

# Prior host feeding experience influences ovipositional but not feeding preference in a polyphagous insect herbivore

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## Abstract

Black vine weevils, *Otiorhynchus sulcatus* (Fabricius) (Coleoptera: Curculionidae), are globally-distributed polyphagous pests of many horticultural crops. We investigated how adult weevils were affected by host switching and, in particular, how host plant species nutritional and defensive chemistry affected subsequent host plant species selection and oviposition. Adults were fed one of three host plant species, blackcurrant [*Ribes nigrum* L. (Grossulariaceae)], raspberry [*Rubus idaeus* L. (Rosaceae)], or strawberry [*Fragaria x ananassa* Duchesne (Rosaceae)], throughout their pre-reproductive periods and then subjected to behavioral choice assays with these plants. Foliar chemistry differed significantly among the three host plant species. Compared to raspberry and strawberry foliage, blackcurrant foliage was 13% lower in nitrogen, 3% higher in carbon, and 28% higher in phenolic compounds. Initial host plant species had a significant effect on weevil mortality, with more weevils dying when previously fed blackcurrant (12%) than strawberry (3%) or raspberry (0%) regardless of subsequent host. Initial host plant species also affected oviposition, with weevils laying only ca. two eggs per week when previously fed blackcurrant, compared to those on raspberry or strawberry (ca. 11 and 15 eggs per week, respectively). When given a choice, weevils discriminated among host plant species and tended to oviposit on plants on which they had previously fed, even when the plant was nutritionally inferior for egg production and adult survival. In contrast, feeding behavior was only affected by the current host plant species. Feeding and oviposition were related to leaf chemistry only in blackcurrant, as leaf consumption was negatively correlated with foliar carbon and zinc concentrations, and positively correlated with foliar phosphorus and potassium concentrations.

## Introduction

Host selection by phytophagous insects is an intricate process, involving a complex set of abiotic and biotic variables, all of which must be interpreted by the insect prior to a decision (West & Cunningham, 2002). Experience-induced changes in host plant preference are often influenced by plant nutritional and defensive chemistry, which can shape both herbivore fitness and host selection (Bernays & Chapman, 1994). In particular, prior experience

with host plants has been linked to associative and non-associative learning (Papaj & Prokopy, 1989; Schoonhoven et al., 2005). Associative learning, in which the herbivore relates a particular stimulus (e.g., odor) with another stimulus (e.g., food), can include aversion behavior (Dethier, 1988), advantageous selection of multiple host plant species (Bernays et al., 1992), or behavior based on oviposition experience (Prokopy et al., 1982; Prokopy & Papaj, 1988). Non-associative learning involves habituation to deterrents (Glendinning et al., 2001; Akhtar & Isman, 2004), sensitization, or induced preferences based on initial host experiences (Jermy et al., 1968).

Induced preference learning, whereby insects are more likely to continue feeding on host plant species they have

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become accustomed to, even when alternate and equally suitable hosts are available, has been widely reported for many insect taxa (Cassidy, 1978; Scriber, 1982; Bernays & Weiss, 1996). In marked contrast, aversion learning has been reported in fewer cases, but is thought to be more common amongst generalist than specialist insect feeders (Dethier, 1980, 1988; Lee & Bernays, 1990). Aversion learning occurs when insect herbivores avoid feeding on host plant species that they have previously experienced the induction of a malaise (Dethier, 1980). Among herbivorous coleopterans, prior feeding may (Hanula, 1988) or may not (Ameen & Story, 1997) influence subsequent host choice, feeding behavior, and oviposition. Although the effects of larval feeding experience on adult host preferences have been well studied, especially in terms of the Hopkin's host selection principle (Barron, 2001), the extent to which changes in feeding experience within the adult phase affect subsequent host preference by adults for feeding and oviposition is not well characterized.

