Tomato Psyllid Behavioral Responses to Tomato Plant Lines and Interactions of Plant Lines with Insecticides

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ABSTRACT Adult tomato psyllid, *Bactericerca* (*Paratrioza*) *cockerelli* (Sulc) (Homoptera: Psyllidae), behavioral responses were evaluated for five tomato plant lines and for the interactions of insecticides with four commercial cultivars. Plant lines tested included the commercial 'Shady Lady', 'Yellow Pear', '7718 VFN', 'QualiT 21', and the plant introduction line PI 134417. Insecticides included a kaolin particle film, pymetrozine, pyriproxyfen, spinosad, and imidacloprid. Psyllids spent significantly more time feeding on 'Yellow Pear' than all other plant lines except '7718 VFN'. In comparisons among plant lines, psyllids exposed to the wild accession PI 134417 showed a 98% reduction in feeding, a significant increase in jumping behavior, and a significant tendency to abandon the leaves, thereby demonstrating repellency, not just an antixenosis response. Interactions between plant lines and insecticides influenced behavioral responses. All insecticides tested significantly reduced feeding durations on all cultivars except the preferred 'Yellow Pear'. However, nonfeeding activities such as walking, probing, resting, and jumping varied substantially with chemical and cultivar combination. The behavior assay results offered insight into host resistance mechanisms, provided a useful technique for measuring effects of interaction of plant lines with insecticides, and generated information for selecting insecticides for specific cultivars used in integrated pest management program for the tomato psyllid.

KEY WORDS *Bactericerca* (*Paratrioza*) *cockerelli*, pymetrozine, pyriproxyfen, spinosad, imidacloprid

The tomato psyllid,, *Bactericerca* (*Paratrioza*) *cockerelli* (Sulc) (Homoptera: Psyllidae), recently has developed high densities on fresh market tomatoes in California and Baja, Mexico. The nymphs (and adults, see Daniels 1954) inject a toxin while feeding on the leaf that causes death in transplants, stunting and curling of the leaves in preflowering plants, and either no production or overproduction of very small, noncommercial grade fruit in larger plants (Pletsch 1947, Al-Jabar 1999). The leaf symptoms are collectively known as "psyllid yellows." As few as 30 nymphs per plant can cause these symptoms on established plants (Blood et al. 1933). Carter (1950) determined that symptoms occurred on transplants from the feeding of a single insect.

The psyllid has an extensive range of acceptable hosts, including species in 20 plant families, but solanaceous species are preferred (Wallis 1955). Increasing urbanization in California, with the planting of vegetable gardens and solanaceous landscape plants, ensures a nearly constant supply of potential hosts. The rapid developmental times, coupled with maximum oviposition in excess of 1,400 eggs per female (Knowlton and James 1931), allow populations to build explosively. In addition, broad-spectrum carbamate pesticides can promote population development (Cranshaw 1985, 1989).

Until recently, sustainable, low-input integrated pest management (IPM) strategies for tomato production in California's $350 million tomato industry were widely adopted. Pesticide use on tomatoes declined by nearly 50% from the late 1980s to the late 1990s (California Department of Food and Agriculture 1989, 1997). However, these recent gains are threatened by the development of large densities of the tomato psyllid and the losses associated with psyllid yellows. Fresh market tomato growers in Baja California, Mexico, suffered major economic losses due to this pest with >85% of the mature tomato plants destroyed in 2001 (J. LeBeouf, California Tomato Commission, personal communication). As a result, growers dramatically increased pesticide use. Typically, combinations of either acephate or methomyl in combination with fenvalerate were used. In Colorado, where the psyllid has become a serious problem on tomatoes and potatoes over the past 6 yr, experts are recommending applications of maximum rates of fenvalerate and esfenvalerate, the chlorinated hydrocarbon endosulfan, as well as the organophosphates methamidophos and phorate (Zink 1998, Cranshaw and Donahue 2002). Use of these materials in California reduces densities of biological control agents, resulting in outbreaks of secondary pests such as *Liriomyza* leafminers and spider mites (Trumble 1990, 1998). The resulting pesticide use pattern is threatening to eliminate sustainable IPM programs in tomatoes and may promote rapid development of resistance.

