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Ovipositional preferences, damage thresholds, and detection of the tomato–potato psyllid *Bactericera cockerelli* (Homoptera: Psyllidae) on selected tomato accessions

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Abstract

The tomato–potato psyllid *Bactericera* [*Paratrioza*] *cockerelli* (Sulc) has recently caused losses exceeding 50% on fresh market tomatoes in California and Baja, Mexico by injecting a toxin that results in a condition known as ‘psyllid yellows’. The objectives of this study were to: (i) document oviposition preferences on a range of tomato cultivars; (ii) determine threshold levels for psyllid densities that would cause psyllid yellows on tomatoes within the first three weeks following transplanting; and (iii) identify the most important ‘psyllid yellows’ symptoms that might be used in surveying and monitoring for this pest. Plant lines tested included the commonly-planted commercial cultivars ‘Shady Lady’ and ‘QualiT 21’, an older, previously commercial cultivar ‘7718 VFN’, a common cultivar planted by consumers ‘Yellow Pear’, and a wild type plant accession, PI 134417. When given a choice, psyllids significantly preferred ‘Yellow Pear’ and avoided PI 134417 for oviposition. Under no-choice conditions psyllids laid significantly fewer eggs on PI 134417, but all the other plant lines were equally good substrates for laying eggs. Thus, oviposition preference is not likely to provide a functional management strategy in large plantings. On ‘Shady Lady’, psyllids preferred to oviposit on plants already infested with adults. On both ‘Shady Lady’ and ‘7718 VFN’ oviposition was significantly greater on plants previously infested by nymphs as compared to uninfested control plants. This suggests that, at least for some cultivars, there is a physiological change in plant attractiveness following psyllid feeding. ‘Yellow Pear’ and ‘QualiT 21’ were relatively tolerant of psyllids, requiring 18 nymphs per plant to produce the disease symptoms. Only eight nymphs per plant were needed on ‘Shady Lady’ and ‘7718 VFN’. For all cultivars, the pest density showed strong correlations with measurements such as the number of yellowing leaves and leaflets and distorted leaves, which were as good as or better than the first factor extracted from principal component analysis. Therefore, such measurements have the potential to simplify field surveys.

Keywords: psyllid yellows, tomato, plant resistance, economic injury level

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Introduction

The tomato–potato psyllid *Bactericera [Paratrioza] cockerelli* (Sulc) (Homoptera: Psyllidae) has recently developed high densities on fresh market tomatoes in California and Baja, Mexico. The populations on the west coast of North America are genetically different from the central and eastern populations, suggesting that a new biotype may have developed (Liu *et al*., 2006). Pletsch (1947) reported that this psyllid could feed on species in 20 plant families, but that the nymphal stage was considerably longer on non-solanaceous hosts. He also noted that the adult female preferred potato plants to other solanaceous hosts for laying eggs. Studies focusing specifically on tomatoes indicated behavioural responses of the psyllid varied with tomato line (Liu & Trumble, 2004). In addition, different psyllid growth and development rates were found on these cultivars (Liu & Trumble, 2005), but no reports are available regarding oviposition preferences or damage thresholds for cultivars used in California or Baja, Mexico.

Psyllid nymphs (and perhaps adults) inject a toxin while feeding on the leaf that can cause death of tomato transplants, and either cause no fruit production or overproduction of very small, non-commercial grade fruit by larger plants (Pletsch, 1947; Al-Jabar, 1999). Garzon *et al*. (1986, 2004) suggested that a phytoplasma may be involved in mainland Mexico populations, but this claim has not been published in a peer-reviewed journal. The symptoms produced in response to the toxin are collectively known as ‘psyllid yellows’, and include retarded growth, erectness of new growth, chlorosis, purpling of leaves, distortion of foliage, and stimulated flower bloom (Al-Jabar, 1999). Previous studies with what are now heirloom lines (or unavailable cultivars) suggested that as few as 30 psyllid nymphs per plant could cause these symptoms on established plants (Blood *et al*., 1933). Carter (1950) stated that symptoms occurred on transplants from the feeding of a single nymph. Thus, transplants historically have been considered the plant stage most at risk. To the best of our knowledge, no studies have been conducted in the last half century on damage thresholds on any commercial tomato plant lines or with the genetically different psyllid populations occurring in California and Baja, Mexico.