The black vine weevil, *Otiorhynchus sulcatus* (Fabricius) (Coleoptera: Curculionidae), is a globally-distributed polyphagous herbivore with a host range of over 100 plant species, many of which are horticultural crops (Masaki et al., 1984; Moorhouse et al., 1992). Adult feeding can cause considerable economic losses (Cone, 1963; Penman & Scott, 1976; Cram, 1978). Larval feeding can severely damage roots, resulting in reduced plant growth and survival (Penman & Scott, 1976; Moorhouse et al., 1992). Adults are parthenogenic and have a wider host range than the larvae. The flightless adults can move from host to host during their teneral and ovipositional periods (Maier, 1978). Thus, unlike larvae, which are relatively non-mobile in soil and restricted to feeding on the host on which adults deposit the eggs, adults can potentially sample several plant species prior to ovipositing. The effects of these encounters on subsequent host choice are unknown.

Hanula (1988) examined the effect of host switching on adult *O. sulcatus* oviposition using several horticultural crop plants. Under no-choice conditions, weevils preferentially oviposited on the first host plant species they consumed as adults regardless of the subsequent host presented (Hanula, 1988). Apart from total nitrogen (N) concentration being positively associated with feeding (e.g., Hesjedal, 1984), the effect of plant chemistry on such behavioral patterns remains largely uncharacterized for *O. sulcatus*.

Our goal was to determine whether the influence of initial host plant species affected subsequent preferences when given a choice of three host plant species midway through this weevil's adult lifecycle. In particular, we examined how differences in key mineral nutrients and secondary metabolites might underpin such patterns. This study quantified N, carbon (C), zinc (Zn), calcium (Ca),

potassium (K), phosphorus (P), and phenolic compounds. Phenolic compounds were selected as likely defensive compounds because they are common in such perennial crops, and have been shown to have negative and deterrent effects on many generalist herbivores (Hartley & Firn, 1989; Harborne, 1994; Hartley & Jones, 1997), including curculionid pests (Nerio et al., 2009; Stevenson et al., 2009). We hypothesized that adult *O. sulcatus* would preferentially consume foliage and oviposit on the most suitable host plant species, regardless of the initial host plant species they were reared on (i.e., behavior that was more typical of aversion learning rather than induced preference learning). We also hypothesized that host plant species would differ in their nutritional and defensive chemistry, and some of these differences would be associated with weevil behavior.

## Materials and methods

### Plant material

Blackcurrant [*Ribes nigrum* L. cv. Ben Gairn (Grossulariaceae)], raspberry [*Rubus idaeus* L. cv. Glen Ample (Rosaceae)], and strawberry [*Fragaria x ananassa* Duchesne cv. Symphony (Rosaceae)] plants were used in this study, as this represents the most likely combination of species at commercial fruit growing sites. Plants were grown from high health root stock maintained at the Scottish Crop Research Institute, Invergowrie, UK (56°27'N, 3°4'W) in 150-mm diameter pots containing 1.17 kg insecticide-free compost (peat-sand-perlite mix containing 17N:10P:15K; William Sinclair Horticulture, Lincoln, UK). Propagation and bioassays were conducted in a glasshouse with optimum conditions for plant production (20 ± 5 °C and L16:D8 photoperiod provided by supplemental lighting from overhead lamps; Philips 400 W SON-T AGRO, Lanarkshire, Scotland, UK). We used plants that were 6–8 weeks old throughout the study, which were propagated on a weekly basis.

### Experimental procedure

We collected primarily teneral *O. sulcatus* adults, and some pupae, from a field site containing blackcurrant, raspberry, and strawberry in Perthshire, UK (56°27'N, 3°4'W). Teneral adults were whitish in color, showed minimal movement, and likely had no prior feeding experience. Adults that emerged from pupae were added to the existing colony. One hundred and fifty weevils were maintained at 19 °C and L16:D8 photoperiod in separate Petri dishes (9 cm diameter) that were lined with dampened filter paper. Feeding history was established by randomly dividing weevils according to three diets of freshly excised leaves: 50 each from blackcurrant, raspberry, and strawberry.

Larval feeding can affect adult host selection behavior in some holometabolous insects (see discussion by Barron, 2001), but the fully randomized experimental design should have randomly distributed any adults with a predisposition for a particular host plant species. Leaves were changed every other day for the duration of the weevils' pre-reproductive period (Cram, 1958) which lasted 4 weeks.