Insect herbivores have evolved a variety of behavioral responses to various toxins, the nature of these responses can reflect toxin apparency, mode of action, and the extent to which lethal and sublethal effects influence behavior (Hoy et al. 1998). Changes in pest activity as a result of the surface residues may contribute positively or negatively to the ultimate effect. Similarly, insects respond variably to cultivar differences (Eigenbrode and Trumble 1994). Not surprisingly, response of an insect species to insecticides can vary with the mode of host plant resistance and also between cultivars (reviewed by van Emden 1991 and Eigenbrode and Trumble 1994). Because both adult and nymphal tomato psyllids cause plant damage by injecting toxins while feeding (Daniels 1954), behavioral analyses can be used to evaluate responses to plant lines and pesticides that potentially impact population development. Therefore, a series of plant cultivars and chemicals with potential value in IPM programs were evaluated for tomato psyllid behavioral responses.

Materials and Methods

Insects. Adults collected from fresh market tomatoes in Orange County 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) h. 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 from which they had been 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 d. Because adults are difficult to sex, and oviposition does not occur within the first 3 d (Knowlton and James 1931), selection of 2–3-d-old adults eliminated problems with oviposition status variability.

Plants. Tomato plants used in all tests were grown in 15-cm-diameter pots with UC mix (Matkin and Chandler 1957) and fertilized three times weekly with the label rate of Miracle Gro nutrient solution (Scotts Company, Marysville, OH). All plants used were between 1 and 2 mo of age, at the developmental stage achieved approximately 1 wk after transplanting in the field. Although damage can occur at any time, young plants are particularly susceptible (Carter 1950). Plant leaves used as substrates for the behavioral assays were standardized by selecting the uppermost fully expanded leaf.

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. 'Yellow Pear' is commonly planted by consumers in personal gardens. 'QualiT 21' and 'Shady Lady' are widely used commercial cultivars in California, whereas Petoseed '7718 VFN' is an older commercial cultivar 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 and Kennedy 1992, Eigenbrode and Trumble 1993). All of these varieties are available commercially and from the Charles Rick collection at University of California-Davis (Davis, CA).

Pesticides. We evaluated five pesticides: one soil-applied systemic material and four that were applied to foliage. All pesticides were selected for their potential usefulness in sustainable IPM programs that include beneficial insects (Trumble and Alvarado-Rodriguez 1993, Trumble et al. 1994). Chemicals and rates included in the study were pyriproxyfen (Pyrigro, Whitmire Micro-Gen Research Laboratories, Inc., St. Louis, MO; 0.78 ml/liter, applied as a leaf dip), a kaolin clay particle film (Surround WP, Engelhard Corporation, Iselin, NJ; 50g/liter, applied with a pressurized sprayer), pymetrozine (Fulfill, Syngenta, Greensboro, NC; 1.873 g/liter, applied as a leaf dip), spinosad (Conserve SC, Dow AgroSciences Inc., Indianapolis, IN; 1.72 ml/liter, applied as a leaf dip), and imidacloprid (Admire 2 Flowable, Bayer Corporation, Kansas City, MO; 0.94 ml Admire/liter, applied to the soil at 100 ml per pot). All doses used were the maximum field rates recommended by the manufacturers. Leaves were used within 24 h after treatment for all insecticides except imidacloprid. Plants in soil treated with imidacloprid were used 1 wk after treatment.

None of the chemicals have reported activity against hymenopterous parasitoids but do provide suppression of other psyllids and related insects. Pyriproxyfen, a juvenile hormone mimic, is labeled for pear psylla, *Cacopsylla pyricola* Foerster, on pome fruits, and also reduces egg hatch and adult eclosion of greenhouse whitefly, *Trialeurodes vaporariorum* Westwood (Ishaaya et al. 1994, Bi et al. 2002). The kaolin clay material forms a white barrier film on plants, providing control of various insect species (Jifon and Syvertsen 2003). Spinosad is a secondary metabolite from the aerobic fermentation of *Saccharopolyspora spinosa* (a soil-dwelling bacterium) on nutrient media (McPherson et al. 2003) and has minimal impact on parasites of *Liriomyza* species in fresh market tomatoes (Carson et al. 1996). Pymetrozine, in the group of azomethine pyridines, has a spectrum of activity that covers sucking pests such as aphids, whiteflies, and planthoppers, yet it has no negative effects on natural enemies (Sechser et al. 2002). Imidacloprid is a systemic, chloro-nicotinyl insecticide used for the control of insects that is already included in current tomato recommendations to control whiteflies and other pests (Zalom et al. 2000).

