Mechanisms of woolly aphid [*Eriosoma lanigerum* (Hausm.)] resistance in apple

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*Ms. received: June 15, 2005; accepted: August 12, 2005*

**Abstract:** The sourcing of new resistant accessions and understanding their resistance mechanisms are significant aspects of a breeding strategy for durable resistance. Resistance of a number of apple accessions to the woolly apple aphid (*Eriosoma lanigerum* (Hausm.)) was assessed based on the biological parameters of the insect. Two experiments were conducted under glasshouse conditions in two consecutive years during January–February of 2002 and 2003. In Expt 1 in 2002, settlement, development and survival of the aphids were assessed on five apple accessions (Roter Eiserapfel (RE), Freiherr von Berlepsch (FvB), Braeburn (B), Willie Sharp (WS) and Royal Gala (RG)). RG was the most susceptible and WS the most resistant accession to WAA. RG and WS were included as references in Expt 2 in 2003, with 11 further accessions (*Malus floribunda* 821 OP (open-pollinated) G01-078 (MF), Korichnoe Polosatoje OP G01-104 (KP), Geneva (G), Raritan (R), Malus 6 (M-6), Twenty Ounce (TO), Winter Majetin (WM), Aotea (A), Irish Peach (IP), Court Pendu Plat (CPP) and Colonel Vaughan (CV)). Daily reproductive rate and colony establishment were added to the parameters assessed in Expt 1. The overall results showed resistance in G, MF, WS and KP to settlement and development with low survival at the larval stage of the aphid, whereas R showed resistance in all the parameters tested. RG and CPP have proved to be susceptible while A, WM, TO, M-6, IP and CV were partially resistant.

**Key words:** apple accessions, biological parameters, resistance, simulation, woolly apple aphid

1 Introduction

Woolly apple aphid (WAA) *Eriosoma lanigerum* (Hausm.) (Homoptera, Aphididae) is native to eastern North America and has now become a cosmopolitan pest of apples. It weakens the apple tree by feeding on bark and roots, which reduces tree fitness, thus preventing wounds from healing. In addition to feeding on small branches and wounds, WAA may be found year-round on roots of mature trees where they often go unnoticed. However, the root systems of nursery stock are more susceptible to damage, and severe root infestations can stunt or kill young trees. Resistant varieties have been used to prevent underground infestations and the Malling-Merton (MM) rootstock series were specifically bred to provide resistance to WAA (Staniland, 1923; Crane et al., 1936; Cummins and Aldwinckle, 1974).

Woolly apple aphids are effectively controlled by chemicals. As a result, the breeding of scion cultivars resistant to WAA has been of minor importance to date compared with major diseases, such as apple scab, powdery mildew and fire blight. However, the increased interest of growers in organic production, and the variable success of biological control, leaves breeding for resistance as a major means to control this pest in the orchard. The apple germplasm is a rich source of resistance to WAA (Le Pelley, 1927; Bus et al., 2000), which enables the development of cultivars with durable resistance. The necessity of breeding cultivars with pyramided resistance has been demonstrated by the development of biotypes of WAA that can overcome the *Er1* (Giliomee et al., 1968) or the *Er3* (Sandanayaka et al., 2003) genes. The fact that apple accessions behave differently in different countries (Knight et al., 1962) indicates that biotypes of WAA may be a common phenomenon. Moreover, strong resistances to WAA often have to be sourced from crabapples, which require more generations of backcrossing into a commercial cultivar than those from large-fruited cultivars. However, the combined use of partial resistance in large-fruited cultivars and biological control can overcome the long development time associated with using crabapples as the source of WAA resistance. Biological control by the parasitoid, *Aphelinus mali* (Haldeman) (Hym., Aphelinidae), has been found to play a significant role in reducing WAA populations above ground (Mols, 1996). However, the parasitoid is usually less effective in cooler climates.
because of a slower development rate compared with that of WAA early in the growing season, particularly on highly susceptible cultivars (e.g. ‘Fuji’). Hence, partial resistance of apple cultivars can delay the development of WAA sufficiently for A. mali to provide full control during the warmer period of the growing season.

