$  SE;  $n = 6-8$ ).

behaviour. For example, Glen Moy had the second highest N concentrations but the lowest numbers of eggs laid, whereas Tulameen had among the lowest Mg concentrations but highest numbers of eggs laid.

Although no plant biometrics or nutrients affected egg-laying behaviour in choice tests, there was a positive relationship between number of eggs laid and leaf area consumed ( $F_{1,70} = 13.21$ ,  $P < 0.001$ ) and soil moisture content ( $F_{1,70} = 4.37$ ,  $P = 0.04$ ) in the choice test.

## Discussion

Adult weevil feeding significantly differed between the nine raspberry cultivars investigated. When given a choice, weevils



**Figure 4** Number of eggs laid in relation to (a) leaf nitrogen and (b) leaf magnesium concentrations on no-choice tests ( $n = 64$ ) (two plants excluded as a result of contamination).

preferred to feed on Tulameen and avoided feeding on Glen Moy, whereas, in a no-choice situation, adult weevils consumed a high quantity of leaf material on Glen Moy and Glen Rosa. The contrast between feeding behaviour on Glen Moy in the choice and no-choice experiments could be a result of the highly polyphagous nature of the vine weevil adult, in so much that they will accept a host plant for survival, even if it is undesirable. This is consistent with the findings of Coyle *et al.* (2011), who reported that vine weevil adults would readily switch between host plants for feeding but tended to lay eggs on plant species that they had been reared on. The results obtained in the present study also emphasize the need to conduct both choice and no-choice feeding experiments when considering varietal susceptibility. Weevils avoided feeding on Glen Moy when given an option; however, if Glen Moy was the only cultivar grown by a particular grower, then it may be susceptible to heavy damage, as indicated by the no-choice test.

When scaled for differences between choice and no-choice experiments, weevils consumed significantly more foliage in the latter than the former for all cultivars. The nutritional chemistry was similar for plants used in both tests, and we suggest that this is not the result of a compensatory feeding response (i.e. weevils consuming more foliage of lower nutritional quality; Johnson *et al.*, 2010b) but that reduced feeding may be a result of the extra time spent moving between plants in the choice tests.

Because the major plant biometric features and nutritional content of the foliage was not related to weevil feeding, this suggests that other (unmeasured) plant properties may influence

weevil feeding behaviour. For example, leaf hairs were found to be one of the factors determining the acceptance of strawberry cultivars for vine weevil feeding, although it was proposed that another undetermined property was also important (Cowles, 2004). Differences in plant defences between the cultivars may affect the feeding behaviour of the weevils, although Coyle *et al.* (2011) found no evidence of phenolic compounds influencing host selection by *O. sulcatus*.

Vine weevil egg-laying behaviour differed significantly between the nine raspberry cultivars investigated, which is similar to the findings of Cram and Daubeny (1982) who used different raspberry cultivars. In the no-choice tests, egg-laying behaviour was influenced by leaf N and Mg concentrations. The number of vine weevil eggs laid was found to be positively (if weakly) correlated with concentrations of both nutrients. This has not previously been reported for raspberry but similar patterns have been observed in strawberry for leaf N and egg laying (Hesjedal, 1984), although this relationship was not apparent in the study of Maier (1981).

Although vine weevil larvae feed belowground and would not directly benefit from elevated foliar N concentrations, adult weevils may associate the increased nitrogen as an indication of a nutritionally superior host plant. In particular, early-instar insect larvae are susceptible to nitrogen availability, which can affect both growth rates and survival (White, 1993). Therefore, according to the preference–performance hypothesis (Jaenike, 1978) maternal oviposition should favour host plants with optimal nitrogen availability for offspring, even when they feed above- and belowground, respectively (Johnson *et al.*, 2006).

Even though plants received identical irrigation and showed no symptoms of water stress, there was inevitable variation in soil water content between plants (e.g. differences in uptake, transpiration, etc.). We observed that higher soil water content was associated with higher numbers of eggs in choice tests, which may also reflect ovipositional behaviour geared to benefit soil-dwelling offspring that are particularly susceptible to desiccation (Villani & Wright, 1990; Johnson *et al.*, 2010a).

In some polyphagous insects where the relationship between adult oviposition and offspring performance is not strongly linked, as predicted by the preference–performance hypothesis (Jaenike, 1978), it has been suggested that egg-laying behaviour is predominantly influenced by the nutritional status of the host plant for the maternal insect (Scheirs & De Bruyn, 2002). In this case, adult feeding takes precedence over egg laying; hence, eggs tend to be laid where the adults feed. In the present study, when vine weevils were given a choice of raspberry cultivars, leaf consumption and egg-laying behaviour were positively correlated. However, the quantity of leaf material consumed was not related to foliar N content, unlike egg laying, although a significant relationship between foliar N and plant consumption has been reported previously in strawberries (Cowles, 2004). Thus, although eggs were laid where weevils fed in the choice experiment, the nitrogen content of leaves did not dictate where the weevils fed.

Using whole plants, rather than excised leaves, we have established differences in the susceptibility of different raspberry cultivars to attack by vine weevils. In particular, the present study demonstrates the importance of conducting both choice and no-choice experiments when assessing a crop

for susceptibility to insect attack because weevils demonstrated an aversion to feeding on particular cultivars (e.g. Glen Moy) when offered a choice but caused significant damage to these cultivars when offered no alternative.

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