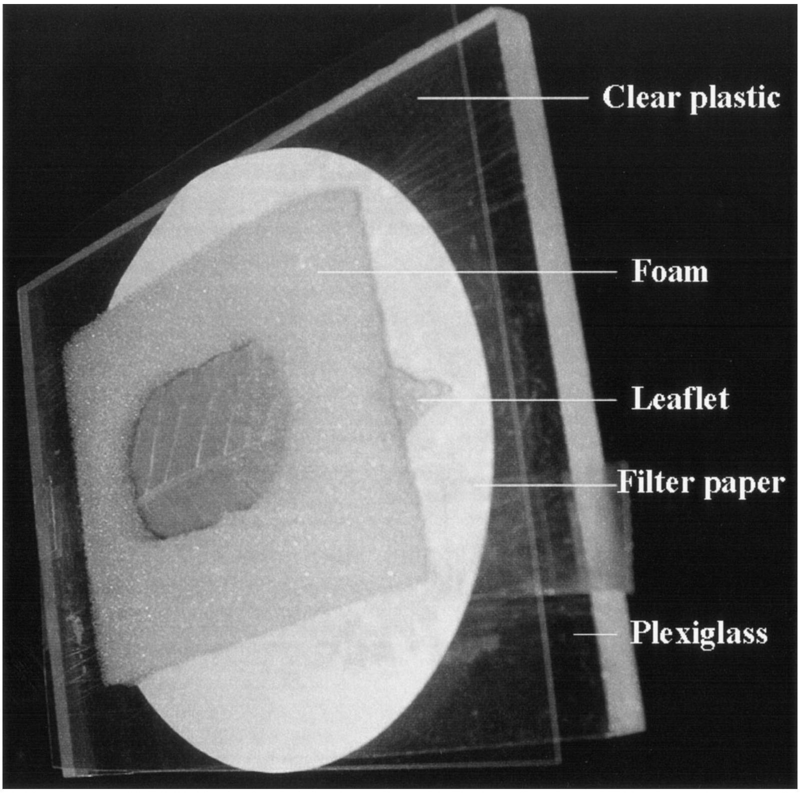

Fig. 1. Arena for observing and recording psyllid behaviors.

Behavioral Assays. All assays were conducted in arenas made by layering the following: a Plexiglas rectangle (9 by 12 cm) serving as a base, a moistened 9-cm-diameter filter paper placed on the Plexiglas, the test leaflet, a foam (1 by 3 by 6 cm) with a hole (2 by 4 cm) cut in it, and an additional piece of clear plastic that covered the arena to prevent psyllids from escaping during observation (Fig. 1). A newly emerged adult was introduced into the arena and allowed to adjust to the microenvironment for 5 min before initiating behavioral recording. An observation period lasted for 15 min. Preliminary studies indicated that the 15-min observation period was adequate for the psyllids to exhibit most of the behaviors that were recorded. Observation times >15 min could force insects to return to plants that were judged unsuitable and would be abandoned under field conditions. Because the time period was adequate for multiple occurrences of all behaviors, the insects had sufficient time to abandon the leaf if it was not acceptable. The observations were recorded using the Noldus Observer program (Noldus, Wageningen, The Netherlands), which provides data on the cumulative duration of each behavior as well as the number of occurrences of each behavior.

Specific behaviors recorded included cleaning (using legs to cleanse or wipe antennae, appendages, or abdomen), feeding (proboscis inserted in the leaf tissue), jumping (leaping from one point to another on the leaf), resting (not moving, mouthparts not in contact with leaf), off leaf (exiting or abandoning the leaf surface), walking (walking on leaf surface), and probing (tapping the mouthparts on the leaf surface intermittently, presumably to place olfactory receptors in contact with the surface). Forbes (1972) stated that stylets of a closely related psyllid contain nerves that are involved in chemoreception. Thus, probing is believed to assist in selection of feeding sites and host plant choice. Jumping occurs so rapidly that accurately recording duration times was not possible; therefore, only numbers of occurrences were recorded. These are typical behaviors that are routinely monitored in many studies assessing antixenosis effects of plant cultivars (Berdegue and Trumble 1996). Behavioral observations were replicated 20 times for all plant lines and for all of the combinations of commercially available plant lines and insecticides.

Insects may have variable responses to excised leaves (Palaniswamy et al. 1997, Tune and Dussourd 2000). To document whether the excision process would have any impact, behavioral responses to leaves on intact plants were compared with excised leaves, and no differences in any of the behaviors were significant at the $P < 0.1$ level ($n = 20$ replicates each on intact and excised leaves, Mann–Whitney U test). Accordingly, we chose to work with excised leaves which were easier to manipulate.

