Insect Science (2006) 13, 195–204

Differential responses to feeding by the tomato/potato psyllid between two tomato cultivars and their implications in establishment of injury levels and potential of damaged plant recovery

DEGUANG LIU, LINDSEY JOHNSON and JOHN T. TRUMBLE
Department of Entomology, University of California, Riverside CA, USA

Abstract An invasive new biotype of the tomato/potato psyllid (*Bactericera* [*Paratrioza*] *cockerelli* [Sulc.]) (Homoptera: Psyllidae) recently has caused losses exceeding 50% on fresh market tomatoes in western North America. Despite these extensive losses, little is known regarding the threshold levels at which populations must be suppressed in order to prevent economic losses. A series of experiments were therefore designed using combinations of two common tomato cultivars (QualiT 21 and Yellow Pear), five pest-densities (0, 20, 30, 40 and 50 nymphs/plant), and three feeding-duration (5 days, 10 days, and lifetime) treatments to test the relative importance of pest density, feeding period, and cumulative psyllid-days to establish economic threshold levels for psyllids. The cultivars differed considerably in their response to the toxin injected by the psyllid nymphs. 'Yellow Pear' plants could recover from feeding by up to 40 nymphs for as long as 10 d, whereas 'QualiT 21' plants were irreparably damaged by densities of 20 nymphs feeding for only 5 days. On 'Yellow Pear', all plant measurements such as the number of yellow leaves and plant height were significantly better correlated with cumulative psyllid-days than with either pest density or feeding duration. On 'QualiT 21', all plant measurements other than the number of yellow leaflets and leaves were significantly better correlated with pest density than with feeding duration or cumulative psyllid-days, and pest density was a better predictor of psyllid damage. Potential reasons for the variable responses between cultivars and the implications for psyllid sampling and integrated pest management are discussed.

Key words IPM, psyllid yellows, tomato cultivar, toxic saliva
DOI 10.1111/j.1744-7917.2006.00082.x

Introduction

The tomato/potato psyllid (*Bactericera* [*Paratrioza*] *cockerelli* [Sulc.]) (Homoptera: Psyllidae) recently has developed high densities in western North America and caused losses exceeding 50% on fresh market tomatoes in California, USA and Baja, Mexico (Liu *et al*., 2006).

Correspondence: Deguang Liu, Department of Entomology, University of California, Riverside, CA 92521, USA. Tel: 951 827 4297; e-mail: dliu001@student.ucr.edu

Feeding by this psyllid results in a condition known as 'psyllid yellows', where leaves become yellow or purple and the plant is stunted. Psyllid yellows was first reported by Richards (1928), who stated the yellow and stunting effects were caused by a toxic saliva produced by the nymphs (Pletsch, 1947; Carter, 1950). Garzón *et al*. (1986, 2004) have suggested that a phytoplasma may be involved in tomato plant toxicity for some populations of this psyllid in mainland Mexico, but this claim has not been substantiated.

Key physiological and histological changes in diseased plants were documented by Eyer (1937) and Al-Jabar

(1999), including protein breakdown, reduced nitrogen levels, increased sucrose levels but reduced overall starch levels, altered carbohydrate metabolisms, and localized inhibition of translocation. In addition, chloroplasts frequently appeared smaller, lighter in color, and distorted. Complete disruption of chloroplasts, lighter pigmentation, and reduced levels of chlorophyll and carotene were observed in heavily damaged tissues (Eyer, 1937). Daniels (1954) and Al-Jabar (1999) listed 'psyllid yellows' symptoms in tomato as retarded growth, erectness of new growth, chlorosis and purpling of the leaves, stunting of growth for weeks to months, stimulated flower bloom, and production of numerous small and poor quality fruit.

Early reports suggested the first symptoms of psyllid yellows appeared after three days of feeding, but the complete symptomology was not obtained unless the nymphs fed continuously for 36 days (Carter, 1939). Although damage could occur at any stage of plant development, young plants were particularly susceptible, and plant size appeared to be a critical element in susceptibility to this insect (Carter, 1950).

In our previous experiments, the number of psyllid nymphs needed to cause psyllid yellows symptoms on 3–4-week-old tomato plants varied among cultivars 'QualiT 21' (18 nymphs), 'Yellow Pear' (18 nymphs), 'Shady Lady' (8 nymphs) and '7718 VFN' (8 nymphs) (Liu & Trumble, 2006). This variation may have been due, in part, to cultivar-specific behavioral responses (Liu & Trumble, 2004) and psyllid growth and development rates (Liu & Trumble, 2005). Therefore, the occurrence of psyllid yellows was closely associated with the number of nymphs on plants, duration of feeding, and crop cultivar, as well as plant age and size.

The phytotoxic effects of insect feeding commonly vary 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). As a result, the recovery of such diseased plants with systemic physiological changes is likely to be much more difficult than those plants with localized damage. The literature on plants recovering from psyllid yellows is quite limited and somewhat variable: affected tomato plants tended to recover when the psyllid feeding period was less than 26 days (Carter, 1939) or 16 days (Richards & Blood, 1933). Blood *et al.* (1933) reported that symptoms were not induced by inoculation with less than 30 psyllids, and if insects were removed, plants would recover even after extended periods of feeding. Subsequently, Carter (1950) determined that symptoms could occur on transplants from the feeding of a single nymph. The potential for plant recovery from toxin injection is a critical factor in establishment of an economic threshold level for psyllids. Documentation of the pest densities and feeding durations that permit plants to recover is necessary for the development of an integrated pest management (IPM) program and will allow the most effective use of pesticides. Therefore, our primary objectives were to determine if current tomato cultivars could recover from psyllid feeding, and if so, was recovery dependent on pest density and insect feeding duration.