Many researchers have tested the resistance of apple varieties to WAA (e.g. Le Pelley, 1927; Knight et al., 1962; Rock and Zeiger, 1974), and immunity is often assessed by a simple technique of inoculating gernplasm and observing it after a set time. However, more accurate methods based on biological parameters (e.g. survival, growth rate and fecundity), are required to assess partial plant resistance to insects (Kembabonta and Odebiyi, 2001; Wearing et al., 2003), including WAA (MacKenzie and Cummins, 1982). Other measures of resistance that have been used are the size of the galls induced by WAA (Staniland, 1923) and the electrical penetration graph (EPG) technique (Sandanayaka et al., 2003).

The main objective of this study was to source partial resistances in apple cultivars that, in combination with A. mali, may provide sufficient control of WAA during the growing season without the need for the application of chemicals. We compare the resistance of a number of apple accessions based on the assessment of several biological parameters including settlement, development, survival, daily reproductive rates and colony establishment. Most of the accessions were selected for their larger fruit size, which is expected to reduce the number of generations required for the development of new cultivars. Several accessions that had been reported resistant in previous evaluations, were included.

2 Materials and Methods

2.1 Plant material

Two experiments were performed. In Expt 1, WAA first instar settlement, larval survival and development were assessed on five apple accessions: ‘Roter Eiserapfel’ (RE), ‘Freiherr von Berlepsch’ (FvB), ‘Braeburn’ (B), ‘Willie Sharp’ (WS) and ‘Royal Gala’ (RG) in January–February 2002. Two of these accessions (WS and RG) were used again as references in the Expt 2 conducted in January–February 2003, to study WAA resistance in a further 11 accessions: Malus floribunda 821 OP (open-pollinated) G01-078 (MF), ‘Korichnoe Polosatoe’ OP G01-104 (KP), ‘Geneva’ (G), ‘Raritan’ (R), ‘Malus 6’ (M-6), ‘Twenty Ounce’ (TO), ‘Winter Majetin’ (WM), ‘Aotea’ (A), ‘Irish Peach’ (IP), ‘Court Pendu Plat’ (CPP), and ‘Colonel Vaughan’ (CV). Bench-grafted trees on WAA-resistant M.793 rootstock, were used in both experiments. The trees were grafted in the same year as the experiments were performed and grown in 5L plastic bags with potting mix in the nursery. All the experiments were carried out in the glasshouse, where the trees were grown under optimal conditions (25 ± 3°C with 16 : 8 h light : dark). The experiments commenced when the trees had one or two 1-month-old shoots. Five trees of each accession were randomly distributed in the glasshouse and the performance of the aphids on each tree was monitored.

2.2 Insects

A colony of WAA was established from a single apterous virginoparae adult on a RG tree in a glasshouse (at 25 ± 5°C). Later generations were used to infest either RG or B trees. Subsequent colonies were reared in the glasshouse at 25 ± 5°C with 16 : 8 h light : dark conditions inside fine net cages to avoid parasitism. Aphids reared on B trees for three or four generations were used for experiments. Young adult apterous virginoparae aphids were separated from the colony and left in closed plastic square Petri dishes (9 × 9 × 2 cm) for 12 h to produce nymphs. Twenty-five nymphs < 4 h old were collected in a plastic vial (3 × 1.5 cm) with a 3-mm-diameter hole at the bottom, plugged with cotton. The longest shoot of each tree was inoculated by attaching the plastic vial to a leaf node in the middle of the shoot with Blu-Tack® (Bostik (Australia) Ltd). The cotton plug was then removed to release the nymphs. A funnel-shaped trap made of laboratory film (Parafilm™ “M” (Pechiney Plastic Packaging, Wisconsin, USA)) was attached to the base of the tree at 3 cm above the graft union and filled with Vaseline™ (Lever Rexona, New Zealand) to trap the nymphs attempting to escape and moving from one tree to another.

2.3 Settlement

The first reading of WAA settlement was taken on the fifth day following inoculation. The number of aphids that had settled on each plant was counted along with the numbers left in the plastic vial attached to that plant. The percentage settlement was calculated by taking the numbers settled on the plant, as a percentage of the total number inoculated initially minus the number remaining in the plastic vials. Arcsine-transformed percentage data were subjected to a one-way ANOVA, followed by a multiple comparison of mean values using the Tukey–Kramer HSD test (SAS Institute, 1995).