Table 1. Duration (in seconds) and number of occurrences of selected behaviors of the tomato psyllid in response to five tomato plant lines

Category	Plant line	Probing	Feeding	Cleaning	Jumping	Resting	Walking	Off leaflet
Duration	'7718 VFN'	1.0a	687.3bc	25.1ab		115.0a	18.4a	53.1a
Duration	'QualiT 21'	0.1a	565.6b	67.4b		246.9b	4.6a	15.3a
Duration	'Shady Lady'	4.3b	574.4b	28.1ab		205.1ab	47.7b	39.8a
Duration	'Yellow Pear'	0.8a	756.1c	8.6a		87.3a	27.8ab	19.3a
Duration	'PI 134417'	1.3ab	15.2a	12.8a		272.3b	121.9c	470.5b
Occurrences	'7718 VFN'	0.1A	1.7B	0.6BC	0.4AB	0.6A	1.0A	0.2A
Occurrences	'QualiT 21'	0.1A	1.7B	0.9C	0.1A	1.2AB	0.2A	0.2A
Occurrences	'Shady Lady'	0.6B	2.3C	0.3AB	1.5B	1.8B	2.7B	0.3A
Occurrences	'Yellow Pear'	0.1A	1.7B	0.4AB	0.3AB	0.6A	0.9A	0.2A
Occurrences	'PI 134417'	0.1A	0.1A	0.1A	13.3C	3.9C	11.6C	3.7B

Values for each plant line were based on 20, 15-min observations; values within the same category in each column followed by the same letter are not significantly different at the $P < 0.05$ level, ANOVA followed by Fisher's protected LSD test (SAS Institute 1998).

Although nymphal feeding is the primary cause of toxin injection, handling this normally sessile stage presents significant problems. We therefore focused on antixenosis effects on adults, which would likely impact population development. A primary assumption inherent in this project is that plant or chemical avoidance by adults would reduce feeding and thereby reduce oviposition. Our working hypothesis was that because tomato accessions are unusually variable in defensive chemistry and physical defenses (Eigenbrode and Trumble 1994), and because pesticides frequently induce behavioral effects, the combination of plant accession selection and pesticide effect could interact to cause variable behavioral responses in adult psyllids.

Statistical Analysis. All data were analyzed by analysis of variance (ANOVA) ($P < 0.05$ level). A post hoc test, Fisher's protected least significant difference (LSD) test (SAS Institute 1998), was used to compare means at the $P < 0.05$ level.

Results

Behavioral Responses to Plant Lines. Psyllids spent the most time feeding on 'Yellow Pear', and the least time feeding on the wild accession PI 134417 (Table 1). The antixenosis observed for PI 134417 was substantial, with feeding duration reduced by nearly 98% compared with 'Yellow Pear'. Not surprisingly, the psyllids spent significantly more time off the leaves ($F = 39.47$; df = 4, 95; $P < 0.01$) and significantly more time walking ($F = 19.68$; df = 4, 95; $P < 0.01$) on PI 134417 than on any other plant line. However, on PI 134417 the times spent cleaning or probing were not significantly less than any other plant line.

The durations of feeding on '7718 VFN', 'Shady Lady', and 'QualiT 21' were intermediate between 'Yellow Pear' and PI 134417, but only the psyllids on 'Shady Lady' and 'QualiT 21' showed significant reductions in feeding times compared with 'Yellow Pear' ($F = 30.05$; df = 4, 95; $P < 0.01$) (Table 1). The duration of cleaning was significantly increased for 'QualiT 21' compared with 'Yellow Pear' and PI 134417 ($F = 2.33$; df = 4, 95; $P < 0.01$). Among the commercially available plants, differences were detected for walking, resting, and probing, but there were no consistent patterns.

Numbers of occurrences of each behavior also were recorded on each plant line (Table 1). Differences between plant lines were most evident for PI 134417, where feeding occurrences were rare ($F = 18.01$; df = 4, 95; $P < 0.01$), and cleaning ($F = 3.32$; df = 4, 95; $P < 0.05$), jumping ($F = 137.82$; df = 4, 95; $P < 0.01$), resting ($F = 15.61$; df = 4, 95; $P < 0.01$), abandoning the leaves ($F = 55.89$; df = 4, 95; $P < 0.01$), and walking ($F = 66.17$; df = 4, 95; $P < 0.01$) occurred more

Table 2. Duration (in seconds) and number of occurrences of selected behaviors of the tomato psyllid in response to chemical treatment of commercial 'Shady Lady'