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℃, and a photoperiod of 14:10 (L: D), and all of the experiments were conducted under the same conditions. Host plants for the colony 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 (1984 a,b) demonstrated that some insect species developed a preference for the host species on which they were reared.

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 g/L, Scotts Company, Ohio, USA). All tests were initiated using plants between two and three weeks of age.

Two tomato cultivars of *Lycopersicon esculentum* Mill. (Petoseed 'Yellow Pear' and Rogers 'QualiT 21') were tested. The 'Yellow Pear' cultivar is a variety commonly planted by consumers in personal gardens, and commercially grown for restaurants and specialty stores. The cultivar 'QualiT 21' is a widely-used commercial fresh market cultivar in California. Both of these cultivars were more tolerant of tomato psyllid damage than other tested cultivars in our previous experiments (Liu & Trumble, 2006), and are therefore more likely to be planted. Both cultivars are commercially available.

Bioassay

To determine the relationship between psyllid damage and plant recovery potential, 2-week-old plants were ex-

posed to ovipositing adults and numbers of resulting nymphs were manipulated by removing eggs or nymphs to achieve predetermined density ranges. Initially, psyllid numbers were manipulated to generate densities of 0, and approximately 20, 30, 40, and 50 nymphs per plant for the 'Yellow Pear', with 0, 20, 30 and 40 nymphs per plant for 'QualiT 21'. At day 3 and again one week later, the numbers of nymphs/plant were examined to make certain that the only replicates used in the experiment contained 0, 19−23, 28−33, 38−43, and 48−53 nymphs on the control, 20-nymph, 30-nymph, 40-nymph and 50-nymph density treatments, respectively. For the 20−50-nymph treatments, nymphs were maintained at these densities for either 5 days, 10 days, or their lifetime (about 25 days in our experiments). Thus there were three feeding-duration treatments for each density, except that only 10-day and lifetime treatments were conducted for the 20-nymph density on 'Yellow Pear'. Each combination of density × feeding duration was replicated at least 5 times. In order to differentiate these various combinations, the following conventions were used. Treatments containing psyllids begin with a 'T', which is followed by the pest density and feeding period, such as T205 (20 nymphs feeding for 5 days after hatch), T2010 (20 nymphs feeding for 10 days), and T20L (20 nymphs feeding for their lifetime).

Tomato plants that recover begin to grow again, and symptoms of psyllid yellows disease slowly disappear (Carter, 1950). Plants that do not recover remain stunted permanently, and psyllid yellows symptoms persist (Blood *et al*., 1933). Thus, plants either make a complete recovery and produce marketable fruit or never develop further and do not produce any useful fruit. We therefore used a series of symptoms, including chlorosis, leaf curling, and plant height to characterize recovery. We examined all these plant symptoms 20 days after insect removal, and compared them with the control plants. Disappearance of leaf symptoms demonstrates plant recovery, but the plant height may still be lower than the control due to the stunting that occurred during the period the insects were present and feeding. However, from the viewpoint of a grower, allowing plants that can recover to survive and produce fruit (perhaps 1−2 weeks later than expected) still makes more economic sense than replanting and loosing 4−5 weeks and incurring the costs of new transplants and field preparation.

After completion of the specific feeding duration, the insects were removed and the plants were allowed to grow without any insect feeding for at least 20 days. The 20-day time limit was chosen because growers would not likely maintain plants that did not recover within this time period. The plants under 5-day treatments were allowed to recover for 40 days, under 10-day treatments for 30 days and under lifetime treatments for 20 days. In this way, plant stage was standardized to facilitate comparison with control. At day 45 after hatching, plant heights, the length of the three uppermost leaves (all of which developed after the nymphs were removed), and the length of the uppermost leaflet of the three uppermost leaves of treated plants were measured. In addition, the total numbers of yellow leaves and yellow leaflets were counted. A leaf or leaflet was defined as yellow if 50% or more of the leaf was yellow. These data collectively provided evidence of the recovery of the plants from toxin injection during psyllid feeding.

Statistical analysis and experimental design

The experiments were performed using a completely randomized block design for all tests. Two-way ANOVA was conducted in SAS (2002) to identify possible interactions between pest density and feeding period, but no interactions were found. Therefore, a one-way ANOVA followed by Tukey's HSD test were used to identify differences between controls and psyllid treatments, and differences among treatments with a particular pest density or feeding period (SAS, 2002). The correlations between plant measurements and pest density, pest feeding duration and psyllid-days were calculated using the correlation Z-test procedure of StatView (1998), the *t*-statistic was used to assess the significance of difference between correlations in the same sample while taking their dependence into account (Cohen & Cohen, 1983). Psyllid-days were calculated as the number of nymphs on a plant times the duration of feeding.

Results

Pest density and feeding durations

'Yellow Pear' In treatments where 30, 40 and 50 nymphs fed on a plant for only 5 days, the plants recovered as indicated by the negligible numbers of yellow leaves (Fig. 1.1) and leaflets (Fig. 1.2), and the normal lengths of the top three leaves (Fig. 2.1) and leaflets (Fig. 2.2) (compared to controls). Plants exposed to 20, 30, or 40 nymphs for 10 days also recovered. However, in the treatment with a pest density of 50 nymphs per plant and a feeding period of 10 days, the plants did not recover (Figs. 1−3). Treated plants did not recover in the 20, 30, 40 or 50 nymph treatments where the insects were allowed to feed until adult eclosion (Figs. 1−3).