Experiments were conducted in a glasshouse using 30 mesh cages (0.25 × 0.25 × 0.7 m), with a wood floor that contained three 150-mm diameter holes to hold plant pots. Three similar sized plants (blackcurrant, raspberry, and strawberry) were transferred to each of the cages. To allow egg recovery (as described in Johnson et al., 2010), a fine mesh (<100 µm) circular sheet was placed around the stem of each plant, which was then covered with washed gravel (coarse grit, lime-free horticultural grade; J. Arthur Bowers, Lincoln, UK) that had been sieved to 2–8 mm. Nine cages were selected at random and each received four weevils, starved for 24 h prior to assay initiation, that had been fed exclusively on blackcurrant. A further nine cages received four weevils fed on raspberry, and another nine cages received four weevils fed on strawberry. The remaining three cages were maintained as insect-free controls to determine whether weevil activity affected plant chemistry. The experiment ran for 7 days, after which eggs were manually recovered from leaves and from the gravel surface by submerging the mesh sheet in saturated KCl solution (see Johnson et al., 2004).

Plants were destructively harvested by cutting the stem at the soil line. Fresh aboveground mass was recorded. Leaves were removed from the shoot, and leaf consumption was quantified by comparing photocopied images of damaged leaves with images in which the intact leaf perimeter had been estimated (by filling feeding notches) using a leaf area meter (LI-300; Li-Cor, Lincoln, NE, USA) (see Johnson et al., 2010). Leaf area was converted to dry mass using regression equations derived from measuring area and dry mass for the three host plants (Johnson et al., 2002). Leaves were then snap-frozen in liquid nitrogen before being freeze-dried and ball-milled to a fine powder for chemical analyses.

#### Chemical analysis

The C and N concentrations of leaves were determined using an Exeter Analytical CE440 Elemental Analyzer (EAI, Coventry, UK). The C and N concentrations were calculated using a standard (acetanilide) with known C and N concentrations. Benzoic acid was also used as a standard and to check the nitrogen blanks. For measurement of P, Mg, K, Ca, and Zn, powdered leaf samples (0.05 g) were subjected to acid digestion for 20 min at 180 °C in 3 ml of 15.8 M HNO<sub>3</sub> (Aristar grade; VWR International,

Poole, UK) followed by oxidation for 20 min at 180 °C with 1 ml of H<sub>2</sub>O<sub>2</sub> in closed vessels using a MARS-Xpress microwave oven (CEM, Buckingham, UK). Digested samples were diluted to a final volume of 50 ml with de-ionized water. Total mineral concentrations were quantified by inductively coupled plasma-mass spectrometry (Elan DRC-e; Perkin-Elmer, Beaconsfield, Bucks, UK).

Phenolic analysis was carried out using the enzymatic method described by Johnson et al. (2011), originally based on the protocol described by Stevanato et al. (2004). Phenolics were extracted in a 10:1 ratio from 50 mg freeze-dried leaves by incubating in 0.5 ml 50% methanol at 80 °C for 2.5 h. The aqueous phase was removed and cleared by centrifugation. A 1 ml enzymatic reaction was set up using 50 µl of the resultant supernatant mixed with 740 µl 100 mM potassium phosphate buffer (pH 8.0), 100 µl 30 mM 4-aminophenazone, 100 µl 20 mM hydrogen peroxide, and 1 U horseradish peroxidase dissolved in 10 µl potassium phosphate buffer. The reaction was incubated at room temperature for 15 min and absorbance read at a wavelength of 500 nm. Absorbance data were converted to catechin equivalents using a standard curve produced by serial dilution (0–0.10 mg ml<sup>-1</sup> catechin). All chemicals were obtained from Sigma-Aldrich (Dorset, UK).

