OXFORD

Plant Resistance

Effects of High-Level Acylsugar-Producing Tomato Lines on the Development of Tomato Psyllids (Hemiptera: Triozidae)

Zhenyu Li,[1] Gregory Kund,[2] Darlene M. De Jong,[3] Xia Feng,[1] Martha A. Mutschler,[3] and John T. Trumble[2,4]

[1]Institute of Plant Protection, Guangdong Academy of Agricultural Sciences, Guangzhou 10 510640, China, [2]Department of Entomology, University of California, Riverside, CA 92521, [3]Section of Plant Breeding and Genetics, School of Integrative Plant Science, Cornell University, Ithaca, NY 14853 and [4]Corresponding author, e-mail: john.trumble@ucr.edu

Abstract

Acylsugars have been shown to provide activity against numerous insect pests of tomatoes. Comparison of acylsugar levels in four tomato plant lines, FA7/AS, FA2/AS, CU071026, and 'Yellow Pear', found that the acylsugar contents in the elevated acylsugar lines were significantly higher than the commercial Yellow Pear (control) tomato plant line. Adult choice tests indicated that the tomato psyllid, *Bactericera cockerelli*, preferred to settle on the Yellow Pear and FA2/AS lines over the line with the highest content of acylsugars, FA7/AS, and the parental line, CU071026. The no-choice test demonstrated that adults laid fewer eggs on the high acylsugar tomato lines than on the control tomato line, Yellow Pear. For all high acylsugar lines, the relative growth index of the psyllid was significantly lower compared with the commercial line, indicating a reduced potential for population growth. Although some tomato psyllids completed their life cycle on the high acylsugar tomato plant lines, the percent survival of psyllids to the adult stage when developing on the high acylsugar lines was significantly less (range = 43.7–57.1%) than on the commercial tomato line (83.8%). All mortality occurred during the early stages of development (egg stage to third instar), which has implications for acquisition and transmission of *Candidatus* Liberibacter solanacearum, the causal agent of tomato vein greening disease. Therefore, with reduced attractiveness for tomato psyllids and significantly reduced survival, the high-acylsugar tomato plant lines have the potential to be part of an integrated pest management program for this pest.

Key words: host plant resistance, potato psyllid, tomato vein greening

The tomato psyllid, *Bactericera cockerelli*, is a serious pest of tomatoes (*Solanum lycopersicum* L.), peppers (*Capsicum* spp.), and potatoes (*S. tuberosum* L.) in North and Central America, New Zealand (Butler and Trumble 2012), and more recently in western Australia (https://www.interstatequarantine.org.au/producers/biosecurity-alert-tomato-potato-psyllid/) and Norfolk Island, an Australian Territory in the western Pacific Ocean (Thomas et al. 2018).

This pest causes significant injury to crop plants by feeding and transmitting the bacterial pathogen, *Candidatus* Liberibacter solanacearum (Lso; a.k.a. *Ca*. L. psyllaurous), with losses up to 85% in commercial tomato crops (Liu and Trumble 2004). There have been many publications reporting management strategies to control this pest since the first recorded outbreaks in the early 1900s (Prager and Trumble 2018). Several studies have attempted to incorporate host plant resistance as a management strategy for tomato psyllids on either tomatoes or potatoes. While there have been some potato lines reported that have potential economic use (Rubio-Covarrubias et al. 2017, Anderson et al. 2018, Prager et al. 2018), no field tomato lines have been identified with enough resistance to have commercial potential (Liu and Trumble 2004, Casteel et al. 2007, Mayo-Hernández et al. 2018).

Nearly all of the tomato psyllid management strategies used to date on either potatoes or tomatoes focus on repeated applications of pesticides (e.g., Guenthner et al. 2012, Greenway 2014, Prager et al. 2016). Although psyllid populations may be suppressed with pesticides, some crops will still show commercially unacceptable losses from Lso (Prager et al. 2013). Unfortunately, resistance has developed to some neonicotinoids, including those that are most commonly applied (Prager and Trumble 2018, Szczepaniec et al. 2019). Despite some success using two natural enemy species in greenhouses (Calvo et al. 2018), repeated attempts to use biological control to manage tomato psyllid populations on any field crops have not proven commercially effective (Knowlton and Allen 1936, Pletsch 1947, Al-Jabr 1999, Butler and Trumble 2012).