In all 20−50-nymph density treatments, plant heights were significantly lower than those of control plants (Fig. 3). Within the 5-day feeding period treatments, no differences

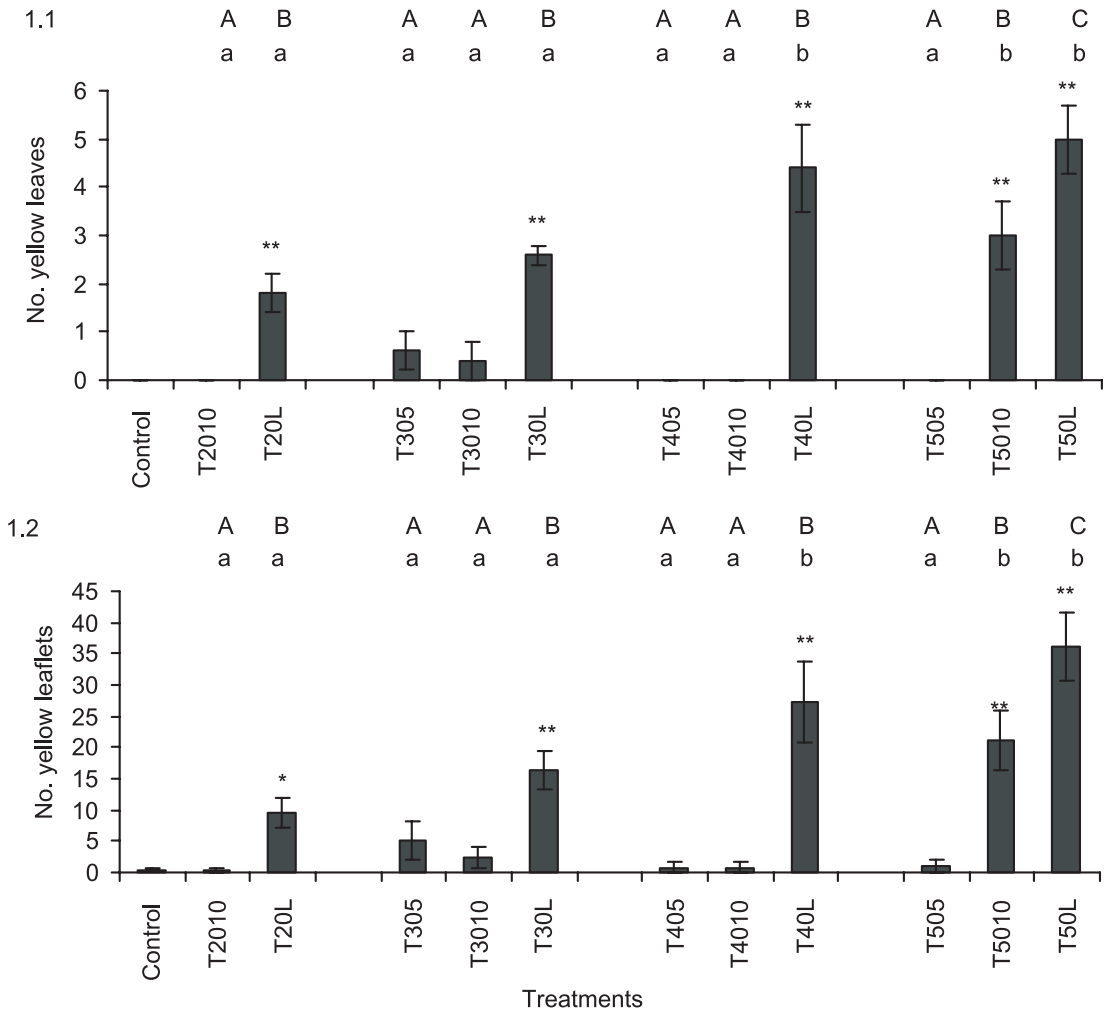

Fig. 1 Comparisons of the number of yellow leaves (Fig. 1.1) or yellow leaflets (Fig. 1.2) under different density and feeding period treatments on the tomato cultivar 'Yellow Pear'. Note: no bar indicates 0 yellow leaves or leaflets; different letters above bars indicate significant differences among treatments with the same pest density (capital letters) or within the same feeding period (small letters); significant differences between treatments and controls are indicated with *$P < 0.05$, ** $P < 0.01$.

in plant heights were found among the density treatments where nymphs were present (e.g., 20−50 nymphs per plant). Within the 10-day feeding period treatments, plants with a pest density of 50 nymphs per plant were significantly smaller than those with 20, 30 or 40 ($F = 7.48$; df = 11,50; $P < 0.01$). In the 20-nymph density treatments, no significant differences in plant heights were found between treatments of the 10-day and lifetime feeding periods. In 30 and 40-nymph density treatments, plants fed upon by nymphs for 5 and 10 days were significantly taller ($F = 7.48$; df = 11,50; $P < 0.01$) than those fed upon until adult eclosion. Within the 50-nymph density treatments, plants with a feeding period of 5 days were significantly taller than those with a feeding period of 10 days or lifetime ($F = 7.48$; df = 11,50; $P < 0.01$).

'QualiT 21' For all the 20−40-nymph density treatments with feeding periods of 5 days, 10 days, or until adult eclosion, the plants did not recover as shown by significantly more yellow leaves (Fig. 4.1) and leaflets (Fig. 4.2), significantly shorter leaves (Fig. 5.1) and leaflets (Fig. 5.2), and significantly reduced plant heights. Five-day feeding by 30 nymphs caused significantly more yellow leaves ($F = 6.80$; df = 9,40; $P < 0.01$) and leaflets ($F = 5.48$; df = 9, 40; $P < 0.01$) than by 20 nymphs, but not by 40 nymphs. Within the 10-day feeding period treatments, no differences in the number of yellow leaves or leaflets were found. Feeding until adult eclosion by 20 or 40 nymphs caused significantly more yellow leaves and leaflets than