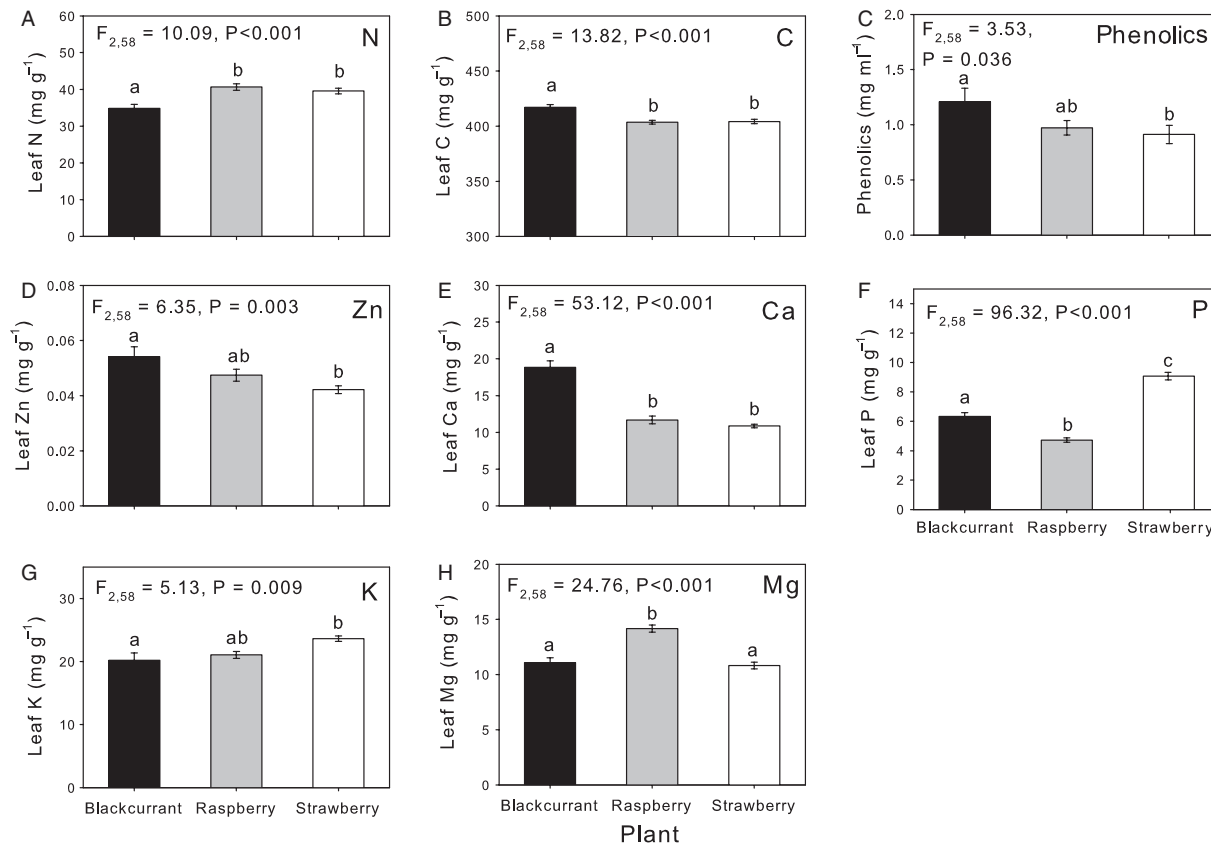
#### Statistical analysis

Plant mass and chemistry were analyzed using analysis of variance (ANOVA) with cage treated as a block term. Data from control plants and plants treated with weevils were pooled because there was no statistical effect of weevil presence on any aspect of plant chemistry measured. Tukey's post-hoc tests were used to indicate statistical differences among plant species. Weevil mortality on initial host plant species was analyzed with a generalized linear mixed model (GLMM) with a binomial error structure and logit link function. Weevil oviposition and feeding responses were scaled to reflect mortality during the experiment. Oviposition was analyzed with a GLMM with a Poisson error structure and log link function, whereas feeding was transformed (square root-log) and analyzed with a restricted maximum likelihood (REML) mixed model. Initial host plant species and current host plant species (and an interaction of the two) were fixed terms in the model, with cage included as a random term. Relationships between weevil responses and plant chemistry were analyzed with Spearman's rank correlations for each plant species.