One potential host plant resistance mechanism for tomato psyllids that has not been studied is the incorporation of type IV trichomes producing high acylsugar levels. Many species of the Solanaceae family produce high levels of acylsugars, including *Solanum pennellii* Correll, *Solanum galapagense* S.C. Darwin and Petalta, *Solanum habrochaites*, *Solanum berthaultii* (Hawkes), and *Nicotiana tabacum* L. (Schilmiller et al. 2015, Vosman et al. 2018). Acylsugar-producing tomato lines have been tested against a variety of insect herbivores, including silverleaf whiteflies (*Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodoidae)), potato aphids (*Macrosiphum euphorbiae* (Thomas) (Hemiptera: Aphididae)), thrips (*Frankliniella fusca* (Hinds) (Thysanoptera: Thripidae)), western flower thrips (*F. occidentalis* (Pergande) (Thysanoptera: Thripidae)), serpentine leafminers (*Liriomyza trifolii* (Burgess) (Diptera: Agromyzidae)), tomato fruitworms (*Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae)), beet armyworms (*Spodoptera exigua* (Hubner) (Lepidoptera: Noctuidae)), and green peach aphids (*Myzus persicae* (Sulzer) (Hemiptera: Aphididae)) (Goffreda and Mutschler 1989, Hawthorne et al. 1992, Rodriguez et al. 1993, Juvik et al. 1994, Liedl et al. 1995, Fancelli et al. 2005, Leckie et al. 2016, Weinhold et al. 2017). In nearly all of these studies, acylsugars provided some benefit for pest population suppression.

The objective of our study was to determine whether high-level acylsugar tomato lines could provide a sustainable mechanism for management or suppression of tomato psyllid populations. To document this potential, we examined tomato lines with variable levels of acylsugars and conducted experiments to determine feeding and ovipositional preferences, as well as possible impacts on psyllid development and survival.

Materials and Methods

Characterization of Tomato Plant Lines

Four tomato lines were tested that contained high but variable levels of acylsugars. The FA2/AS and FA7/AS lines were created by individual introgressions of the quantitative trait loci FA2 and FA7 into the acylsugar chemotype line of CU071026 to create these tomato sister lines (Leckie et al. 2014). The line FA2/AS has an elongation of branched chain fatty acids and the line FA7/AS reduces elongation of fatty acids by two carbons (Smeda et al. 2017). The lines FA2/AS, CU071026, and FA7/AS contain moderate to high levels of acylsugars, and the control was the commercial line 'Yellow Pear', with low acylsugar content. All of these tomato plants were cultivated in the Insectary & Quarantine Facility greenhouse at the University of California Riverside and maintained at 21–26°C with a photoperiod of 16:8 (L:D) h. All plants were grown in UC potting mix (Matkin and Chandler 1957) and fertilized weekly with Miracle Groä (Scotts Miracle Gro Company, Marysville OH) at the recommended rate. Three weeks after germination, all plants were transferred into individual 0.9-liter greenhouse pots. Experiments were initiated when the plants in the preflowering stage reached a height of 20 cm (~5 wk following germination).

Leaf samples of tomato plants grown concurrently with the plants used in the experiments were collected for the analysis of acylsugar content. Wide-mouth 20-ml plastic scintillation vials from Laboratory Products Sales (Rochester, NY) were used for collecting samples. Each leaflet, from the top fully expanded leaf, was excised carefully with forceps and a clean razor blade to preserve acylsugar levels and avoid cross-contamination. Each sample vial contained two leaflets and was considered a replicate. Six replicate samples were collected for each tomato line. Leaflet samples were dried in an oven for 4 d at 26.5–29°C. When the samples were dry, they were analyzed for total acylsugar level using the methods

detailed in Leckie et al. (2012) and Smeda et al. (2016). This technique measures acylsugar content in terms of moles of glucose per mole of acylsugar. Acylsugar fatty acids for all plants were characterized by gas chromatography-mass spectrometry according to methods described in Leckie et al. (2014).

Psyllid Colonies

The tomato psyllid colony was originally established from a field population near Weslaco, TX, and was held in mesh cages 96 cm in length by 56 cm in width by 56 cm in height (Bugdorm from Bioquip, Rancho Dominguez, CA). The colony was maintained on potatoes ('Atlantic') and several commercial tomato cultivars including the cultivar Yellow Pear at a photoperiod of 16:8 (L:D) h. Environmental conditions were maintained at 21–26°C and 35–45% relative humidity in a greenhouse. The colony was examined using the method of Swisher et al. (2012) and confirmed as the 'central haplotype'. Approximately 6 mo before the experiment, insects were removed from the colonies and tested to confirm infection with Lso using qPCR (after Butler et al. 2011). The adults were tested in 10 groups of 3 insects. All groups tested positive for Lso infection. Voucher specimens from the *B. cockerelli* colony have been deposited in the University of California, Riverside Entomology Research Museum.