Category	Treatment	Probing	Feeding	Cleaning	Jumping	Resting	Walking	Off leaflet
Duration	Imidacloprid	7.7b	245.8a	58.9b		307.7ab	80.5b	196.2b
Duration	Pymetrozine	1.0a	278.9a	17.7ab		246.9ab	69.3ab	284.1bc
Duration	Pyriproxyfen	5.8ab	156.0a	7.5a		311.0ab	49.5a	366.2c
Duration	Spinosad	1.2a	264.5a	13.5ab		375.1b	87.5b	156.9ab
Duration	Surround WP	4.8ab	256.0a	115.2c		393.5b	39.4a	90.5a
Duration	Control	4.3ab	574.4b	28.1ab		205.1a	47.7a	39.8a
Occurrences	Imidacloprid	0.8C	1.4B	1.0B	6.2C	3.1B	6.6C	1.5B
Occurrences	Pymetrozine	0.1A	1.0AB	0.3A	4.2BC	2.4AB	5.0BC	1.4B
Occurrences	Pyriproxyfen	0.4ABC	0.6A	0.1A	4.4BC	2.9AB	4.1AB	1.6B
Occurrences	Spinosad	0.2AB	1.2AB	0.4A	2.8AB	3.5B	5.2BC	1.1AB
Occurrences	Surround WP	0.6ABC	1.6BC	1.5B	1.4A	3.2B	2.5A	0.5A
Occurrences	Control	0.6BC	2.3C	0.3A	1.5A	1.8A	2.7A	0.3A

Values for each plant line were based on 20, 15-min observations; values within the same category in each column followed by the same letter are not significantly different at the $P < 0.05$ level, ANOVA followed by Fisher's protected LSD test (SAS Institute 1998).

Table 3. Duration (in seconds) and number of occurrences of selected behaviors of the tomato psyllid in response to chemical treatment of commercial 'QualiT 21'

Category	Treatment	Probing	Feeding	Cleaning	Jumping	Resting	Walking	Off leaflet
Duration	Imidacloprid	3.8a	276.9a	57.8a		303.2ab	29.3abc	225.9b
Duration	Pymetrozine	1.8a	178.9a	20.3a		341.1ab	70.4c	286.3b
Duration	Pyriproxyfen	0.8a	279.7a	95.6ab		424.2b	16.1ab	83.2a
Duration	Spinosad	1.0a	314.6a	78.1a		411.5ab	17.0ab	77.6a
Duration	Surround WP	18.1a	209.3a	172.4b		365.5ab	55.4bc	78.4a
Duration	Control	0.1a	565.6b	67.4a		246.9a	4.6a	15.3a
Occurrences	Imidacloprid	0.4B	1.1AB	1.0AB	3.6C	3.0CD	3.0B	1.4BC
Occurrences	Pymetrozine	0.2AB	0.8A	0.3A	3.0C	1.8AB	2.9B	1.9C
Occurrences	Pyriproxyfen	0.2AB	1.4AB	1.3BC	1.0AB	1.6AB	1.3A	0.4A
Occurrences	Spinosad	0.1AB	1.4AB	0.8AB	0.5A	2.2BC	1.1A	0.4A
Occurrences	Surround WP	0.3AB	1.7B	1.8C	2.2BC	3.4D	3.2B	0.7AB
Occurrences	Control	0.1A	1.7B	0.9AB	0.1A	1.2A	0.2A	0.2A

Values for each plant line were based on 20, 15-min observations; values within the same category in each column followed by the same letter are not significantly different at the $P < 0.05$ level, ANOVA followed by Fisher's protected LSD test (SAS Institute 1998).

frequently than on any of the other plant lines (Table 1).

Behavioral Responses to Interactions of Plant Lines with Pesticides. There were differences between plant lines for tomato psyllid responses to insecticides. Compared with untreated controls, imidacloprid reduced duration of feeding on 'Shady Lady', '7718 VFN', and 'QualiT 21' by 57, 51, and 69%, respectively (Tables 2, 3, and 4) but not on 'Yellow Pear' (Table 5). On 'Yellow Pear', imidacloprid significantly increased the time spent cleaning compared with all other insecticide treatments ($F = 4.51$; df = 5, 114; $P < 0.01$), but this pattern was not seen for other plant lines (Tables 2–5). Resting duration was significantly increased on '7718 VFN' ($F = 3.42$; df = 5, 114; $P < 0.01$) but not on other cultivars. Imidacloprid also increased time spent walking on 'Shady Lady' compared with the control but not on other cultivars ($F = 3.17$; df = 5, 114; $P < 0.05$). Similarly, tomato psyllids on imidacloprid treatments spent significantly less time compared with control on the leaves of 'Shady Lady' ($F = 5.23$; df = 5, 114; $P < 0.01$) and 'QualiT 21' ($F = 5.79$; df = 5, 114; $P < 0.01$) but not on 'Yellow Pear' or '7718 VFN'. There were no differences in probing duration between the imidacloprid treatment and control on any cultivar.