## Results

#### Plant chemistry

The three host plant species all had approximately the same fresh aboveground mass at harvest (ca. 8 g)



**Figure 1** Foliar chemistry in blackcurrant, raspberry, and strawberry (mean concentrations  $\pm$  SE): (A) nitrogen, (B) carbon, (C) phenolic compounds (expressed as catechin equivalents), (D) zinc, (E) calcium, (F) phosphorus\*, (G) potassium, and (H) magnesium. Different superscripts within chemicals indicate significant differences among plants (Tukey's post-hoc tests:  $P < 0.05$ ). All chemicals:  $n = 30$ , except for phosphorus:  $n = 28$  (two outliers were removed). \*Data were log transformed prior to analysis.

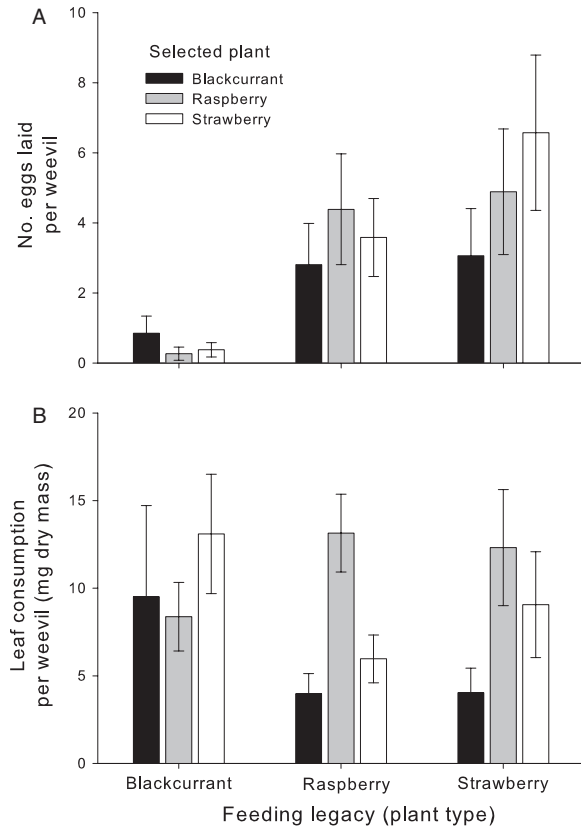
( $F_{2,58} = 1.09$ ,  $P = 0.34$ ). There were, however, very large differences in foliar chemistry among host plant species (Figure 1). Values for all minerals were above the critical level for growth, and were generally within the adequate to high range (Reuter & Robinson, 1986). Foliar N concentration was significantly lower in blackcurrant than raspberry or strawberry (Figure 1A), but C concentration was significantly higher in blackcurrant (Figure 1B). Phenolic compounds were highest in blackcurrant (Figure 1C), as was Zn (Figure 1D), and Ca (Figure 1E). Strawberry had the highest concentration of P (Figure 1F) and K (Figure 1G), whereas raspberry was particularly rich in magnesium (Figure 1H).

#### Weevil responses

Mortality on target host plant species was significantly higher among *O. sulcatus* that had originally been fed blackcurrant (12.1%) compared to those fed strawberry (2.9%) or raspberry (0%) ( $F_{2,24} = 3.27$ ,  $P = 0.038$ ).

Weevils previously fed blackcurrant laid significantly fewer eggs than those fed raspberry or strawberry (Figure 2A, Table 1), with the vast majority of eggs (97%) being recovered from the soil rather than the plant. In addition to initial host plant species influencing the overall oviposition capacity of weevils, there was a significant interaction between initial and current host plant species (Table 1), whereby weevils tended to oviposit on host plant species on which they had previously fed (Figure 2A). Feeding behavior was only influenced by the current host plant species (Table 1), with most feeding taking place on raspberry, most notably in those weevils previously fed raspberry (Figure 2B).