The objectives of this study therefore were to: (i) document oviposition preferences on a range of tomato lines; (ii) determine threshold levels for psyllid densities that causes psyllid yellows on tomatoes within the first three weeks following transplanting; and (iii) identify the most important ‘psyllid yellows’ symptoms to be used in surveying and monitoring for this pest.

Materials and methods

Insects

Adults collected from fresh market tomatoes in Orange County, California, USA in December 2002 were used to establish a laboratory colony. The colony was maintained at 25 ± 1°C, and a photoperiod of 14 : 10 (L : D). All of the following tests were conducted under the same conditions. Host plants were potatoes (*Solanum tuberosum*, VanZyverden Russett, Meridian, MS). A plant genus other than *Lycopersicon* was chosen as the rearing host because Tavormina (1982) and Via (1984a,b) demonstrated that some insect species developed a preference for the host species on which they were reared. Adults used in all tests were standardized by selection of insects with teneral coloration (light or pale green) indicating that they had emerged within the previous 2–3 days. Because oviposition does not occur within the first 3 days (Knowlton & James, 1931), selection of 2- to 3-day- old adults eliminated problems with variability in oviposition status.

Plants

Tomato plants used in all tests were grown in 15-cm diameter pots with UC Soil Mix (Matkin & Chandler, 1957) and fertilized three times weekly with Miracle Gro nutrient solution (rate: $3.8\,\mathrm{g\,l^{-1}}$, Scotts Company, Ohio, USA). All plants used were between two and six weeks of age. Although damage can occur at any time, young plants are particularly susceptible (Carter, 1950).

Five tomato varieties were tested, including four cultivars of *Lycopersicon esculentum* Mill. (Petoseed ‘7718 VFN’, Petoseed ‘Yellow Pear’, Rogers ‘QualiT 21’, and Sunseeds ‘Shady Lady’) and a *Lycopersicon hirsutum* f. *glabratum* accession, PI 134417. The ‘Yellow Pear’ cultivar is a variety commonly planted by consumers in personal gardens. The cultivars ‘QualiT 21’ and ‘Shady Lady’ are widely used commercial varieties in California, while Petoseed ‘7718 VFN’ is an older commercial variety known to be susceptible to many insect pests (Eigenbrode *et al*., 1993). PI 134417 is a wild-type accession with considerable insect resistance that has been studied extensively (Farrar & Kennedy, 1992; Eigenbrode & Trumble, 1993). All of these varieties are available commercially and from the Charles Rick collection at University of California, Davis, California.

Bioassay

For no-choice oviposition tests of plant lines, newly emerged adults were held on fresh potato leaves in a Petri dish for 3 days, after which 10 adults (5 males and 5 females) were caged on each plant (one plant per replicate) and allowed to oviposit for 5 days. All eggs were then counted. Ten replicates were conducted for each plant line tested. For the no-choice tests, experiments were initiated with plants with 4–5 fully expanded leaves (3–4 weeks of age).

In choice tests for oviposition on plant lines, five different plants (one plant from each plant line), which were similar in size and vigour, were evenly placed along the circumference in an opaque plastic container with a height of 37 cm and with a diameter 45 cm. The top of the container was covered with cheese cloth. As in the previous test, newly emerged adults were held on fresh leaves in a Petri dish for 3 days, after which 20 adults (10 males and 10 females) were released in the middle of each tub and allowed to oviposit for 3 days, the eggs were then counted. Each treatment was replicated 10 times. For the oviposition tests, experiments were initiated with plants with 4–5 fully expanded leaves (3–4 weeks of age).