Host Plant Preference

Choice experiments were conducted to determine whether psyllid adults demonstrated a behavioral preference for settling and feeding on any of the tomato lines tested (FA7/AS, FA2/AS, CU071026, and Yellow Pear). We hypothesized that the higher levels of acylsugars in trichomes of the putatively resistant lines would reduce settling by the psyllids. To test for possible preferences, four plants, one from each of the test lines, were randomly placed in the corners of each cage (80 × 50 × 50 cm). Sixty pairs of mating adults from the main colony were collected and released from a vial placed in the center of the plants. After allowing 24 h for the adults to acclimate, the numbers of adults on each plant were counted every 24 h (between 10 am and noon) and the position of plants was rotated every day. This experiment was conducted for 12 d to ensure that all plants would survive until the experiment completed. Because some insects died over time and others were occasionally on the sides of cages, we calculated the percent of insects found on each line based on the total number of psyllids that were found on plants at each sampling date. Total numbers of adults on the plants in each cage on across all sample dates varied between 75 at the beginning of the experiment to about 30 at the end of the trial. These tests were replicated four times.

No-Choice Oviposition Experiment

Plants of each tomato line (FA7/AS, FA2/AS, CU071026, and Yellow Pear) were tested in the oviposition experiment. The two largest leaves (third and fourth leaves from the apex) of each plant were used as a replicate with a total of seven replicates per line. To retain the adult psyllids on a specific leaf, the leaf (still attached to the plant) was placed into an 18- × 15- × 16-cm clear plastic container with foam gaskets. Five pairs of mating adults were released into the container for a period of 48 h. After 48 h, the adults were removed from the container and the number of eggs was counted. An effort was made to avoid touching the leaves to prevent disrupting the trichomes and thereby reducing acylsugar content.

Growth, Survival, and Development

The same experimental design for the growth and development study was used as in the oviposition experiment. After 48 h, the

adults and the containers were removed from the plants. The numbers of all life stages were counted every 24 h. This experiment was replicated seven times and lasted for 23 d until the majority of the nymphs developed to the adult stage. Day 14 was selected for the relative growth index (RGI) analysis (Zhang et al. 1993), because this day gave the best overall coverage of multiple life stages from nymph to adult.

Data Analyses

Acylsugar level data were analyzed using analysis of variance (ANOVA) in JMP Pro 12 (SAS Institute Inc. 2015), and means were separated by Tukey–Kramer HSD ($P < 0.05$). Percent mortality data and percent survival data to the adult stage were normalized by the arcsine square root transformation prior to an ANOVA. Values were then converted back into percent mortality for presentation. Means
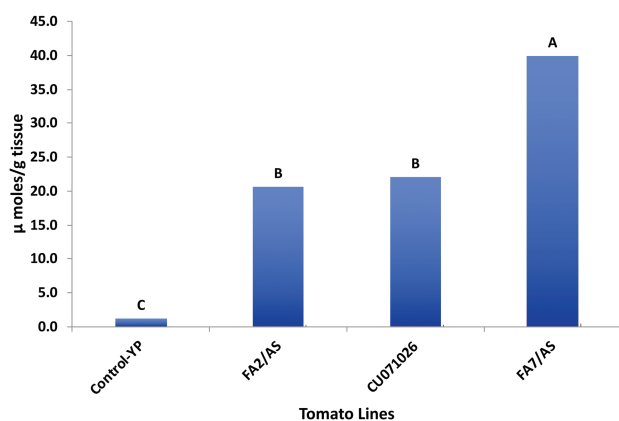
were compared with Tukey's HSD test. Oviposition data were analyzed with ANOVA followed by Tukey's HSD test.

The RGI (Zhang et al. 1993) was used to evaluate the development of the psyllid population. RGI values were calculated as

$$GI = \frac{\sum_{i-1}^{i\max} [n_{(i)}i] + \sum_{i-1}^{i\max} [n'_{(i)}(i-1)]}{Ni_{\max}},$$

where $i_{\max} = 3$ is the highest attainable stage of the insect at day 14, $n_{(1)}$ is the number of insects alive at stage i, $n'_{(i)}$ is the number of insects dead at stage i, and N is the total number of insects tested. Stages were chosen as 1 = instars 1 + 2, 2 = instars 3 + 4 + 5, and 3 = adult. This index provides an indication of the developmental stage reached by the cohort of test insects at the completion of the experiment, with values approaching one indicating a large proportion reaching the adult stage and values near zero indicating few insects surviving beyond stage 1 (first and second 185 instars).