Imidacloprid increased the number of occurrences of jumping and abandoning leaves compared with the controls on all commercially available plant lines except the preferred 'Yellow Pear' (Tables 2–5). Similarly, occurrences of both resting and walking were significantly increased on all cultivars except 'Yellow Pear' (Tables 2–5). The occurrence of feeding also was reduced on 'Shady Lady' ($F = 4.61$; df = 5, 114; $P < 0.01$) but not on the other cultivars.

Pymetrozine significantly decreased feeding duration (range 51–68%) on all cultivars compared with controls ('Shady Lady': $F = 5.49$; df = 5, 114; $P < 0.01$; 'Yellow Pear': $F = 5.36$; df = 5, 114; $P < 0.01$; 'QualiT 21': $F = 4.79$; df = 5, 114; $P < 0.01$; and '7718 VFN': $F = 6.85$; df = 5, 114; $P < 0.01$) (Tables 2–5). Tomato psyllids also spent significantly more time off leaves that were treated with pymetrozine ('Shady Lady': $F = 5.23$; df = 5, 114; $P < 0.01$; 'Yellow Pear': $F = 3.93$; df = 5, 114; $P < 0.01$; 'QualiT 21': $F = 5.79$; df = 5, 114; $P < 0.01$; and '7718 VFN': $F = 3.52$; df = 5, 114; $P < 0.01$). Although a few other differences in durations of specific behaviors were found, no additional patterns were evident.

Compared with the control, the occurrences of walking were increased by pymetrozine application for all cultivars except the preferred 'Yellow Pear' ('Shady Lady': $F = 4.25$; df = 5, 114; $P < 0.01$; 'QualiT 21': $F = 5.56$; df = 5, 114; $P < 0.01$; and '7718 VFN': $F = 3.19$; df = 5, 114; $P < 0.01$) (Tables 2–5). Pymetrozine

Table 4. Duration (in seconds) and number of occurrences of selected behaviors of the tomato psyllid in response to chemical treatment of commercial '7718 VFN'

Category	Treatment	Probing	Feeding	Cleaning	Jumping	Resting	Walking	Off leaflet
Duration	Imidacloprid	2.8a	213.1a	81.5ab		379.1c	45.0a	177.1ab
Duration	Pymetrozine	0.1a	325.7a	24.8a		181.2ab	89.0b	277.9b
Duration	Pyriproxyfen	2.0a	279.1a	154.2b		319.8bc	22.1a	122.4a
Duration	Spinosad	1.0a	270.8a	16.0a		457.1c	44.5a	110.0a
Duration	Surround WP	8.9b	371.9a	104.3ab		321.3bc	39.3a	54.0a
Duration	Control	1.0a	687.3b	25.1a		115.0a	18.4a	53.1a
Occurrences	Imidacloprid	0.3A	1.1AB	1.1BCD	3.1C	2.0C	3.1B	1.2B
Occurrences	Pymetrozine	0.1A	1.0A	0.3A	2.1BC	1.2AB	2.5B	1.1B
Occurrences	Pyriproxyfen	0.2A	1.2ABC	1.4D	1.0AB	1.7BC	1.0A	0.8AB
Occurrences	Spinosad	0.1A	1.3ABC	0.7ABC	1.4AB	2.1C	2.7B	0.6AB
Occurrences	Surround WP	0.8B	1.8C	1.2CD	0.6A	2.1C	1.7AB	0.3A
Occurrences	Control	0.1A	1.7BC	0.6AB	0.4A	0.6A	1.0A	0.2A

Values for each plant line were based on 20, 15-min observations; values within the same category in each column followed by the same letter are not significantly different at the $P < 0.05$ level, ANOVA followed by Fisher's protected LSD test (SAS Institute 1998).