In a related study, psyllid adults were also given a choice between infested plants and healthy, non-infested plants. Since the psyllid is never likely to experience the chance to make a choice in the field between the infested and the non-infested plants of the wild accession, the wild accession was not included in the tests of choice between infested and control plants. Paired infested plants and healthy plants of similar size of each plant line were placed in the containers described in the previous experiments. Twenty adult psyllids were then released in the middle of the container and allowed to oviposit for 3 days. Five replicates were conducted for each treatment. For each plant line, three treatments were tested. The first treatment examined the effect of a previous adult infestation: one plant was previously infested by 15 preovipositional adults for 3 days (adults then removed) and compared with a control plant that was never infested. In a second treatment a non-infested control plant was compared against a plant infested with 30–35 third-instar nymphs which remained on the plant throughout the test. The third treatment examined the effect of a previous nymphal infestation: one plant was previously infested by 30–35 nymphs for 3 days, the nymphs were then removed, and this plant was compared with a control plant that was never infested. A 3-day infestation was chosen because induced plant responses generally occur rapidly in tomatoes with other sucking insects (Cooper & Goggin, 2005) and at least peroxidase and lipoxygenase activities can remain at high levels for an extended period (Stout *et al.*, 1998). Thirty to 35 nymphs were used to infest the plants, because such densities are frequently reached before pesticide application in commercial planting of tomatoes in Baja, Mexico (J. Trumble, personal observation). No information is available about how many psyllid adults it would take to induce plant responses: 15 adults were chosen as a maximum that would typically be tolerated by growers on young plants in commercial crops.

To determine the damage threshold for psyllid nymphs, plants about two weeks old were exposed to ovipositing adults and numbers of resulting nymphs were manipulated by removing extraneous eggs or nymphs. Initially, 0, 8, 18, 28, 38, 48, 58 or 68 nymphs were maintained on plants. One week later, the numbers of nymphs per plant were examined to make certain that the only replicates used contained 0, 5–8, 13–18, 23–28, 33–38, 43–48, 53–58 and 63–68 nymphs on 8-nymph, 18-nymph, 28-nymph, 38-nymph, 48-nymph, 58-nymph and 68-nymph treatments, respectively. Nymphs were maintained at these densities for 3 weeks. Thus, there were eight density treatments for each cultivar, and each treatment was replicated at least five times. After 3 weeks, plant heights, the length of three uppermost leaves, and the length of the uppermost leaflet of the three uppermost leaves of the control plants were measured. At the end of the experiments, the 6-week-old control plants averaged 10 leaves for 'Yellow Pear', and 6 for the remaining three cultivars ('QualiT 21', 'Shady Lady' and '7718 VFN'). On plants that became stunted, measurements were standardized by including only the equivalent leaves or leaflets from leaf number 8, 9 or 10, depending on which were available (in our numbering system, leaf no. 1 was the oldest on the plant). In addition, the total numbers of leaves, yellow leaves, yellow leaflets, curled leaves, and curled leaflets were counted. A leaf or leaflet was defined as curled if over 30% of the leaf edge was curled upwards. A leaf or leaflet was defined as yellow if 50% or more of the leaf was yellow.

Statistical analysis

Choice test data were analysed using Mann-Whitney U-test, and no-choice test data using ANOVA ($P < 0.05$ level, StatView, 1998). Due to the non-normal distribution of plant measurement data, pairwise comparisons of plant measurements between controls and other treatments were made using the Mann-Whitney U-test (StatView, 1998).

For the damage threshold experiments, principal component analysis (PCA) (Proc PRINCOMP) and correlation analysis (Proc Pearson CORR) were performed for each cultivar separately as well as for all cultivars combined after the raw counts and measurements were log transformed (SAS, 2002). The factor weightings for each replicate in the PCA were calculated and the resulting values were used as a composite plant factor in subsequent correlation analyses. Using this approach, the correlations of pest density and the first factor extracted from PCA could be compared with correlations of direct plant measurements and pest density. The linear regression analyses (Proc Reg) between the numbers of yellowing leaflets and pests were conducted using SAS (2002).

Results

Ovipositional preference

When given a choice, psyllids significantly preferred 'Yellow Pear' and avoided PI 134417 for oviposition (fig. 1, Mann-Whitney U-test, $P < 0.01$). No differences in oviposition were detected among the other plant lines. Under no-choice conditions psyllids laid significantly fewer eggs on PI 134417, but all the other tested plant lines were equally good substrates for laying eggs (fig. 2, $F = 10.91$; $df = 4, 45$; $P < 0.001$).