Results and Discussion

Characterization of Acylsugars Within the Tomato Lines

The tomato lines had significant differences in acylsugar content ($F = 181.1$, df = 3, $P < 0.01$; Fig. 1). The concentration of acylsugars in the control line (Yellow Pear) was substantially lower at 1.2 µmoles/g tissue. The acylsugar contents in CU071026 and FA2/AS were at least 18 times higher than the control line, whereas that of FA7/AS was 33 times higher than the control line (Fig. 1). The highest level of acylsugars was 39.9 µmoles glucose/g in the FA7/AS tomato plants.

The total acylsugar range for the CU070126 line was previously reported as 13.6–20.8 µmoles glucose/g (Leckie et al. 2012). The mean concentration found in CU070126 in our study was 22.0 µmoles glucose/g. These results suggest that different growing conditions may have an effect on the content of acylsugars in tomato plants.
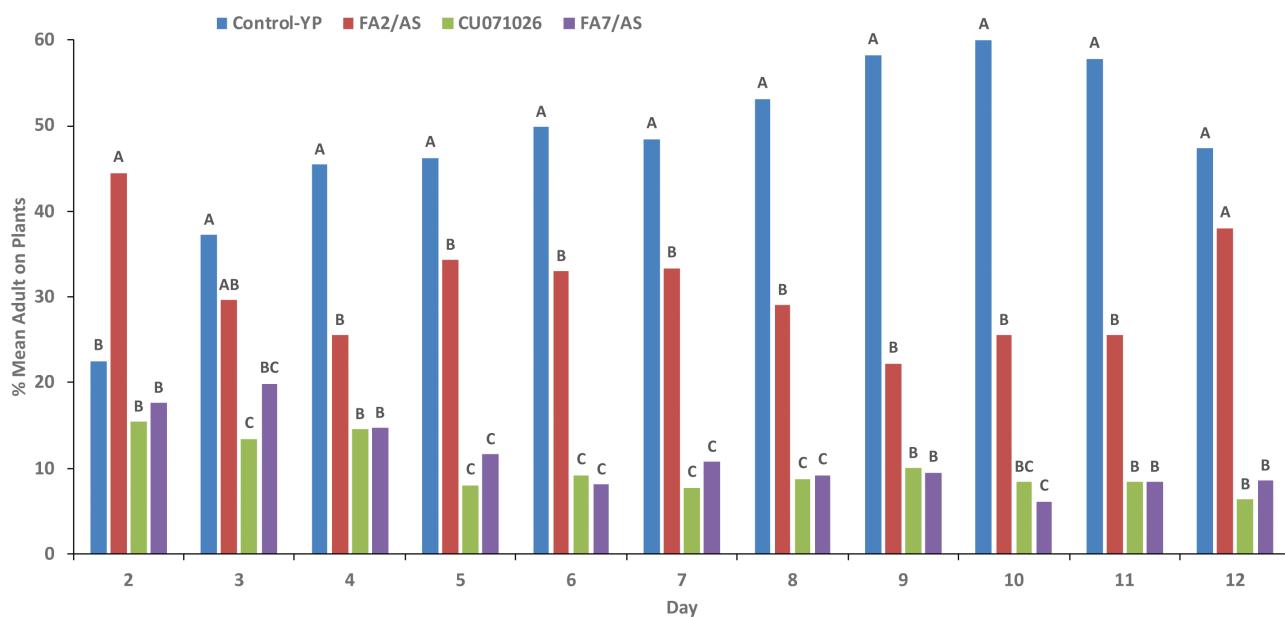

Fig. 1. Acylsugar contents of Yellow Pear (Control-YP), FA7/AS, FA2/AS, and CU071026 tomato lines. Plant lines not sharing the same letter are significantly different in acylsugar content (ANOVA, Tukey–Kramer HSD test, $F = 181.1$, df = 3, $P < 0.01$).

Fig. 2. Percent of tomato psyllid adults settling on Yellow Pear (Control-YP), FA2/AS, CU071026, and FA7/AS tomato lines over time. Within sampling dates, plant lines not sharing the same letter are significantly different (ANOVA, Tukey's HSD test, $F = 6.26$, df = 3, $P < 0.01$).