Table 5. Duration (in seconds) and number of occurrences of selected behaviors of the tomato psyllid in response to chemical treatment of commercial 'Yellow Pear'

Category	Treatment	Probing	Feeding	Cleaning	Jumping	Resting	Walking	Off leaflet
Duration	Imidacloprid	2.6a	627.6bc	79.3c		97.7a	53.0ab	39.5a
Duration	Pymetrozine	0.1a	363.9a	9.1a		256.8b	52.6ab	216.8b
Duration	Pyriproxyfen	2.4a	386.9a	49.9b		279.5b	86.7b	94.0a
Duration	Spinosad	3.4a	673.8c	16.7a		78.0a	73.5ab	54.3a
Duration	Surround WP	12.7b	499.8b	16.1a		108.4a	152.5c	90.5a
Duration	Control	0.8a	756.1c	8.6a		87.3a	27.8a	19.3a
Occurrences	Imidacloprid	0.5A	2.1B	1.1B	0.7AB	1.0AB	2.1AB	0.3A
Occurrences	Pymetrozine	0.1A	1.2A	0.4A	1.8C	1.1AB	2.2AB	1.1B
Occurrences	Pyriproxyfen	0.3A	1.5AB	0.8AB	1.2AB	1.5B	2.7BC	0.7AB
Occurrences	Spinosad	0.3A	3.0C	0.7AB	0.6AB	0.7A	2.8BC	0.6AB
Occurrences	Surround WP	1.2B	2.6BC	0.4A	1.4BC	1.1AB	4.1C	0.6AB
Occurrences	Control	0.1A	1.7AB	0.4A	0.3A	0.6A	0.9A	0.2A

Values for each plant line were based on 20, 15-min observations; values within the same category in each column followed by the same letter are not significantly different at the $P < 0.05$ level, ANOVA followed by Fisher's protected LSD test (SAS Institute 1998).

also increased the numbers of occurrences of jumping and leaf abandonment on all cultivars.

Feeding duration was significantly reduced on all cultivars in pyriproxyfen treatments compared with the control (range 49–72%; 'Shady Lady': $F = 5.49$; df = 5, 114; $P < 0.01$; 'Yellow Pear': $F = 5.36$; df = 5, 114; $P < 0.01$; 'QualiT 21': $F = 4.79$; df = 5, 114; $P < 0.01$; and '7718 VFN': $F = 6.85$; df = 5, 114; $P < 0.01$) (Tables 2–5). Cleaning durations increased on '7718 VFN' ($F = 3.00$; df = 5, 114; $P < 0.05$) and 'Yellow Pear' ($F = 4.51$; df = 5, 114; $P < 0.01$). Pyriproxyfen increased resting duration on all cultivars except 'Shady Lady' ('Yellow Pear': $F = 3.42$; df = 5, 114; $P < 0.01$; 'QualiT 21': $F = 1.21$; df = 5, 114; $P < 0.05$; and '7718 VFN': $F = 5.07$; df = 5, 114; $P < 0.01$). No consistent differences in durations were observed for the other behaviors. Whereas some significant differences were observed for numbers of occurrences of specific behaviors between treatments, no consistent patterns were evident (Tables 2–5).

Compared with the control, spinosad application reduced feeding duration by 54, 44, and 60% on 'Shady Lady', 'QualiT 21', and '7718 VFN' respectively (Tables 2–5) but did not significantly affect feeding duration on 'Yellow Pear'. No differences were found in durations of probing, jumping, and abandoning the leaves on any cultivar. Although some significant differences were observed for durations of specific behaviors between treatments, no consistent patterns were evident across cultivars (Tables 2–5).

Interestingly, spinosad application increased the number of feeding occurrences on 'Yellow Pear' ($F = 5.36$; df = 5, 114; $P < 0.01$) compared with the control (Table 5). This pattern was not seen for other insecticides, regardless of cultivar (Tables 2–4). In addition, the numbers of occurrences of resting and walking increased on all cultivars except 'Yellow Pear' (Tables 2–5).

Treatment with kaolin clay significantly reduced feeding duration compared with controls by 55, 34, 63, and 46% on 'Shady Lady' ($F = 5.49$; df = 5, 114; $P < 0.01$), 'Yellow Pear' ($F = 5.36$; df = 5, 114; $P < 0.01$), 'QualiT 21' ($F = 4.79$; df = 5, 114; $P < 0.01$), and '7718 VFN' ($F = 6.85$; df = 5, 114; $P < 0.01$), respectively (Tables 2–5). Probing duration increased on 'Yellow Pear' ($F = 4.30$; df = 5, 114; $P < 0.01$) and '7718 VFN' ($F = 4.31$; df = 5, 114; $P < 0.01$) but not on 'Shady Lady' or 'QualiT 21'. Cleaning, walking, and resting durations increased on two of the four cultivars, so consistent responses to this insecticide were not observed across cultivars. No differences were found in time spent off the leaves.