The history of psyllid infestation affected psyllid oviposition for two of the plant lines tested. In choice tests between plants previously infested by adults and control plants that were never infested (fig. 3), the psyllids preferred the previously-infested plants for the cultivar 'Shady Lady' (Mann-Whitney U-test, $P = 0.047$), but no such preferences were found on other cultivars. If 30–35 nymphs per plant were present at the time of oviposition, no significant differences in oviposition were seen for any plant line except 'Shady Lady', where adult psyllids preferred to oviposit on uninfested control plants (fig. 4, Mann-Whitney U-test, $P = 0.047$). In the experiments where nymphs were allowed to feed on plants for 3 days, and then were removed, the psyllid laid more eggs on infested plants than on control plants on 'Shady Lady'(Mann-Whitney U-test, $P = 0.048$) and

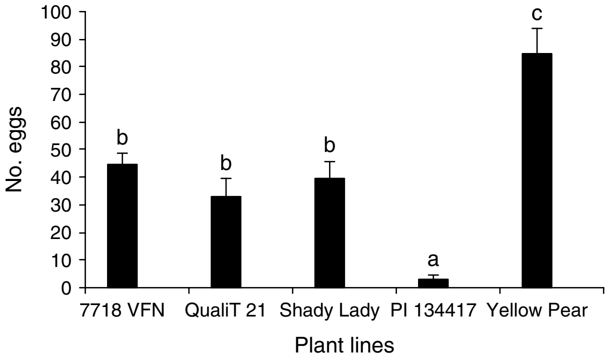

Fig. 1. Psyllid ovipositional preference among tomato plant lines under choice conditions. Values are significantly different if letters above bars differ (Mann-Whitney U-test, $P < 0.05$).

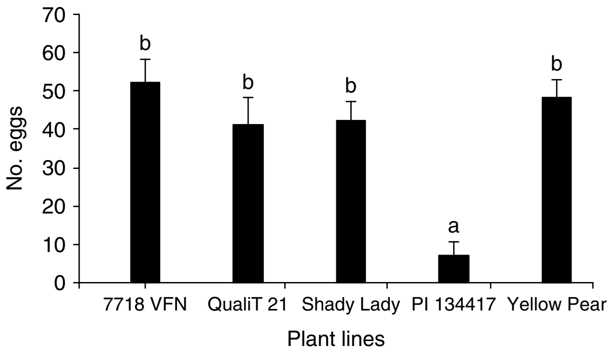

Fig. 2. Psyllid ovipositional preference among tomato plant lines under no-choice conditions. Values are significantly different if letters above bars differ (ANOVA, $P < 0.001$).

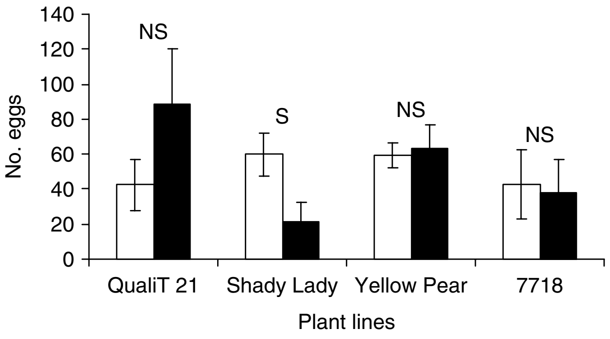

Fig. 4. Psyllid ovipositional choice between nymph-infested and control tomato plants. S indicates a significant difference between control (□) and treatment (■) (Mann-Whitney U-test, $P < 0.05$); NS, no significant difference.

'7718 VFN' (Mann-Whitney U-test, $P = 0.043$) (fig. 5), but not on the other two cultivars.

Damage threshold

For the cultivars 'Shady Lady' and '7718 VFN' exposed to treatments of eight or more nymphs per plant, the infested plants had significantly higher numbers of yellowing leaves and leaflets, greater numbers of distorted leaves, the lengths of the three uppermost leaves were significantly shorter, and total plant height was significantly lower (table 1, Mann-Whitney U-test, $P < 0.05$). For the cultivars 'Yellow Pear' and 'QualiT 21', significant differences in plant measurements were detected between infested and control plants once densities increased to 18 nymphs per plant (table 1, Mann-Whitney U-test, $P < 0.05$). The damage threshold was therefore defined as the pest density at which significantly more yellowing leaves and leaflets were found than control, and height of treated plants was significantly smaller.