2.4 Development

Each aphid that had settled on a plant was assigned a number including the name of the accession and the tree number. The development of WAA aphids from first instar to adult was observed daily in both experiments. Development through the instars of each aphid was studied by counting the number of exuviae (indicating ecdysis) around them, which were removed using a fine needle without disturbing the aphid. The duration of each developmental stage was counted as the number of days between two ecdyses. The data were tested using a one-way ANOVA and the mean values compared using a Tukey–Kramer HSD test (SAS Institute, 1995).

2.5 Survival

Survival in each developmental stage was recorded daily by counting the number of aphids feeding on each plant of the different apple accessions. The movements of aphids from one feeding site to another were recorded. Aphids that disappeared and could not be located on the trees were considered to be dead. Angular-transformed percentage survival rates of aphids in each instar on each accession were analysed in a one-way ANOVA and the mean values were compared using the Tukey–Kramer HSD test (SAS Institute, 1995).

2.6 Reproduction

In the Expt 2, once the nymphs had developed into adults, the observations were carried out in two groups, with each group comprising all the apple accessions but excluding those
that could not support the development of nymphs up to the adult stage. In group 1, the daily reproductive output of an individual aphid was counted and the offspring produced by each individual was then removed without disturbing the adult aphid. These observations were carried out for the 17 days from the onset of reproduction. All the recordings were taken at the same time of the day starting from 12.00 hours. The sequence of the reading (order of the plants) was not changed in order to minimize the variability in results. Offspring from aphids in group 2 were left for 12 days after the first observation in order to establish a colony. Because the second generation was likely to begin to reproduce on the 13th day of the first generation, the individual aphid colonies were collected into Petri dishes using a fine brush to avoid mixing nymphs of two generations. The total numbers of offspring of each virginooparar in each colony were counted under a microscope. Offspring produced by the adults over a 12-day period in both groups were analysed using the Poisson generalized linear model (GLM) procedure with the statistical package R (R Development Core Team, 2004). Differences between accessions and the variation between trees were examined by an analysis of variance of the GLMs produced. As an examination of a plot of the residuals associated with an anova showed them to be approximately normally distributed, Tukey’s HSD was used to make the multiple comparisons between the accessions.

2.7 Simulation

The combined effects of the various aspects of apple resistance to WAA were assessed by simulating aphid population development based on settlement, survival, development and reproduction rates. Settlement data were used to calculate a constant probability of survival throughout the simulation period. Beginning with an arbitrary number of 50 nymphs, the proportion surviving to adulthood in each generation was simulated by generating random numbers from a binomial distribution with that constant probability. Settlement data were used to calculate a constant probability of survival throughout the simulation period. For each settled immature aphid, sampling simulated the number of days until maturity with replacement from the development data. For each aphid reaching maturity, reproduction was simulated by sampling from group 1 of the reproduction data, which recorded the daily reproductive output of individual aphids up to 17 days. Aphids that failed to reach reproductive maturity on the accessions G, MF, KP, and WS were not included in the simulation. The total number of offspring after an arbitrary number of 45 days for each accession were compared using Tukey’s HSD as above. The numbers are not to be taken literally and serve only to compare the relative susceptibility of the accessions to WAA.

3 Results

3.1 Settlement

Percentage settlement of WAA varied among the accessions in both Expt 1 ($F_4, 97 = 13.53$, d.f. = 5, $P < 0.05$) and 2 ($F_4, 49 = 4.44$, d.f. = 5, $P < 0.05$). In Expt 1, the percentage settlement ranged from 33% on RE to 7% on WS (fig. 1a). In Expt 2, the percentage settlement was highest (41.08%) on RG and lowest (3.76%) on G (fig. 1b). Settlement numbers on WM, TO, CPP and RG were significantly different only from that on G. Although the mean percentage settlement differed considerably among the accessions in each experiment, there were also considerable variations within accessions, hence in many cases the differences were not significant at $P < 0.05$, except for those between the extremes. The means were then back transformed to obtain the percentage values for the histogram (fig. 1a, b). The error bars are not given in the histogram, as they would be meaningless on the back-transformed scale.