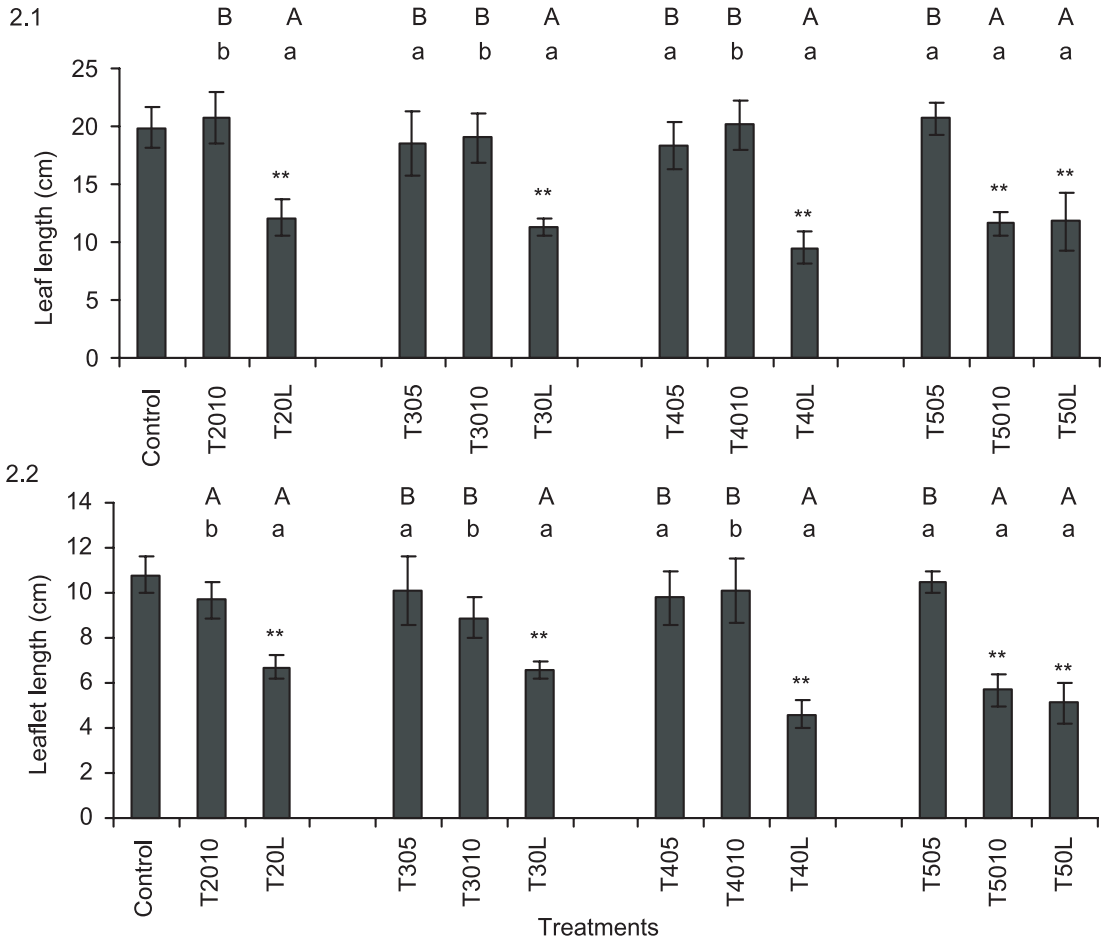

Fig. 2 Comparisons of the length of the top 3 yellow leaves (Fig. 2.1) or leaflets (Fig. 2.2) under different density and feeding period treatments on the tomato cultivar 'Yellow Pear'. Note: no bar indicates 0 yellow leaves or leaflets; different letters above bars indicate significant differences among treatments with the same pest density (capital letters) or within the same feeding period (small letters); **significant differences between treatments and controls ($P < 0.01$).

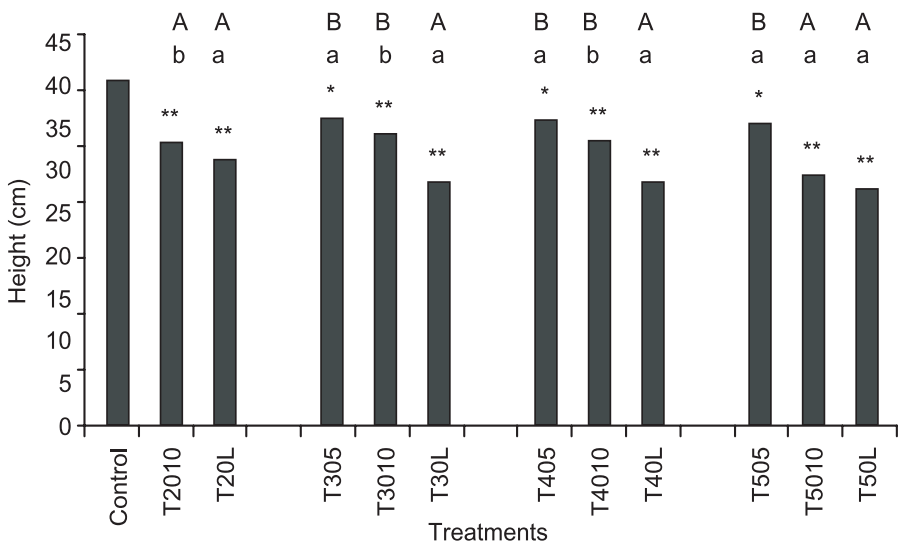

Fig. 3 Comparisons on the plant heights under different density and feeding period treatments on the tomato cultivar 'Yellow Pear'. Note: no bar indicates 0 yellow leaves or leaflets; different letters above bars indicate significant differences among treatments with the same pest density (capital letters) or within the same feeding period (small letters); significant differences between treatments and controls are indicated with *$P < 0.05$, ** $P < 0.01$.