Principal component analysis

In this analysis, the first four principal component axes explained 99% of the total variation in plant measurements (table 2). The number of yellowing leaves and leaflets, and the numbers of distorted leaves contributed the most to the first principal component (PC 1). The PC 2 comprised the number of upcurled leaves versus the number of yellowing leaves and leaflets, and was dominated by the number of upcurled leaves and leaflets. The number of distorted leaves and the length of three uppermost leaves contributed the most to PC 3 and PC 4 respectively.

Correlation and regression analyses

Correlations of psyllid nymph density and plant measurements are shown in table 3. On '7718 VFN', the best correlation was found between the number of distorted leaves and pest density ($r = 0.86$), but the numbers of yellowing leaves ($r = 0.81$) and leaflets ($r = 0.81$) also correlated well with pest density. The number of yellowing leaves ($r = 0.86$) and leaflets ($r = 0.86$) correlated best with nymphal density for 'Yellow Pear', followed by plant height ($r = -0.69$). On 'QualiT 21, plant height correlated best with nymphal density ($r = -0.75$), followed by the number of yellowing leaves ($r = 0.60$) and leaflets ($r = 0.60$). For 'Shady Lady', the best correlation was found between the number of distorted leaves and nymph density ($r = 0.85$),

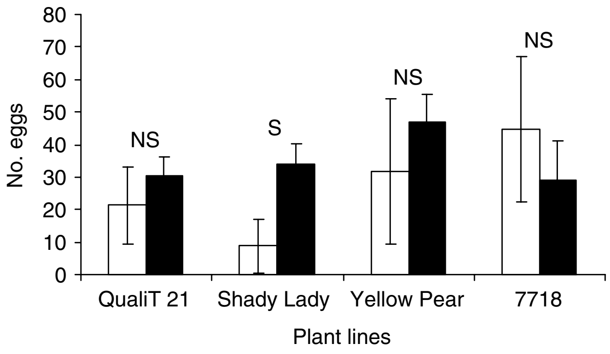

Fig. 3. Psyllid ovipositional choice between tomato plants previously infested by adults and control plants. S indicates a significant difference between control (□) and treatment (■) (Mann-Whitney U-test, $P < 0.05$); NS, no significant difference.

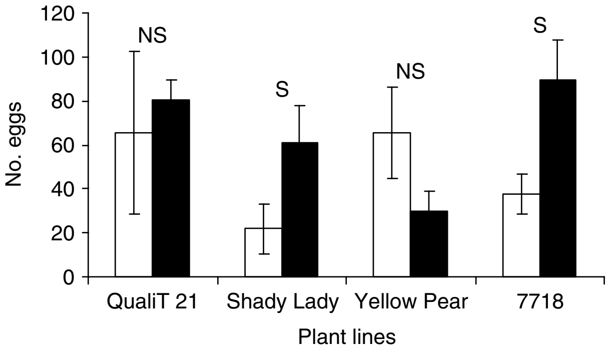

Fig. 5. Psyllid ovipositional choice between tomato plants previously infested by nymphs and control plants. S indicates significant difference between control (□) and treatment (■) (Mann-Whitney U-test, $P < 0.05$); NS, no significant difference.

Table 1. Quantifying leaf symptoms and plant height for five psyllid densities on four tomato cultivars[a].