3.2 Survival

One hundred per cent survival was recorded on B and RG in Expt 1. Mortality in early larval stages was recorded on WS and RE accessions, while low levels of larval mortality occurred continuously during development on FVB. WS showed a similar pattern of survival in both experiments, but significantly low survival after the first instar in Expt 2 (table 1). In Expt 2, no survival was recorded on G after the first instar, or on MF after the second instar. The nymphs on KP were alive up to the fourth instal and only a single nymph on WS developed to the adult stage (2.45 mean percentage survival). Aphids on R, WM and M-6 showed a more or less steady mortality rate during all instars, which continued after the nymphs turned into adults.

Fig. 1. (a) Mean percentage settlement of first instar woolly apple aphid nymphs on five apple accessions in Expt 1. Mean values that share the same letter are not significantly different at $P < 0.05$ (Tukey–Kramer test). (b) Mean percentage settlement of first instar woolly apple aphid nymphs on different apple accessions in Expt 2. Mean values that share the same letter are not significantly different at $P < 0.05$ (Tukey–Kramer multiple comparison test)
Table 1. Mean percentage survival of each developmental stage of woolly apple aphid from the first instar to adulthood on different apple accessions

<table>
<thead>
<tr>
<th>Accession</th>
<th>First instar</th>
<th>Second instar</th>
<th>Third instar</th>
<th>Fourth instar</th>
<th>Adult</th>
</tr>
</thead>
<tbody>
<tr>
<td>WS</td>
<td>81.29 ± 0.85</td>
<td>52.39 ± 0.85</td>
<td>52.39 ± 0.85</td>
<td>52.39 ± 0.85</td>
<td></td>
</tr>
<tr>
<td>FvB</td>
<td>92.24 ± 0.78</td>
<td>68.81 ± 0.78</td>
<td>66.15 ± 0.78</td>
<td>66.15 ± 0.78</td>
<td></td>
</tr>
<tr>
<td>RE</td>
<td>97.34 ± 0.91</td>
<td>91.86 ± 0.91</td>
<td>91.86 ± 0.91</td>
<td>91.86 ± 0.91</td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>100.00 ± 0.00</td>
<td>100.00 ± 0.00</td>
<td>100.00 ± 0.00</td>
<td>100.00 ± 0.00</td>
<td></td>
</tr>
<tr>
<td>RG</td>
<td>100.00 ± 0.00</td>
<td>100.00 ± 0.00</td>
<td>100.00 ± 0.00</td>
<td>100.00 ± 0.00</td>
<td></td>
</tr>
<tr>
<td>MF</td>
<td>50.00 ± 0.00</td>
<td>44.34 ± 0.00</td>
<td>26.71 ± 0.00</td>
<td>26.71 ± 0.00</td>
<td></td>
</tr>
<tr>
<td>KP</td>
<td>100.00 ± 0.00</td>
<td>26.71 ± 0.00</td>
<td>26.71 ± 0.00</td>
<td>26.71 ± 0.00</td>
<td></td>
</tr>
<tr>
<td>WS</td>
<td>79.32 ± 0.21</td>
<td>24.52 ± 0.21</td>
<td>24.52 ± 0.21</td>
<td>24.52 ± 0.21</td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>81.94 ± 0.47</td>
<td>91.86 ± 0.47</td>
<td>91.86 ± 0.47</td>
<td>91.86 ± 0.47</td>
<td></td>
</tr>
<tr>
<td>FvB</td>
<td>50.00 ± 0.00</td>
<td>44.34 ± 0.00</td>
<td>26.71 ± 0.00</td>
<td>26.71 ± 0.00</td>
<td></td>
</tr>
<tr>
<td>RE</td>
<td>97.34 ± 0.91</td>
<td>91.86 ± 0.91</td>
<td>91.86 ± 0.91</td>
<td>91.86 ± 0.91</td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>100.00 ± 0.00</td>
<td>100.00 ± 0.00</td>
<td>100.00 ± 0.00</td>
<td>100.00 ± 0.00</td>
<td></td>
</tr>
<tr>
<td>RG</td>
<td>100.00 ± 0.00</td>
<td>100.00 ± 0.00</td>
<td>100.00 ± 0.00</td>
<td>100.00 ± 0.00</td>
<td></td>
</tr>
</tbody>
</table>