Host Plant Preference

There were significant differences in psyllid preference between the lines ($F = 6.26$, df = 3, $P < 0.01$). Yellow Pear and FA2/AS had the highest mean percent of adults that settled on plants, together accounting for 70–85% of the total population throughout the experiment. Consistently, the fewest adults were found on CU071026 and FA7/AS (Fig. 2). Additionally, the percentage of adults on the highest acylsugar tomato lines showed an overall decline over time, suggesting adults continued to move to the more acceptable lines for oviposition and nymphal survival throughout the trial. If this occurs in field plantings, there are two possible outcomes (after Kennedy 1976). First, the most commonly reported outcome is that the infected adults could leave the field to find more suitable hosts, thereby reducing both oviposition and the potential for transmission of the pathogen. A second possibility is that the increased movement of the adults would minimize the edge effects that are currently seen in the field (Prager et al. 2014a) by causing the psyllids to search for suitable hosts further into the crop. This could increase spread of the pathogen in the field and likely require changes in current sampling strategies. Large-scale field trials will be needed to document either possibility.

Although the FA2/AS line and CU071026 are related in terms of acylsugar content (FA2/AS is single-line integration with CU071026), the percentages of adults on these lines were not different on five of the sampling dates and were different on seven dates (Fig. 2). Therefore, while the preferences for FA2/AS over CU071026 are not consistent, this suggests that additional research will be needed to
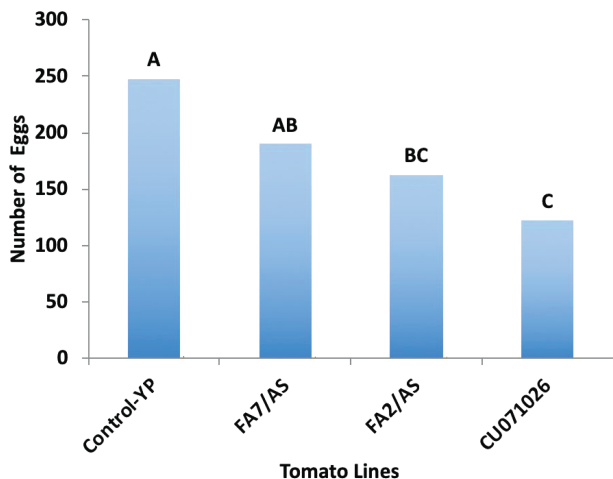
fully exploit possible additional factors in CU071026 responsible for attraction or repellency.

No-Choice Oviposition Experiment

Significant differences were found between plant lines for mean numbers of eggs oviposited in the no-choice experiment ($F = 6.31$, df = 3, $P < 0.05$). In general, the mean numbers of eggs oviposited on the high acylsugar lines were lower than on the control line (Fig. 3). The females laid a mean of 122 eggs on plants of CU071026, which was the lowest among all lines. The largest numbers of eggs were found on the Yellow Pear line, with a mean of 248 eggs. This reduced oviposition on the high-acylsugar lines is consistent with previous studies conducted on thrips and silverleaf whiteflies (Leckie et al. 2016, Smeda et al. 2018).

While there was no significant difference between mean numbers of eggs on FA7/AS and the Yellow Pear control line ($P = 0.057$), there was significantly more oviposition ($P < 0.01$) on 'Yellow Pear' than on the FA2/AS and the CU071026 lines (Fig. 3). Oviposition on the acylsugar lines may have been increased by forcing the insects to remain on these lines throughout the no-choice experiment. However, a previous study found a rather weak association between oviposition preference and subsequent nymphal developmental rates, suggesting that while the adults generally oviposit more on the most suitable plants, host plant choice is not based entirely on plant suitability for nymphal growth (Prager et al. 2014b). Regardless, any significant reductions in oviposition or survival would lower the potential for subsequent transmission of the pathogen by simply reducing the numbers of infected adults that could be generated from a cohort on an infested plant in the field.

Growth, Survival, and Development

Psyllid populations developing on the high-acylsugar tomato lines had less growth potential and reduced survivorship compared with the commercial cultivar. For all high-acylsugar plant lines, the RGI was significantly reduced compared with the commercial line, Yellow Pear ($F = 5.34$, df = 3, $P < 0.05$; Table 1). The RGI of the parental CU071026 line was the lowest at 0.37, with less than half the growth potential seen in the control line (Yellow Pear, RGI = 0.79). There were no significant differences in RGI between any of the acylsugar lines.

The majority of psyllid nymphs that died did so in the first and second instars. All nymphs successfully completing the third instar survived to the adult stage. Although some psyllids completed development to the adult stage on the high-acylsugar lines, the percent survival of psyllids reared on these lines was significantly less (range = 43.7–57.1%) than on the cultivated tomato control (83.8%) ($F = 6.05$, df = 3, $P < 0.05$).