Cultivar	Treatment	No. leaves yellowing (mean ± SE)	No. leaflets yellowing (mean ± SE)	Plant height (mean ± SE) (cm)	No. leaves distorted (mean ± SE)	Length of three uppermost leaves (mean ± SE) (cm)
Yellow Pear	Control	0	0	21.3 ± 0.8	0	20.4 ± 1.9
Yellow Pear	8-nymph	0	0	21.5 ± 0.5	0	25.1 ± 2.4
Yellow Pear	18-nymph	1.8 ± 0.5*	9.8 ± 2.8*	16.8 ± 0.6**	0.6 ± 0.4	13.1 ± 1.7*
Yellow Pear	28-nymph	1.7 ± 0.7*	7.8 ± 3.9*	14.9 ± 1.3**	0.8 ± 0.4*	8.9 ± 2.9**
QualiT 21	Control	0	0	15.2 ± 0.3	0	26.3 ± 2.2
QualiT 21	8-nymph	0.2 ± 0.2	0.2 ± 0.2	14.0 ± 0.5	0	30.0 ± 2.0
QualiT 21	18-nymph	1.2 ± 0.4*	6.2 ± 2.5*	10.6 ± 1.3*	1.3 ± 0.6*	13.3 ± 5.2*
QualiT 21	28-nymph	2.0 ± 0.2**	10.0 ± 2.1**	11.8 ± 1.7*	2.2 ± 0.5**	16.0 ± 7.8*
Shady Lady	Control	0	0	14.8 ± 0.5	0	39.5 ± 1.5
Shady Lady	8-nymph	1.4 ± 0.4*	3.0 ± 1.0*	9.1 ± 0.8**	1.2 ± 0.4*	31.8 ± 1.4**
Shady Lady	18-nymph	1.5 ± 0.4*	5.1 ± 0.6*	9.6 ± 1.0**	1.5 ± 0.4*	16.8 ± 3.5**
Shady Lady	28-nymph	1.7 ± 0.6*	5.7 ± 0.4*	10.2 ± 1.3*	2.0 ± 0.5**	21.3 ± 2.1**
7718 VFN	Control	0	0	17.1 ± 0.5	0	30.6 ± 2.6
7718 VFN	8-nymph	1.3 ± 0.3**	5.3 ± 2.2**	10.3 ± 0.6**	1.3 ± 0.3**	19.9 ± 2.2**
7718 VFN	18-nymph	1.5 ± 0.3**	7.3 ± 1.9**	11.1 ± 2.0**	1.8 ± 0.5**	23.9 ± 5.2**
7718 VFN	28-nymph	2.1 ± 0.1**	10.1 ± 1.2**	11.2 ± 0.6**	2.1 ± 0.4**	23.5 ± 3.5**

[a] * Significant difference compared to control (Mann-Whitney U test, $P < 0.05$); ** $P < 0.01$.

followed by plant height ($r = -0.82$) and number of leaves ($r = -0.62$). If measurements for all cultivars are combined, nymphal density correlated well with the number of yellowing leaves ($r = 0.71$) as well as the number of distorted leaves ($r = 0.71$) and yellowing leaflets ($r = 0.71$). However, a higher correlation coefficient was found between nymph density and the first factor extracted from the principal component analysis. When PCA was conducted individually for each cultivar, correlations of most plant measurements and nymphal densities were found to be as good as that of correlations of nymphal densities and the first factor extracted from PCA on '7718 VFN', 'Yellow Pear', 'QualiT 21' and 'Shady Lady'.

The linear relationship between the numbers of yellowing leaflets and pests was found to be as follows: Log (No. yellowing leaflets) = −1.6616 + 0.8801*Log (No. pest) for 'QualiT 21' ($R^2 = 0.36$, $P < 0.01$), and Log (No. yellowing leaflets) = −1.0088 + 0.8609*Log (No. pest) for 'Yellow Pear' ($R^2 = 0.74$, $P < 0.01$).

Discussion

Plant preference

When psyllids have the option of ovipositing on all plant lines, they preferred 'Yellow Pear', and avoided PI 134417 (fig. 1). This finding is consistent with the results of previous studies (Liu & Trumble, 2004, 2005), where PI 134417 proved highly resistant to psyllids and 'Yellow Pear' was highly susceptible. We suspect that the resistance of PI 134417 identified in our studies has the potential to be incorporated into commercial tomato cultivars. However, under no-choice conditions, all plant lines except the wild type PI 134417 were equally good substrates for laying eggs. Therefore, when tomatoes are planted over large areas, selecting a specific cultivar based on a lack of an ovipositional preference in choice tests is likely to fail to provide an effective management. Although this approach has been attempted for some crops, there is ample evidence that oviposition preference of adults and performance of

Table 2. Results of principal component analysis (PCA) used to describe the main sources of variation in plant measurements for all cultivars combined.