Table 2. Duration of the development stages of woolly apple aphid (Mean ± SE) on five accessions in Expt 1

<table>
<thead>
<tr>
<th>Accession</th>
<th>First instar</th>
<th>Second instar</th>
<th>Third instar</th>
<th>Fourth instar</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>WS</td>
<td>6.86 ± 0.36</td>
<td>3.33 ± 0.36</td>
<td>3.33 ± 0.36</td>
<td>3.44 ± 0.34</td>
<td>17.22 ± 1.06</td>
</tr>
<tr>
<td>FvB</td>
<td>6.03 ± 0.22</td>
<td>2.72 ± 0.13</td>
<td>3.14 ± 0.24</td>
<td>3.54 ± 0.29</td>
<td>15.32 ± 0.52</td>
</tr>
<tr>
<td>RG</td>
<td>4.91 ± 0.17</td>
<td>2.57 ± 0.09</td>
<td>2.51 ± 0.12</td>
<td>2.69 ± 0.11</td>
<td>12.69 ± 0.25</td>
</tr>
<tr>
<td>RE</td>
<td>4.94 ± 0.12</td>
<td>2.68 ± 0.06</td>
<td>2.50 ± 0.07</td>
<td>2.52 ± 0.06</td>
<td>12.65 ± 0.17</td>
</tr>
<tr>
<td>B</td>
<td>5.00 ± 0.15</td>
<td>2.49 ± 0.09</td>
<td>2.36 ± 0.08</td>
<td>2.49 ± 0.10</td>
<td>12.34 ± 0.19</td>
</tr>
</tbody>
</table>

had the highest simulated reproduction, while those on TO, M-6, IP and CV showed low to intermediate levels, which were significantly different from each other as well as from the rest of the accessions (fig. 3). As expected with Poisson distribution of count data, larger populations showed higher variability.

Reactions of the plants to WAA infestation was observed as galls started to appear on shoots of the accessions where aphids managed to feed on. Gall size, though not measured, exhibited a tendency to follow a pattern similar to that of the number of offspring produced.

### 4 Discussion

This study demonstrated that different apple accessions have different (combinations of) resistance mechanisms to WAA. To measure these aspects of WAA resistance, a sensitive method based on monitoring the settlement and development of the aphids on the accessions was employed.

Table 3. Duration of the development stages of woolly apple aphid (Mean ± SE) on 10 apple accessions in Expt 2