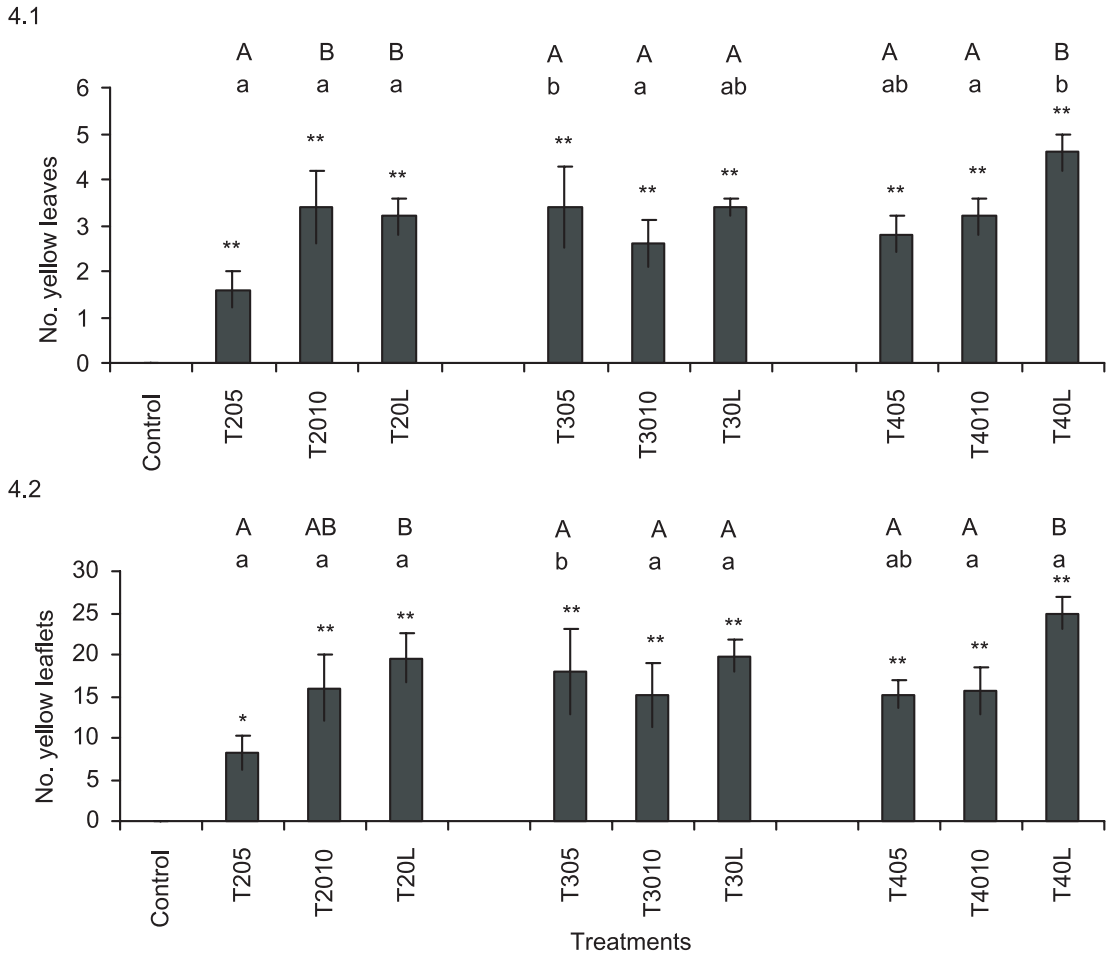

Fig. 4 Comparisons on the number of yellow leaves (Fig. 4.1) or leaflets (Fig. 4.2) under different density and feeding period treatments on the tomato cultivar 'QualiT 21'. Note: no bar indicates 0 yellow leaves or leaflets; different letters above bars indicate significant differences among treatments with the same pest density (capital letters) or within the same feeding period (small letters); significant differences between treatments and controls are indicated with $*P < 0.05$, $**P < 0.01$.

feeding for 5 days or 10 days. Within the 20-nymph density treatments, feeding for the psyllid's lifetime caused significantly more yellow leaves and leaflets than for 5 days. However, no differences in the number of yellow leaves or leaflets were found within feeding durations with a 30-nymph pest density. For the 40-nymph density treatments, feeding for lifetime caused more yellow leaves and leaflets than for 5 days and 10 days. No patterns were apparent for the length of the top three leaves and leaflets (Fig. 5): feeding until the adult stage did not necessarily cause shorter leaves or leaflets than for 5-day or 10-day feeding periods, regardless of density.

Because all 'QualiT 21' plants were strongly affected by the presence of nymphs, no significant differences in plant heights were found among treatments containing nymphs with the same feeding period (5 days, 10 days, or lifetime). Similarly, no differences were found in plant height within the same pest density (20, 30 or 40 nymphs per plant).

Correlation analyses

On 'Yellow Pear', correlation of the number of yellow leaves with psyllid-days ($r = 0.83$) was significantly better than with feeding duration ($r = 0.37$) or pest density ($r = 0.42$) (Table 1). The same general pattern was found for the other plant measurements including the number of yellow leaves, plant height, the length of top three leaves, and the length of the top three leaflets (Table 1).