Measurements	Principal components[a]			
	PC 1	PC 2	PC 3	PC 4
Total number of leaves	−0.0080	−0.0035	0.0394	0.0096
Number of yellowing leaves	0.5409	−0.1832	0.2879	0.0185
Number of yellowing leaflets	0.6470	−0.2220	0.3487	0.0321
Number of upcurled leaves	0.1778	0.6453	0.0829	−0.0555
Number of upcurled leaflets	0.1925	0.7007	0.0935	−0.0780
Plant height	−0.0268	−0.0064	0.0570	0.0318
Length of three uppermost leaves	−0.0738	0.0708	0.1344	0.7139
Length of three uppermost leaflets	−0.0730	0.0672	0.1140	0.6609
Number of distorted leaves	0.4568	0.0065	−0.8626	0.2073
% variance explained in PCA				
Proportion	62.1	21.8	8.5	7.4
Cumulative	62.1	83.9	92.4	99.8

[a] Principal component analysis performed in SAS (2002).

Table 3. Best correlations identified by Pearson's correlation coefficient between insect density and plant measurements compared to correlations between insect density and factor 1 from principal component analysis[a].

Cultivar	Factor 1	Best correlations (correlation coefficient/measurement)				
		1	2	3	4	5
7718 VFN	0.86	0.86/NDL	0.81/NLY	0.81/NLTY	−0.61/PH	−0.52/TNL
Yellow Pear	0.50	0.86/NLY	0.86/NLTY	−0.69/PH	0.59/NDL	−0.47/TNL
QualiT 21	0.40	−0.75/PH	0.60/NLY	0.60/NLTY	0.57/NDL	−0.49/TNL
Shady Lady	0.50	0.85/NDL	−0.82/PH	−0.62/TNL	0.60/NLTY	0.60/NLY
All cultivars combined	0.78	0.71/NLY	0.71/NDL	0.71/NLTY	−0.63/PH	0.37/NUL

[a] All correlations shown above are significant ($P < 0.01$, SAS, 2002); NDL, number of distorted leaves; NLY, number of yellowing leaves; NLTY, number of yellowing leaflets; PH, plant height; TNL, total number of leaves; NUL, number of upcurled leaves.

offspring are not always linked in the field (Berdegue *et al.*, 1998; Kagata & Ohgushi, 2001).

Implications of choices between infested and control plants

On 'Shady Lady', psyllids preferred to oviposit on plants previously infested by either adults or nymphs compared to control plants. Because most insect infestations in field crops are not distributed evenly on all plants (Trumble, 1993), the previously infected plants are likely to be more attractive if populations have been eliminated or severely reduced by pesticides. However, no information is available regarding plant recovery from psyllid yellows following single infestations, much less multiple infestations.

On 'Shady Lady', psyllids preferred to oviposit on plants previously infested by either adults or nymphs as compared to control plants. Also, psyllids preferred control plants to infested plants on which there were 30–35 nymphs. This pattern was not found on other cultivars tested. We suspect the response may be due to variations in inducible defensive chemistry, because our observations were consistent with those of Underwood (1998) where: (i) induced plant responses were variable (and could even be reversed) with the time length of insect feeding; and (ii) different responses were found between closely-related plant cultivars.

Hodkinson & Hughes (1982) reported that the survival of Australian eucalyptus psyllid increased from 20 to 80% as nymph density increased from 2 to 10 per leaf disc, suggesting feeding by psyllids caused biochemical or mechanical alteration of foliage resulting in higher quality food sources for psyllids. However, in the present experiments adult tomato–potato psyllids oviposited more readily on uninfested plants as compared to plants colonized by 30–35 psyllid nymphs. Given the small size of the tomato plants tested and the relatively large numbers of psyllids per plant, we suspect that the psyllids are capable of limiting the potential for over exploitation of the host resource. This ability to limit intraspecific competition by restricting oviposition has been reported for another psyllid species (Luft & Paine, 1997; Luft *et al.*, 2001). Regardless, additional studies on previously infested plants documenting psyllid growth and development as well as potential changes in plant chemistry would be beneficial. In particular, it would be beneficial to determine whether chemical changes in tomatoes typically associated with induced resistance in other phloem-feeding insects on tomatoes such as the potato aphid *Macrosiphum euphorbiae* (Thomas) (Aphididae) (Stout *et al.*, 1998; De Ilarduya *et al.*, 2003) or the silverleaf whitefly *Bemisia argentifolii* Bellows & Perring (Aleyrodidae) (Mayer *et al.*, 1996, 2002) also occur in response to psyllids and result in either an induced resistance effect or an enhanced growth of psyllid populations.