<table>
<thead>
<tr>
<th>Accession</th>
<th>First instar</th>
<th>Second instar</th>
<th>Third instar</th>
<th>Fourth instar</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>R</td>
<td>6.58 ± 0.45 b (n = 12)</td>
<td>3.33 ± 0.21 bd (n = 6)</td>
<td>3.00 ± 0.00 a (n = 4)</td>
<td>3.00 ± 0.00 a (n = 4)</td>
<td>15.25 ± 0.48 b (n = 4)</td>
</tr>
<tr>
<td>WS</td>
<td>5.33 ± 0.29 a (n = 9)</td>
<td>4.00 ± 1.00 b (n = 3)</td>
<td>3.00 a (n = 1)</td>
<td>2.00 a (n = 1)</td>
<td>13.00 abcd (n = 1)</td>
</tr>
<tr>
<td>IP</td>
<td>5.00 ± 0.17 ac (n = 15)</td>
<td>2.33 ± 0.13 ac (n = 15)</td>
<td>2.27 ± 0.12 a (n = 15)</td>
<td>2.80 ± 0.11 a (n = 15)</td>
<td>12.40 ± 0.21 c (n = 15)</td>
</tr>
<tr>
<td>A</td>
<td>4.47 ± 0.17 ac (n = 15)</td>
<td>2.67 ± 0.19 ad (n = 15)</td>
<td>2.60 ± 0.13 a (n = 15)</td>
<td>2.60 ± 0.13 a (n = 15)</td>
<td>12.33 ± 0.21 ac (n = 15)</td>
</tr>
<tr>
<td>RG</td>
<td>4.60 ± 0.13 ac (n = 15)</td>
<td>2.73 ± 0.15 ad (n = 15)</td>
<td>2.33 ± 0.13 a (n = 15)</td>
<td>2.40 ± 0.13 a (n = 15)</td>
<td>12.07 ± 0.18 acd (n = 15)</td>
</tr>
<tr>
<td>CPP</td>
<td>4.73 ± 0.15 ac (n = 15)</td>
<td>2.20 ± 0.11 ac (n = 15)</td>
<td>2.40 ± 0.13 a (n = 15)</td>
<td>2.60 ± 0.13 a (n = 15)</td>
<td>11.93 ± 0.23 acd (n = 15)</td>
</tr>
<tr>
<td>CV</td>
<td>4.50 ± 0.12 ac (n = 18)</td>
<td>2.44 ± 0.12 ac (n = 18)</td>
<td>2.33 ± 0.11 a (n = 18)</td>
<td>2.50 ± 0.12 a (n = 18)</td>
<td>11.78 ± 0.17 acd (n = 18)</td>
</tr>
<tr>
<td>WM</td>
<td>4.58 ± 0.22 ac (n = 12)</td>
<td>2.25 ± 0.13 ac (n = 12)</td>
<td>2.27 ± 0.14 a (n = 11)</td>
<td>2.30 ± 0.15 a (n = 10)</td>
<td>11.40 ± 0.22 ad (n = 10)</td>
</tr>
<tr>
<td>M-6</td>
<td>4.13 ± 0.22 c (n = 15)</td>
<td>2.47 ± 0.13 ac (n = 15)</td>
<td>2.40 ± 0.13 a (n = 15)</td>
<td>2.40 ± 0.13 a (n = 15)</td>
<td>11.40 ± 0.19 d (n = 15)</td>
</tr>
<tr>
<td>TO</td>
<td>4.13 ± 0.19 c (n = 15)</td>
<td>2.00 ± 0.00 c (n = 15)</td>
<td>2.40 ± 0.13 a (n = 15)</td>
<td>2.73 ± 0.12 a (n = 15)</td>
<td>11.27 ± 0.12 d (n = 15)</td>
</tr>
</tbody>
</table>

Accessions with letters in common in each column are not significantly different at P < 0.05 (Tukey-Kramer test). Acronyms of accessions are the same as in table 1.

Fig. 2. Box plots of the total number of offspring produced by the woolly apple aphids on different apple accessions in group 1 (daily reproductive output of an individual aphid) and group 2 (colony establishment). Acronyms of accessions are the same as in Fig. 1. The accessions with letters in common are not significantly different from each other at P < 0.05 (Tukey-Kramer test).
the apple trees was required (MacKenzie and Cummins, 1982) when compared with the more crude methods common to most germplasm evaluations, which usually only involve a single observation on each accession (e.g. Alspach and Bus, 1999). Monitoring biological parameters of an insect settling and feeding on a plant is an effective technique to measure the level of resistance or susceptibility of that plant to the insect (MacKenzie and Cummins, 1982; Kemabonta and Odebiyi, 2001; Wearing et al., 2003). Pimentel (1961) reported that plant resistance was based on both physiological and ecological factors as well as the interaction of both. In our study, we minimized the variability in results because of environmental factors by maintaining the same experimental conditions and carrying out the experiments at the same time of the year in a controlled glasshouse environment. Moreover, the WAA-resistant rootstock, M.793, was used for both experiments. Although no major effects of the rootstock on the expression of resistance are expected (Le Pelley, 1927), our findings may not be applicable to other rootstocks. Moreover, the aphids used in our experiments belonged to the same biotype, having arisen from a single apterous virginoparae adult that founded the colony. Therefore, any behavioural differences that might have arisen from aphids reared from virginoparae adults collected from different source populations, were also limited. On the contrary, the results of this study only represent one biotype of WAA in New Zealand, and the findings might have been different if more complex populations had been used. No information is available on the genetic diversity of WAA in New Zealand, but a biotype capable of infesting accession A (Sandanayaka et al., 2003) has been reported previously.

Three parameters (settlement, survival and development rate) that had proven to be reliable in assessing the level of WAA resistance in apple cultivars (Sandanayaka et al., 2003), were considered in Expt 1. As the settling rates varied considerably within each of the apple cultivars, only the most resistant accessions, WS and G in Expts 1 and 2, respectively, could be separated from the other accessions. The survival and development data showed a more clear separation in partial resistance. The same applied to the two parameters (reproduction and colony establishment) included in Expt 2. RG was chosen over B from Expt 1 as a reference for Expt 2, because the aphid colony was reared on B, which could have a confounding effect on the results of Expt 2.