The mortality observed in the egg stage through the second instar has interesting implications for transmission of the pathogen. Even if eggs were infected at oviposition via transovarial transmission (eggs

Fig. 3. Numbers of tomato psyllid eggs oviposited in no-choice experiment on the tomato lines Yellow Pear (Control-YP), FA7/AS, FA2/AS, and CU071026. Plant lines not sharing the same letter have significantly different numbers of eggs (ANOVA, Tukey's HSD test, $F = 6.31$, df = 3, $P < 0.05$).

Table 1. Acylsugar plant line effects on percent mortality by instar, survival to the adult stage, and RGI of the tomato psyllid

		% Mortality by stage						
	Egg	First instar	Second instar	Third instar	Fourth instar	Fifth instar	% Survival to adult	RGI
Yellow Pear (control)	4.8	4.4	5.6 C	4.0	0	0	83.8 A	0.79 A
FA7/AS	15.8	12.6	24.2 A	2.1	0	0	43.7 B	0.46 B
FA2/AS	9.8	14.7	13.5 AB	3.7	0	0	57.1 B	0.52 B
CU071026	20.5	20.5	9.0 BC	1.6	0	0	47.4 B	0.37 B

Means in columns not sharing the same letter are significantly different at the $P < 0.05$ level (ANOVA, Tukey's HSD test). Percent mortality data and data on percent survival to the adult stage were normalized by Arcsine square root transformation prior to the ANOVA.

show a 15–47% infection frequency, Hansen et al. 2008), then the >50% mortality by the end of the second instar seen in FA7/AS could reduce future spread through the field, because the reduced numbers of adults generated on infected plants would likely slow the movement of the pathogen through the field.

Potential for Use in an IPM Program

Because the high-acylsugar lines demonstrated strong antixenosis, lines containing these compounds have potential for incorporation into integrated pest management programs . Such lines might have benefit as repellant plants on the edges of fields where migrating psyllid adults tend to congregate (Prager et al. 2014a). In addition, these lines provide antibiosis effects that reduce psyllid populations and transmission of *Candidatus* Lso through reduced oviposition and substantially increased nymphal mortality. Collectively, these effects would not only negatively impact population growth within the field but also reduce emigration of infected (and uninfected) adults from these fields. However, large-scale field trials are needed to validate these hypotheses.

Acknowledgments

References Cited

Al-Jabr, A. M. 1999. Integrated pest management of tomato/potato psyllid, *Paratrioza cockerelli* (Sulc) (Homoptera: Psyllidae) with emphasis on its importance in greenhouse grown tomatoes (Ph.D. thesis). Colorado State University, Fort Collins, CO. pp. 186.

Anderson, J. A. D., P. J. Wright, P. Jaksons. A. J. Puketapu, and G. P. Walker. 2018. Assessment of tolerance to zebra chip in potato breeding lines under different insecticide regimes in New Zealand. Am. J. Potato Res. 95: 504–512.

Butler, C. D., and J. T. Trumble. 2012. The potato psyllid *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae): life history, relationship to plant diseases, and management strategies. Terr. Arthropod Rev. 5: 87–111.

Butler, C. D., B. Gonzalez, K. Manjunath, R. F. Lee, R. G. Novy, C. Miller Jr, and J. T. Trumble. 2011. Behavioral responses of adult potato psyllid, *Bactericera cockerelli* (Hemiptera: Triozidae), to potato germplasm and transmission of *Candidatus Liberibacter psyllaurous*. Crop Prot. 30: 1233–1238.

Calvo, F. J., J. C. Velázquez-González, M. B. Velásquez-González, and A. Torres. 2018. Supplemental releases of specialist parasitic wasps improve whitefly and psyllid control by *Dicyphus hesperus* in tomato. BioControl 63: 629–639.

Casteel, C. L., L. L. Walling, and T. D. Paine. 2007. Effect of Mi-1.2 gene in natal host plants on behavior and biology of the tomato psyllid *Bactericera cockerelli* (Sulc) (Hemiptera: Psyllidae). J. Entomol. Sci. 42: 155–162.

Fancelli, M., J. D. Vendramim, R. T. S. Frighetto, and A. L. Lourencao. 2005. Glandular exudate of tomato genotypes and development of *B. tabaci* (Genn.) (Sternorryncha: Aleyrodidae) biotype B. Neotrop. Entomol. 34: 659–665.