Psyllid yellows and psyllid management

The phytotoxic effects of insect feeding on phloem commonly varies from spotting or stippling (due to little diffusion of the toxin and localized destruction of the chlorophyll) to localized tissue malformations such as leaf curling or puckering (Chapman, 1985). However, psyllid yellows is one of the few cases where the toxic effects are systemic and the entire plant is affected (Carter, 1939). This is similar to the systemic disorders found on many vegetable species resulting from feeding by the silverleaf whitefly (McAuslane *et al.*, 2004). Phloem-feeding insects inject saliva into the extracellular spaces as well as in the sieve tubes to limit the response of the plant in the feeding site and to prevent sealing of the sieve elements (van der Westhuizen *et al.*, 1998). The saliva contains peroxidases, β-glucosidases, and other potential signal-generating enzymes (Miles, 1999) which appear to induce transcription of genes associated with salicylic acid or jasmonic acid-dependent responses, and other potential signal-generating enzymes (Miles, 1999) which appear to induce transcription of genes associated with salicylic acid or jasmonic acid-dependent responses, and transcription of stress-related genes (Moran & Thompson, 2001). For example, the silverleaf whitefly induces a number of host plant defences, including pathogenesis-related protein accumulation (e.g. chitinases, beta-1,3-glucanases, peroxidases, chitosanases, etc.) (Mayer *et al.*, 2002). Thus, we speculate that there is an evolutionary advantage for the psyllid to cause stunting in a tomato plant because the host is induced to maintain a suitable state for psyllid development for extended periods, even if the tomato is normally a determinant variety.

On all cultivars, symptoms of psyllid yellows will appear when 8–18 nymphs feed on 2-week-old plants. The cultivars 'Yellow Pear' and 'QualiT 21' were more tolerant of psyllids, requiring 18 nymphs per plant to produce 'psyllid yellows' symptoms. The physiological or mechanical bases for this resistance are not known, but might provide a starting point for molecular investigations while breeding for resistance. The determination that adult psyllids responded uniquely to 'Shady Lady' when nymphal density was high by ovipositing on uninfested plants suggested psyllids would have a tendency to spread more rapidly within fields planted with 'Shady Lady', and the incidence of psyllid yellows would be higher as a result of its lower damage threshold.

Yellowing, upcurled, or distorted leaves were easily identified on infested plants, allowing these characters to be used as indicators that tomato psyllids are present, and thereby showing foliage surveys should be initiated. For all cultivars, the pest density showed very good correlations with physiological effects such as the number of yellowing leaves and leaflets, and distorted leaves. These factors were at least as reliable as the first factor extracted from the principal component analysis. Thus, for greenhouse plants or early season plants during the critical first month following transplanting, some of these plant responses to psyllids could be used in a sampling programme. For example, based on the linear relationships identified above, 1.2 yellowing leaflets per plant would be expected if nine nymphs were found on one-month old 'QualiT 21' plants; 2.2 yellowing leaflets per plant would correspond to the 9-nymph density on 'Yellow Pear'. Because simply recording yellowing leaves is faster and easier than counting nymphs, this procedure could be much faster and more cost effective than psyllid counts. Of course, the foliage would need to be surveyed to determine if psyllids or some other factors are causing the effects. This approach would not work for a density of nine nymphs on the other cultivars because the threshold for damage would already have been reached. Because all the above tests were done in the laboratory and greenhouse, the current application potential is greatest in greenhouses. These models will require verification from field plantings before use in outdoor systems. Nonetheless, such measurements have the potential to simplify field surveys for this pest, which would play an important role in psyllid integrated pest management.

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