First instar nymphs of WAA took longer time to develop than the older instars irrespective of which accession they fed on. This period was longer on accessions shown to be more resistant (tables 2 and 3), confirming previous findings of Asante et al. (1991) and Sandanayaka et al. (2003). In both experiments, RG displayed consistently susceptible characteristics. Levels of resistance in WS indicated by settlement rates were also consistent across experiments, but survival and duration of the development of nymphs differed. Once the nymphs passed the third instar on this accession, they grew into adults in both experiments.

Wearing et al. (2003) suggested that slow development, reduced growth and higher mortality of leafroller larvae (Lepidoptera, Tortricidae) on apple cultivars were caused by antibiosis. Moreover, low settlement rate of first instar larvae and low fecundity of adult leafroller moths were caused by the antixenosis properties of the host plant. This phenomenon could be applied to our study to characterize resistance in different accessions according to WAA performance in Expt 2. With low settlement rates, slow development and low survival of WAA, the accessions G, MF and R were not significantly different as host plants from WS, which could be interpreted as expressing both antixenotic and antibiotic characteristics towards WAA. MF and KP did not support the development of WAA (table 1) confirming their resistance to WAA (Bus et al., 2000). First instar nymphs settled successfully on KP, R, WM and M-6 irrespective of the suitability of these accessions for subsequent feeding and development. Slow development of WAA on R increases the potential of biological control of WAA with its parasitoid A. mali, which appears later in the season.

A low level of survival was recorded on G, MF, KP, WS, R, WM and M-6 suggesting antibiosis. Similar survival rates were reported by MacKenzie and Cummins (1982) with WAA and Wearing et al. (2003) with leaf rollers on apple cultivars.

Our findings with aphids on WM confirm previous records of Staniland (1923); Le Pelley (1927); Crane et al. (1936); Knight et al. (1962); Cummins and Aldwinckle (1974) and Asante (1994) on resistance to WAA colony establishment. Although the settlement and development of nymphs on TO, IP and A were not significantly different from those on RG the low reproduction of WAA, resulting in a lower level of colony establishment, indicated an expression of resistance. Very little research has been performed on understanding the basis of WAA resistance in apple and how this affects the different aspects of aphid development on the host. Lack of nutrients rather than resistance factors per se, for example, may have

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**Fig. 3.** Box plot of the total number of offspring simulated from 50 woolly apple aphids on each apple accession after 45 days (○; outliers). Acronyms of accessions are the same as in fig. 1b.
affected WAA fecundity on some accessions. The influence of dietary constituents on polymorphism and reproduction in aphids has been demonstrated in studies on plants resistant to aphids in general (Auclair, 1964), while having an effect on the colonization rates of WAA in specific (Sen Gupta and Miles, 1975). The resistance in Northern Spy has been attributed to a chemical substance present in the bark of this cultivar, whereas wood structure was not thought to be implicated in resistance (Roach, 1937). However, it has been suggested that resistance is correlated with the amount of sclerenchyma present in the circumference of the stem, the effectiveness of which may be reduced by tears in the tissue (Staniland, 1924).

In the simulation of total reproduction experiments, A demonstrated a resistant property (fig. 3) which is significantly lower than that of TO, M-6, IP, CV, RG and CPP. Sandanayaka et al. (2003) reported that first instar WAA nymph settlement on A was significantly lower than that on RG. In concordance with Taylor (1981), this evidence further corroborates the possible role of antixenosis in A resistance to WAA. CPP was not significantly different from RG in all the parameters as well as simulation, confirming susceptibility.

Although the simulation was considered to give a better representation of population development, there will also be a tendency for it to give an artificially low estimate, as the history is recorded up to 17 days only. The simulation assumed that no offspring were produced after 17 days. In contrast, the numbers of the offspring will be somewhat artificially high as the estimate, as the history is recorded up to 17 days only. Therefore a similarEnemies, or the response of offspring to crowding were produced after 17 days. In contrast, the numbers of the offspring will be somewhat artificially high as the

References


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