For 'QualiT 21', plant height correlated much better with pest density ($r = -0.67$) than with feeding duration ($r = -0.47$) or psyllid-days ($r = -0.42$) (Table 1). Similar

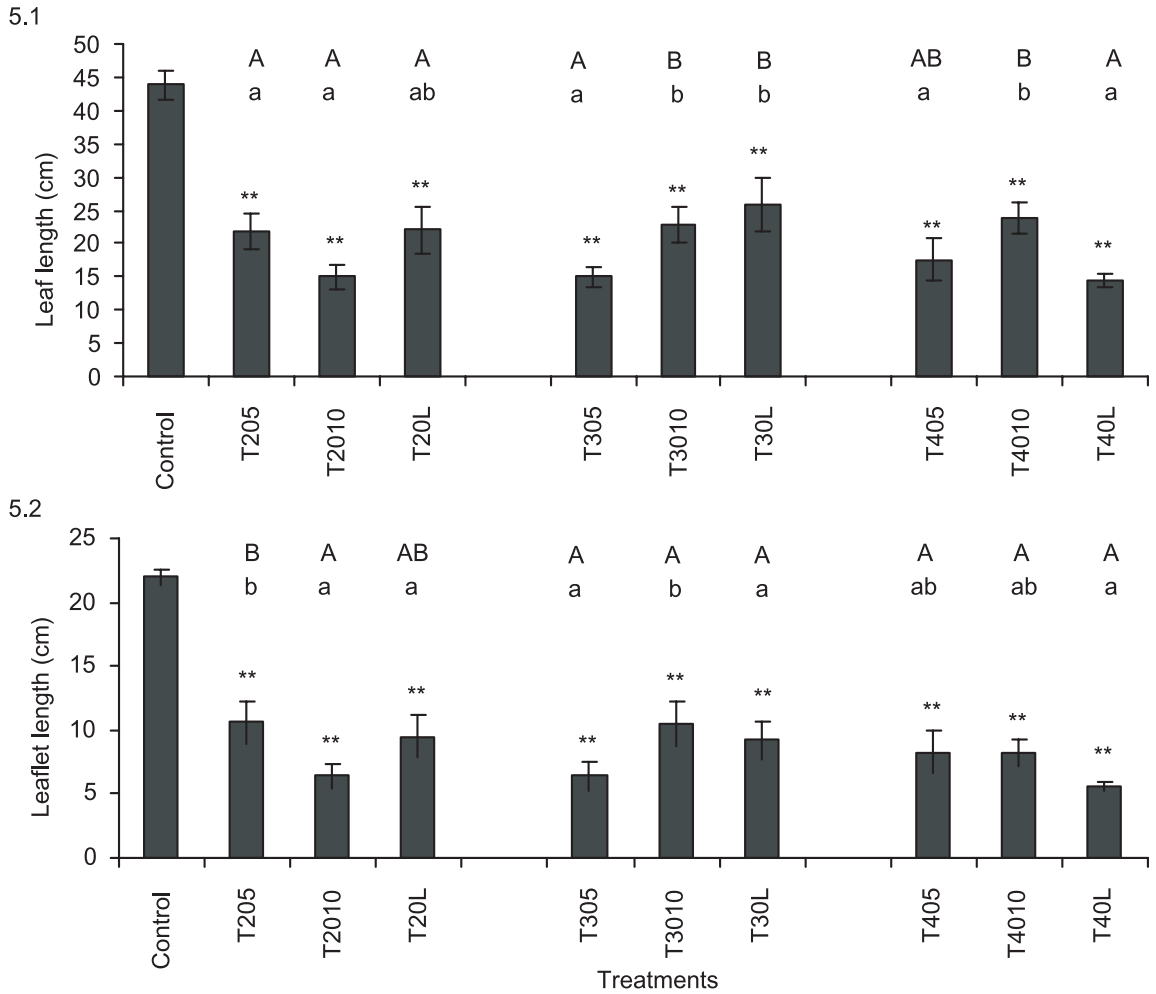

Fig. 5 Comparisons on the leaf length of the top 3 leaves (Fig. 5.1) or leaflets (Fig. 5.2) under different density and feeding period treatments on the tomato cultivar 'QualiT 21'. Note: no bar indicates 0 yellow leaves or leaflets; different letters above bars indicate significant differences among treatments with the same pest density (capital letters) or within the same feeding period (small letters); **significant differences between treatments and controls ($P < 0.01$).

Table 1 Correlation coefficients between plant measurements and pest density, feeding duration and cumulative psyllid-days on two cultivars of tomato.[†]

Cultivar	Pest factors	No. of yellow leaves	No. of yellow leaflets	Plant height	Length of 3 uppermost leaves	Length of 3 uppermost leaflets
QualiT 21	Pest density	0.621 a	0.572 a	−0.673 b	−0.601 b	−0.691 b
QualiT 21	Feeding duration	0.563 a	0.595 a	−0.472 a	−0.294 a	−0.422 a
QualiT 21	Psyllid-day	0.603 a	0.611 a	−0.421 a	−0.303 a	−0.441 a
Yellow Pear	Pest density	0.420 x	0.428 x	−0.543 y	−0.273 x	−0.362 x
Yellow Pear	Feeding duration	0.369 x	0.402 x	−0.322 x	−0.300 x	−0.302 x
Yellow Pear	Psyllid-day	0.830 y	0.814 y	−0.718 z	−0.605 y	−0.671 y

[†]All correlations are significant, $P < 0.05$ (StatView, 1998), different letters indicate significant differences between correlations within a cultivar ($P < 0.05$).

patterns were found for the length of the top three leaves and leaflets: the correlation of the number of yellow leaves with pest density was also better than with feeding duration and psyllid-days, but the correlation coefficient of the number of yellow leaflets with psyllid-days ($r = 0.61$) was nearly the same as that with pest density ($r = 0.57$) or feeding duration ($r = 0.60$) (Table 1).

Discussion and conclusions

Plant recovery from 'psyllid yellows'

In a previous study both 'Yellow Pear' and 'QualiT 21' appeared moderately tolerant of psyllid damage, with a threshold of 18 nymphs per plant feeding until adult eclosion needed to produce a complete symptom picture of 'psyllid yellows' in the early stages of tomato plant development (Liu & Trumble, 2006). As a result, a threshold of 18 nymphs per plant was proposed as an economic injury level (the pest density at which economic losses would occur). However, the earlier experiments did not assess the potential for plant recovery. In the studies reported here, the tested cultivars differed substantially in recovery potential, with 'Yellow Pear' effectively recuperating from feeding by as many as 50 nymphs per plant for 5 days, or up to 40 nymphs per plant for 10 days. In contrast, 'QualiT 21' did not recover from even 20 nymphs feeding for as short as 5 days.