Goffreda, J. C., and M. A. Mutschler. 1989. Inheritance of potato aphid resistance in hybrids between *Lycopersicon esculentum* and *L. pennellii*. Theor. Appl. Genet. 78: 210–216.

Greenway, G., 2014. Economic impact of zebra chip control costs on grower returns in seven US States. Am. J. Potato Res. 91: 714–719.

Guenthner, J., J. Goolsby, and G. Greenway. 2012. Use and cost of insecticides to control potato psyllids and zebra chip on potatoes. Southwest. Entomol. 37: 263–270.

Hansen, A. K., J. T. Trumble, R. Stouthamer, and T. D. Paine. 2008. A new Huanglongbing species, "*Candidatus Liberibacter psyllaurous*," found to infect tomato and potato, is vectored by the psyllid *Bactericera cockerelli* (Sulc). Appl. Environ. Microbiol. 74: 5862–5865.

Hawthorne, D. M., J. A. Shapiro, W. M. Tingey, and M. A. Mutschler. 1992. Trichome- borne and artificially applied acylsugars of wild tomato deter feeding and oviposition of the leaf- miner, *Liriomyza trifolii*. Entomol. Exp. Appl. 65: 65–73.

Juvik, J., J. A. Shapiro, T. E. Young, and M. A. Mutschler. 1994. Acyl-glucoses of the wild tomato *Lycopersicon pennellii* alter behavior and reduce growth and survival of *Helicoverpa zea* and *Spodoptera exigua*. J. Econ. Entomol. 87: 482–492.

Kennedy, G. G. 1976. Host plant resistance and the spread of plant viruses. Environ. Entomol. 5: 827–832.

Knowlton, G. F., and M. Allen. 1936. Three hemipterous predators of the potato psyllid. Proc. Utah Acad. Sci. 13: 293–294.

Leckie, B. M., D. M. DeJong, and M. A. Mutschler. 2012. Quantitative trait loci increasing acylsugars in tomato breeding lines and their impacts on silverleaf whiteflies. Mol. Breed. 31: 957–970.

Leckie, B. M., R. Halitschke, D. M. De Jong, J. R. Smeda, A. Kessler, and M. A. Mutschler. 2014. Quantitative trait loci regulating the fatty acid profile of acylsugars in tomato. Mol. Breed. 34: 1201–1213.

Leckie, B. M., D. A. D'Ambrosio, T. M. Chappell, R. Halitschke, D. M. De Jong, A. Kessler, G. G. Kennedy, and M. A. Mutschler. 2016. Differential and synergistic functionality of acylsugars in suppressing oviposition by insect herbivores. PLoS One. 11: 1–19.

Liedl, B. E., D. M. Lawson, K. K. White, J. A. Shapiro, D. E. Cohen, W. G. Carson, J. T. Trumble, and M. A. Mutschler. 1995. Acylglucoses of the wild tomato *Lycopersicon pennellii* alters settling and reduces oviposition of *Bemisia argentifolii*. J. Econ. Entomol. 88: 742–748.

Liu, D., and J. T. Trumble. 2004. Tomato psyllid behavioral responses to tomato plant lines and interactions of plant lines with insecticides. J. Econ. Entomol. 97: 1078–1085.

Matkin, O. A., and P. A. Chandler. 1957. The U.C.-type mixes, pp. 68–85. *In* K. F. Baker (ed.), The U.C. system for producing healthy container-grown plants, manual 23. University of Califonia, Division of Agricultural Sciences, Agricultural Experiment Station, Extension Service, Berkeley, CA.

Mayo-Hernández, J., A. Flores-Olivas, J. Valenzuela-Soto, Y. Rodríguez-Pagaza, J. Vega-Chávez, F. Hernández-Castillo, and L. Aguirre-Uribe. 2018. *Bactericera cockerelli* sulc oviposition preference and development on three tomato varieties. Southwestern Entomol. 43: 905–910.

Pletsch, D. J. 1947. The potato psyllid, *Paratrioza cockerelli* (Sulc), its biology and control. Montana Agric. Expt. Stn. Bull. 446: 95.

Prager, S. M., and J. T. Trumble. 2018. Psyllids: biology, ecology, and management, pp. 163–181. *In* W. Wakil, G. E. Brust, and T. M. Perring (eds.), Sustainable management of arthropod pests of tomato. Academic Press, Cambridge, MA. ISBN: 9780128024416.