There was a weak positive relationship between oviposition and foliage consumption in raspberry ( $r_s = 0.369$ ,  $P = 0.058$ ), but not in blackcurrant ( $r_s = 0.252$ ,  $P = 0.22$ ) or strawberry ( $r_s = -0.265$ ,  $P = 0.19$ ). In raspberry and strawberry, leaf chemistry was not significantly related to either feeding or oviposition (results not



**Figure 2** Mean ( $\pm$  SE) *Otiorynchus sulcatus* (A) oviposition and (B) leaf consumption in three-way choice tests containing blackcurrant, raspberry, and strawberry plants in relation to initial host plant ( $n = 9$ ). See Table 1 for results of statistical analysis.

shown). In blackcurrant, however, foliage consumption was negatively correlated with concentrations of foliar C (Figure 3A;  $r_s = -0.486$ ,  $P = 0.012$ ) and Zn (Figure 3B;  $r_s = -0.508$ ,  $P = 0.008$ ) and positively correlated with foliar K (Figure 3C;  $r_s = 0.439$ ,  $P = 0.025$ ) and P concentrations (Figure 3D;  $r_s = 0.496$ ,  $P = 0.010$ ). Oviposition was negatively correlated with foliar C in blackcurrant (Figure 4;  $r_s = -0.434$ ,  $P = 0.027$ ).

## Discussion

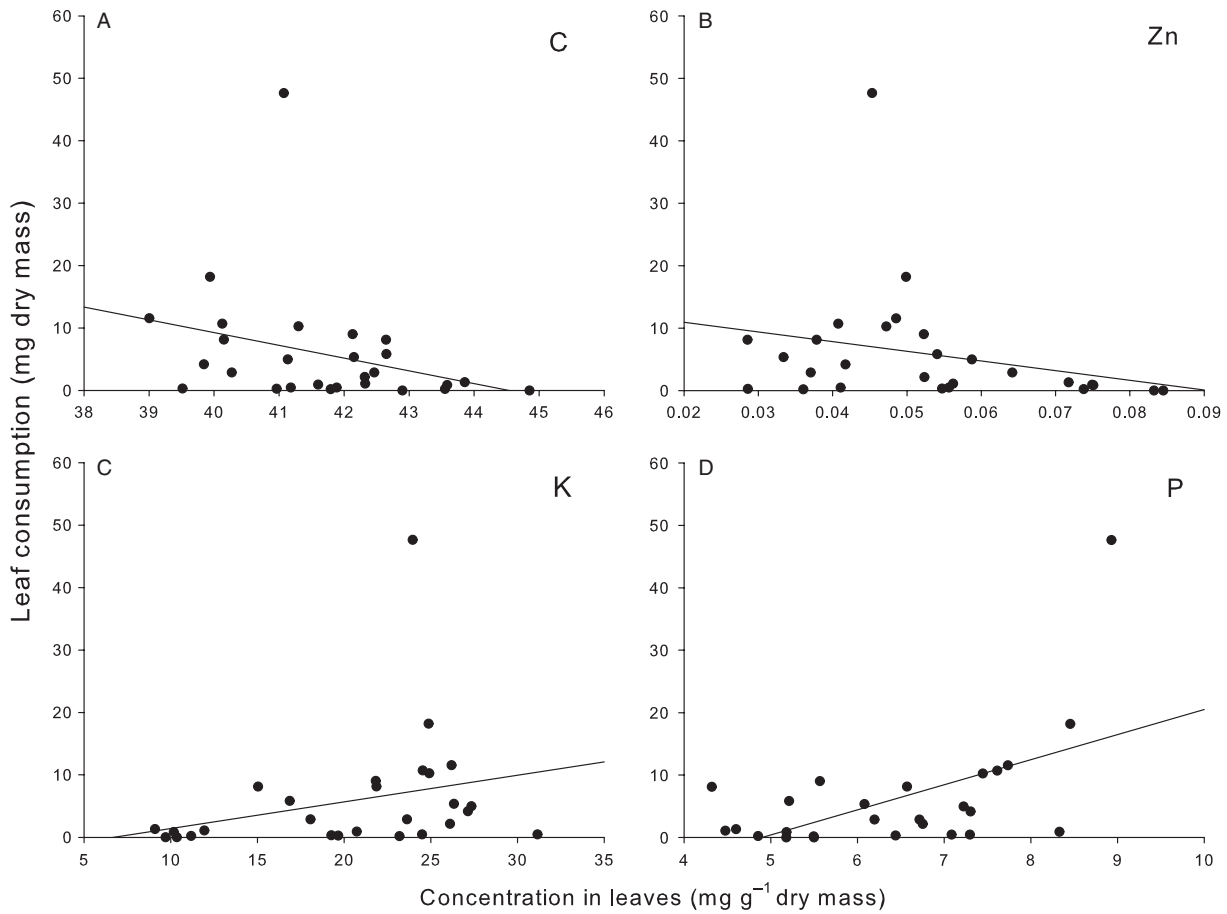
Host history affected the mortality and oviposition behavior of *O. sulcatus*. Specifically, adults suffered higher mortality and laid fewer eggs when initially fed blackcurrant. In terms of those aspects of plant chemistry that have commonly been shown to negatively affect phytophagous insects (low N, high C, high phenolics; Hartley & Jones, 1997), blackcurrant appears to comprise an inferior host, which most likely explains why *O. sulcatus* had lower performance on this species.