The reason for the differential performance of plant recovery on 'Yellow Pear' and 'QualiT 21' is still unknown. The studies on psyllid behavioral responses (Liu & Trumble, 2004) and growth and development (Liu & Trumble, 2005) documented that 'QualiT 21' was both less attractive to the psyllid and a less suitable host than 'Yellow Pear', which suggested different defensive or nutritional chemistries for the two tomato cultivars. 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 transcription of stress-related genes (Moran & Thompson, 2001). For example, the silverleaf whitefly induces a number of host plant defenses, including pathogenesis-related protein accumulation (e.g., chitinases, beta-1,3-glucanases, peroxidases, chitosanases, etc.) (Mayer *et al.*, 2002). Therefore, psyllids' feeding process and plant response may have important implications for late plant recovery. Sucrose synthase, ABC transporter, calmodulin, Pop3 peptide and aquaporin appeared to be actively involved in the process of plant recovery from salt stress (Gu *et al.*, 2004), but the physiological and biochemical pathways involved in plant recovery under psyllids' feeding stress are still unknown. What is evident is that the different chemistries of both tomato cultivars examined in our earlier studies (Liu & Trumble, 2006) contributed to the differential plant responses in recovery for both cultivars.

According to Underwood (1998), induced plant responses were variable (and could even be reversed) with the intensity and time length of insect feeding, different responses were found between closely-related plant cultivars. Therefore, the subsequent recovery process will start with a different physiological and biochemical status following feeding by insects of different density and duration on different cultivars. Plant growth stage is an important factor in this process as well, because plants of small size are more susceptible to psyllid damage (Carter, 1950), and previous infestation by psyllids influenced ovipositional preference with implications for further degree of injury (Liu & Trumble, 2006). In addition, plants in different growth stages may provide different attractiveness to psyllids, and present different physiological responses to psyllid damage.

Relative importance of pest density, feeding duration and psyllid-days

On 'Yellow Pear', all plant measurements were much better correlated to psyllid-days than to pest density or feeding duration (Table 1). Clearly, psyllid-days are a much better predictor of both psyllid damage and plant recovery potential than either pest density or feeding period. For 'Yellow Pear', plants with 50 nymphs feeding for 10 days (500 psyllid-days) failed to recover, but plants with 40 nymphs feeding for 10 days (400 psyllid-days) recovered. Thus, the recovery threshold fell between 400−500 psyllid-days. Interestingly, the predicted economic injury level of 18 nymphs per plant feeding for the nymphal lifetime (about 450 psyllid-days) was nearly the same as the recovery threshold in terms of psyllid-days.

On 'QualiT 21', all plant measurements other than the number of yellow leaflets and leaves were better correlated to pest density than to psyllid-days or feeding duration (Table 1). As a result, psyllid-days were not useful for predicting pest damage on 'QualiT 21', and pest density was a better predictor of psyllid damage. When pest densities were higher than the previously predicted economic injury level of 18 nymphs per plant, feeding durations from 5 days to lifetime completely inhibited plant recovery. Thus, for this cultivar, allowing populations to reach the

previously predicted economic injury level would likely result in the loss of the entire crop. To avoid this problem, we recommend treating when psyllid populations approach 10 nymphs per plant for a period of 5 days.

Implications for psyllid control

Clearly, growers and homeowners have a limited time period following infestation to control psyllids. For 'Yellow Pear', high densities of nymphs are not necessarily a threat to production as long as control activities are initiated in time to prevent the number of accumulated psyllid-days from reaching the non-recovery threshold. Even given the rapid population growth of psyllids (Knowlton & James, 1931), a standard sampling interval of one week would likely be adequate. For 'QualiT 21', densities of psyllids reaching 20/plant in the early stage of tomato development for even a few days could destroy production completely because the plants would fail to recover. Therefore, monitoring of nymphal densities in fields planted with 'QualiT 21' should occur much more frequently, at least twice a week.

Chemical selection for control of psyllids will also be affected by cultivars. Systemic materials that are applied through drip lines or via soil drenches can be very effective (Liu & Trumble, 2005), but the time required for root absorption and translocation to the feeding sites of the psyllids may allow populations to exceed the injury thresholds. Systemic compounds will therefore need to be applied when pest densities are exceedingly low. In addition, materials such as kaolin clay that work by preventing young nymphs from settling on leaves may reduce population growth rate, but are not likely to stop established nymphs from feeding and injecting toxin, and thereby contributing to accumulated psyllid-days. Generally, combinations of a rapid contact material followed by a longer term systemic compound will likely provide the best control.

Although the data presented in this study are immediately applicable to glasshouse culture of tomatoes, extending these results to plants grown in the field should be done with caution. Additional investigations are needed to adjust the identified thresholds for use in commercial outdoor fields.

Acknowledgments

We appreciate the lab and greenhouse assistance of W. Carson and G. Kund. The reviews of J. Morse, R. Stouthamer, W. Carson, P. Jensen, M. Sorensen and G. Kund improved the manuscript. This project was supported in part by grants from the USDA/University of California Exotic Pests and Diseases Program and the California Tomato Commission.

References

Al-Jabar, A. (1999) Integrated pest management of tomato/potato psyllid, *Paratrioza cockerelli* (Sulc) (Homoptera: Psyllidae) with emphasis on its importance in greenhouse grown tomatoes. PhD dissertation, Colorado State University, Fort Collins.

Blood, H.L., Richards, B.L. and Wann, F.B. (1933) Studies of psyllid yellows of tomato. *Phytopathology*, 23, 930.

Carter, R.D. (1950) Toxicity of *Paratrioza cockerelli* to certain solanaceous plants. PhD dissertation, University of California, Berkeley.