Prager, S. M., B. Vindiola, G. S. Kund, F. J. Byrne, and J. T. Trumble. 2013. Considerations for the use of neonicotinoid pesticides in management of *Bactericera cockerelli* (Sulk) (Hemiptera: Triozidae). Crop Prot. 54: 84–91.

Prager, S. M., C. D. Butler, and J. T. Trumble. 2014a. A binomial sequential sampling plan for the psyllid *Bactericera cockerelli* Sulc (Hemiptera: Triozidae) in tomato (*Solanum lycopersicum*). J. Econ. Entomol. 107: 838–845.

Prager, S. M., I. Esquivel, and J. T. Trumble. 2014b. Factors influencing host plant choice and larval performance in *Bactericera cockerelli*. PLoS One. 9: e94047.

Prager, S. M., G. Kund, and J. T. Trumble. 2016. Low input, low cost IPM program helps manage potato psyllid. Calif. Agric. 70: 89–95.

Prager, S. M., C. M. Wallis, M. Jones, R. Novy, and J. T. Trumble. 2018. Association of promising germplasm exhibiting tolerance to psyllids, aphids, and zebra chip disease with foliar host chemistry. J. Econ. Entomol. 111: 327–336.

Rodriguez, A. E., W. M. Tingey, and M. A. Mutschler. 1993. Acylsugars produced by type IV trichomes of *Lycopersicon pennellii* (Corr.) D'Arcy deter settling of the green peach aphid, *Myzus persicae* (Sulzer) (Homoptera: Aphididae). J. Econ. Entomol. 86: 34–39.

Rubio-Covarrubias, O. A., S. M. Prager, C. Wallis, and J. T. Trumble. 2017. Characterization of the tolerance against zebra chip disease in tubers of advanced potato lines from Mexico. Am. J. Potato Res. 94: 342–356.

SAS Institute. 2015. JMP 12.0 program. SAS Institute, Cary, NC.

Schilmiller, A. L., G. D. Moghe, P. Fan, B. Ghosh, J. Ning, A. D. Jones, and R. L. Last. 2015. Functionally divergent alleles and duplicated Loci encoding an acyltransferase contribute to acylsugar metabolite diversity in *Solanum trichomes*. Plant Cell 27: 1002–1017.

Smeda, J. R., A. L. Schilmiller, R. L. Last, and M. A. Mutschler. 2016. Introgression of acylsugar chemistry QTL modifies the composition and structure of acylsugars produced by high-accumulating tomato lines. Mol. Breed. 36: 160.

Smeda, J. R., A. L. Schilmiller, A. Kessler, and M. A. Mutschler. 2017. Combination of QTL affecting acylsugar chemistry reveals additive and epistatic genetic interactions to increase acylsugar profile diversity. Mol. Breed. 37: 104.

Smeda, J. R., A. L. Schilmiller, T. Anderson, S. Ben-Mahmoud, D. E. Ullman, T. M. Chappell, A. Kessler, and M. A. Mutschler. 2018. Combination of acylglucose QTL reveals additive and epistatic genetic interactions and impacts insect oviposition and virus infection. Mol. Breed. 38: 3.

Swisher, K. D., J. E. Munyaneza, and J. M. Crosslin. 2012. High resolution melting analysis of the cytochrome oxidase I gene identifies three haplotypes of the potato psyllid in the United States. Environ. Entomol. 41: 1019–1028.

Szczepaniec, A., K. A. Varela, M. Kiani, L. Paetzold, and C. M. Rush. 2019. Incidence of resistance to neonicotinoid insecticides in *Bactericera cockerelli* across Southwest U.S. Crop Prot. 116: 188–195.

Thomas, J. E., A. D.W. Geering, and G. Maynard. 2018. Detection of "*Candidatus Liberibactor solanacearum*" in tomato on Norfolk Island. Aust. Plant Dis. Notes. 13: 7.

Vosman, B., W. P. C. van't Westende, B. Henken, H. D. L. M. van Eekelen, R. C. H. de Vos, and R. E. Voorrips. 2018. Broad spectrum insect resistance and metabolites in close relatives of the cultivated tomato. Euphitica. 214: 46.

Weinhold, A., C. Ullah, S. Dressel, M. Schoettner, K. Gase, E. Gaquerel, S. Xu, and I. T. Baldwin. 2017. O-Acylsugars protect a wild tobacco from both native fungal pathogens and a specialist herbivore. Plant Physiol. 174: 370–386.

Zhang, M., S. K. Chaudhuri, and I. Kubo. 1993. Quantification of insect growth and its use in screening of naturally occurring insect control agents. J. Chem. Ecol. 19: 1109–1118.