We expected *O. sulcatus* initially fed blackcurrant to exhibit some characteristics of food aversion learning, as is most often associated with generalist orthopterans (Bernays & Lee, 1988) and lepidopterans (Dethier, 1980; Raffa, 1987). Blackcurrant was a much poorer host than either raspberry or strawberry, so we expected *O. sulcatus* to avoid feeding on this host when given a choice. This was not supported by our results, as weevils reared on blackcurrant showed the least discrimination between hosts in terms of feeding preferences. Some polyphagous coleopterans seem incapable of aversion learning (Potter & Held, 1999), whereas results with other species are inconclusive (van Herk et al., 2010). However, suboptimal food is not necessarily harmful food, and animals can and will consume whatever is necessary to survive (Forbes, 2001). Indeed, host selection and feeding by *O. sulcatus* previously fed on blackcurrant seems more like induced feeding preference behavior (Jermy et al., 1968), whereas selection patterns by *O. sulcatus* reared on raspberry or strawberry were more plastic.

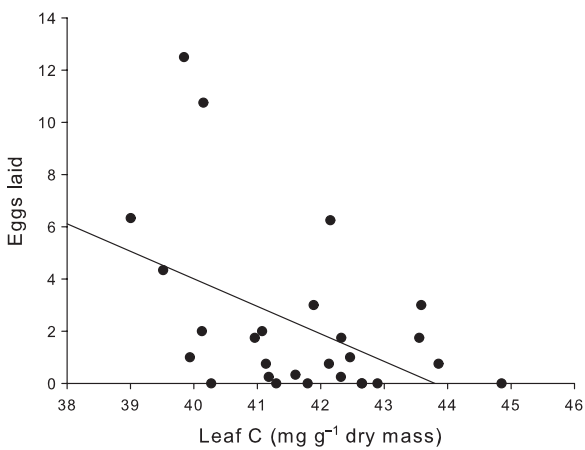
The adaptive significance of induced feeding preference under natural conditions is unclear (see discussion by Schoonhoven et al., 2005), but induced feeding preference may be advantageous if switching hosts decreases resource use efficiency (Scriber, 1982) or imposes fitness costs (Karowe, 1989). However, it seems disadvantageous for insect herbivores to bypass suitable host plants to select specific plant species (Jermy, 1987), especially when the insect has such a broad host range, as does *O. sulcatus*.