Carter, W. (1939) Injuries to plants caused by insect toxins. *The Botanical Review*, 5, 273–326.

Chapman, R.K. (1985) Insects that poison plants. *American Vegetable Grower*, 33, 31–38.

Cohen, J. and Cohen, P. (1983) *Applied Multiple Regression/Correlation Analysis for the Behavioral Sciences*. Hillsdale, N.J.: Lawrence Erlbaum Associates, p. 57.

Daniels, L.B. (1954) The nature of the toxicogenic condition resulting from the feeding of the tomato psyllid *Paratrioza cockerelli* (Sulc). PhD dissertation, University of Minnesota, Twin Cities, 119 pp.

Eyer, J.R. (1937) Physiology of psyllid yellows of potatoes. *Journal of Economic Entomology*, 30, 891–898.

Garzón, T.J.A., Garza, C.A. and Bujanos, M.R. (1986) Determinación del insecto vector de la enfermedad de tipo viral "permanente del tomate" (*Lycopersicon esculentum* Mill.) en la región del Bajío. In: XIII Congreso Nacional de Fitopatología. Tuxtla Gutierrez, Chis. Resúmenes. Soc. Mex. de Fitopatología, A.C. p. 30.

Garzón T.J.A., Bujanos, M.R., Avilés, M.C.G., Byerly, M.K.F., Parga, T.V., Martínez, C.J.L. and Marín, J.A. (2004) *Bactericera (Paratrioza) cockerelli* Sulc, transmisor de toxinas y vectores de fitoplasmas. Memoria del curso "Manejo de plagas en cultivo de tomate, chile y pepino", Sinaloa, México. pp. 80–94.

Gu, R., Fonseca, S., Puskas, L.G., Hackler, L., Zvara, A., Dudits, D. and Pais, M.S. (2004) Transcript identification and profiling during salt stress and recovery of *Populus euphratica*. *Tree Physiology*, 24, 265–276.

Knowlton, G.F. and James, M.J. (1931) Studies on the biology of *Paratriza cockerelli* (Sulc). *Annals of the Entomological Society of America*, 24, 283–291.

Liu, D. and Trumble, J.T. (2004) Tomato psyllid behavioral responses to tomato plant lines and interactions of plant lines with insecticides. *Journal of Economic Entomology*, 97, 1078–1085.

Liu, D. and Trumble, J.T. (2005) Interactions of plant resistance and insecticides on the development and survival of *Bactericera cockerelli* [Sulc] (Homoptera: Psyllidae). *Crop Protection*,

24, 111−117.

Liu, D. and Trumble, J.T. (2006) Ovipositional preferences, damage thresholds, and detection of the tomato/potato psyllid (*Bactericera cockerelli* [Sulc]) on selected tomato accessions. *Bulletin of Entomological Research*, 96, 197−204.

Liu, D., Trumble, J.T. and Stouthamer, R. (2006) Molecular characterization indicates recent introductions of potato psyllid (*Bactericera cockerelli*) into western North America are genetically different from eastern populations. *Entomologia Experimentalis et Applicata*, 118, 177−183.

Matkin, O.A. and Chandler, P.A. (1957) The U. C. −type soil mixes. *The U. C. System for Producing Healthy Container-grown Plants through the Use of Clean Soil, Clean Stock and Sanitation*. California Agricultural Experiment Station Manual 23, Berkeley.

Mayer, R.T., Mccollum, T.G., Mcdonald, R.E., Polston, J.E. and Doostdar, H. (1996) *Bemisia* feeding induces pathogenesis-related proteins in tomato, *Bemisia 1995: Taxonomy, Biology, Damage Control and Management* (eds. Gerling, D. & Mayer, R.T.), pp. 179−188, Intercept Ltd., Andover, Hants, UK.

Miles, P.W. (1999) Aphid saliva. *Biological Reviews*, 74, 41−85.

Moran, P.J. and Thompson, G.A. (2001) Molecular responses to aphid feeding in Arabidopsis in relation to plant defense pathways. *Plant Physiology*, 125, 1074−1085.

Pletsch, D.J. (1947) The potato psyllid *Paratrioza cockerelli* (Sulc), its biology and control. *Montana Agricultual and Experimental Station Bulletin*, 446, 95pp. Montana State College Agricultural Experiment Station, Bozeman, Montana.

Richards, B.L. (1928) A new and destructive disease of the potato in Utah and its relation to potato psylla. *Phytopathology*, 18, 140−141.

Richards, B.L. and Blood, H.L. (1933) Psyllid yellows of the potato. *Journal of Agricultural Research*, 46, 189−216.

SAS Institute (2002) *SAS*. SAS Institute Inc., Cary, NC, USA.

SAS Institute (1998) *StatView*. SAS Institute Inc., Cary, NC, USA.

Tavormina, S.J. (1982) Sympatric genetic divergence in the leaf-mining insect *Liriomyza brassicae* (Diptera: Agromyzidae). *Evolution*, 36, 523−524.

Underwood, N.C. (1998) The timing of induced resistance and induced susceptibility in the soybean-Mexican bean beetle system. *Oecologia*, 114, 376−381.

van der Westhuizen, A.J., Qian, X.M. and Botha, A.M. (1998) Differential induction of apoplastic peroxidase and chitinase activities in susceptible and resistant wheat cultivars by Russian wheat aphid infestation. *Plant Cell Reports*, 18, 132−137.

Via, S. (1984a) The quantitative genetics of polyphagy in an insect herbivore. I. Genotype-environment interaction in larval performance on different host plant species. *Evolution*, 38, 881−895.

Via, S. (1984b) The quantitative genetics of polyphagy in an insect herbivore. II. Genetic correlations in larval performance within and among host plants. *Evolution*, 38, 896−905.

Accepted February 22, 2006