In kaolin clay treatments, the numbers of occurrences of cleaning increased on all cultivars compared with controls except 'Yellow Pear' ('Shady Lady': $F = 6.47$; df = 5, 114; $P < 0.01$; 'QualiT 21': $F = 3.31$; df = 5, 114; $P < 0.01$; and '7718 VFN': $P < 0.01$ $F = 3.91$; df = 5, 114; $P < 0.01$) (Tables 2–5). Similarly, resting occurrences increased on all cultivars except 'Yellow Pear' ('Shady Lady': $F = 2.26$; df = 5, 114; $P < 0.05$; 'QualiT 21': $F = 6.71$; df = 5, 114; $P < 0.01$; and '7718 VFN': $F = 6.05$; df = 5, 114; $P < 0.01$). No differences were found in feeding occurrences. Numbers of occurrences of other behaviors were variable, but no consistent patterns were evident.

Discussion

Behavioral Responses to Plant Lines. Plant lines had variable effects on tomato psyllid behaviors that could reasonably be expected to reduce feeding and associated population parameters that would be impacted. The two common commercial cultivars ('Shady Lady' and 'QualiT 21') reduced feeding by nearly 25% compared with 'Yellow Pear'. The 98% reduction in feeding on PI 134117, and a significant increase in jumping behavior (Table 1), suggested that additional resistance is potentially available in this wild line. The time spent off the leaves also was greatest for this plant line, indicating some repellency, and not just an antixenosis response. Additionally, the numbers of occurrences of abandoning the leaves were low on PI 144117, indicating that once the adults left the leaf they did not return. Initially, we speculated that an increase in cleaning activities should occur due to presence of trichomes, particularly the well known type VI glandular trichomes on PI 134417 (Kennedy 2003). However, this hypothesis could not be substantiated because the duration of cleaning activities on PI 134117 was significantly shorter than the common commercial cultivars, and the repellency of this accession was such that little time was spent on the leaves in contact with the trichomes.

Behavioral Responses to Interactions of Plant Lines with Pesticides. The interactions between plant lines and pesticides can complicate pest control. Variability in pest suppression may be accounted for by unique cultivar characteristics such as planting date (Story et al. 1981, Gonzalez and Wyman 1991), allelochemical factors [such as 2-tridecanone that induce increased tolerance to the pesticide carbaryl in *Helicoverpa zea* (Boddie); Kennedy 1978], and by chemical characteristics such as the degree of suppression of natural enemies (Braman and Joyce 2002). In addition, insecticides have been shown to induce pest resistance to certain plant allelochemicals (Brewer et al. 1995).

Variation in insect control due to interactions of pesticides with plant lines can occur in response to several factors. Pesticide coverage on plant lines may be unequal due to differences in plant morphology (Ahmad et al. 1986). Abro and Wright (1989) demonstrated that feeding rates (and thereby pesticide ingestion) may change with plant line, whereas Eigenbrode and Trumble (1994) described plant line effects on body size and general vigor of insects, both of which influence pesticide susceptibility. However, in general, host plant resistance is either neutral or enhances pesticide efficacy (Creighton et al. 1975, Rose et al. 1988, Eigenbrode and Trumble 1994).

In our study, tomato psyllid behavioral responses to insecticides were influenced by plant line. For insecticides requiring ingestion, such as imidacloprid or pyriproxyfen, decreases in feeding duration could not only reduce toxin injection into the plant but also may reduce mortality rates or the onset of mortality by reducing the dosage obtained. For insecticides with contact toxicity, such as pymetrozine, an increased toxicity could be expected if insects were stimulated into greater activity on the leaf surface. Thus, the variation observed in behaviors between various combinations of insecticides and plant lines could be used to help tailor pesticide use for specific cultivars.

The data presented in our study support the use of behavioral assays for evaluating plant resistance to insects, for measuring potential effects of interactions of plant lines with insecticides, and potentially for selection of insecticides for use with a specific plant line. However, although a behavioral approach can help provide insight into resistance mechanisms, behavioral studies will only provide a portion of the data needed to evaluate plant lines and pesticides for tomato psyllid control. Additional information on tomato psyllid development and mortality in relation to plant lines and pesticides is required. Because tomato plant lines show variation in damage that is not correlated with psyllid population (Abernathy 1991), and psyllid populations within cultivars may increase or decrease substantially with plant age (Cranshaw 1989), more information on the pattern of susceptibility of plant lines to the toxin causing psyllid yellows will be required before a complete IPM program can be developed.

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