**Table 1** Summary of statistical analysis for oviposition (GLMM) and feeding (REML model) behavior of *Otiorynchus sulcatus* in relation to the effects of initial host plant and current host plant (see Figure 2). Where the interaction term was significant, factors were also analyzed separately (given in parentheses)

Behavioral response	Initial host		Current host in choice assay		Initial*current host	
	$F_{2,23}$	P	$F_{2,48}$	P	$F_{4,48}$	P
Oviposition	7.85 (8.20)	0.003 (0.002)	4.13 (3.67)	0.022 (0.033)	2.71	0.041
Leaf area consumption	0.09	0.91	8.97	<0.001	0.81	0.52



**Figure 3** Statistically significant correlations between leaf consumption and leaf chemistry in blackcurrant plants ( $n = 27$ ). Negative correlations with (A) carbon and (B) zinc, and positive correlations with (C) potassium and (D) phosphorus.



**Figure 4** Statistically significant negative correlation between number of eggs laid and leaf carbon in blackcurrant plants ( $n = 27$ ).

(van Tol et al., 2004). In this study, it would seem more likely to see host switching in *O. sulcatus* reared on an inferior host (blackcurrant) compared to adults reared on superior hosts (raspberry and strawberry). These results raise interesting questions about whether *O. sulcatus* adults fed on blackcurrant either began to tolerate poorer hosts or feeding on poorer hosts impacted their discrimination capabilities (e.g., neural capacity) later in their adult life.

Host selection in terms of oviposition was most significantly influenced by prior host feeding, suggestive of induced preference learning, but again this was observed most strongly in *O. sulcatus* fed on blackcurrant. The reduced egg load of weevils reared on blackcurrant may have also influenced the weevils' capacity to identify the best hosts, which has been reported in other species (Minkenberget al., 1992; Jallow & Zalucki, 1998). Induced oviposition preferences, albeit with some plasticity in

*O. sulcatus*, may reflect the fact that root-feeding offspring have limited mobility and are therefore less able to switch hosts post-oviposition (Johnson et al., 2006). Maternal insects may select hosts that they recognize as being more suitable for them rather than risk ovipositing on another species of unknown suitability.

Leaf consumption and oviposition were negatively correlated with foliar C concentrations in blackcurrant. Higher concentrations of C-based compounds, such as structural carbohydrates, often have negative effects on phytophagous insects, as structural compounds can make chewing more difficult and increase the C:N ratio, effectively diluting other nutrients (Awmack & Leather, 2002 and references therein). Although some C-based nutrients (e.g., sugars) stimulate feeding (Chapman, 2003), *O. sulcatus* seemed to avoid feeding on plants that had high concentrations of C, lending credibility to the former explanation. Zinc, known to negatively affect insect feeding and behavior (Mogren & Trumble, 2010), had a negative effect on leaf consumption by *O. sulcatus* in our study. Potassium and P were positively related to blackcurrant foliage consumption by *O. sulcatus*. It was not demonstrated whether such relationships hold true in no-choice situations, but the fact that blackcurrant had the highest concentrations of C and Zn, two conditions known to negatively affect insect performance (Awmack & Leather, 2002; Mogren & Trumble, 2010), is compatible with it being an inferior host in which plant chemistry was influencing *O. sulcatus*.

Although there was no direct correlation between phenolic concentrations and feeding or oviposition, it is noticeable that the comparatively high concentrations of phenolic compounds in blackcurrant were associated with lower survival and egg laying ability later in the adult weevil's life. The negative impact of phenolic compounds on some phytophagous insects, including some beetles, is well documented (Hartley & Firn, 1989; Serratos et al., 1993; Harborne, 1994; Matsuki & MacLean, 1994; Hartley & Jones, 1997; Kestring et al., 2009). Certain phenolic characteristics have the potential to be selected for in soft fruit crop breeding programs (Brennan, 2008; Hall et al., 2008). Unlike some crops, where insect feeding deterrents also have negative effects on crop quality and human diets (e.g., glycoalkaloids in potatoes; Jonasson & Olsson, 1994; Johnson et al., 2008), some polyphenolic compounds are highly desirable in soft fruit as potent antioxidants (Deighton et al., 2000; McDougall et al., 2005). This study suggests that manipulating host plant chemistry has the potential to affect both the fitness and reproductive behavior of *O. sulcatus*, which could ultimately be used in selective plant breeding or integrated pest management programs.

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