Acylsugars of Wild Tomato *Lycopersicon pennellii* Alters Settling and Reduces Oviposition of *Bemisia argentifolii* (Homoptera: Aleyrodidae)

BARBARA E. LIEDL,[1] DARLENE M. LAWSON,[1] KRIS K. WHITE,[2] JOSEPH A. SHAPIRO,[1,3]
DAVID E. COHEN,[1] WILLIAM G. CARSON,[2] JOHN T. TRUMBLE,[2] AND
MARTHA A. MUTSCHLER[1,4]

J. Econ. Entomol. 88(3): 742–748 (1995)

ABSTRACT Acylsugars, the primary components of the exudate secreted by type IV trichomes of *Lycopersicon pennellii* (Corr.) D'Arcy LA716, mediate the resistance of this accession to silverleaf whitefly, *Bemisia argentifolii* Bellows & Perring, n. sp. Reduction in the settling of the adult silverleaf whiteflies correlates with the concomitant increase in applied acylsugars. Oviposition of *B. argentifolii* is also affected by acylsugars, resulting in a reduction in the number of eggs and nymphs found; however, acylsugars do not affect hatching of nymphs. The threshold amount of acylsugars required for deterring settling and oviposition is below the amount of acylsugars (50–70 μg/cm²) required for control of other insects.

KEY WORDS *Lycopersicon pennellii*, insect resistance, acylsugars

WHITEFLIES ARE A global pest affecting many crops (Butler et al. 1986, Byrne et al. 1990). Damage can either be direct, by feeding on the phloem sap and excretion of honeydew, or indirect, by way of transmission of virus diseases (van Lenteren & Noldus 1990). *Bemisia argentifolii* Bellows & Perring, n. sp., previously referred to as *B. tabaci* strain B or poinsettia strain (Bellows et al. 1994), was only identified in the United States in 1986 (Price et al. 1987), but had caused a half billion dollars in damages to the North American agriculture industry by 1991 (Perring et al. 1993).

Damage caused by insects on the tomato crop is economically substantial (Schwartz & Klassen 1981). Quality standards for this crop leave little room for cosmetic damage or contamination by insect parts, requiring the industry to rely heavily on the use of agrochemicals (Farrar & Kennedy 1991). Losses in Florida as a result of irregular ripening caused by *B. argentifolii* were estimated conservatively at $25 million in 1989 (Schuster et al. 1989). Although, control of *B. argentifolii* by a variety of insecticides has been studied (Prabhaker et al. 1989, Schuster et al. 1989), populations of silverleaf whitefly have developed resistances to all classes of commercially available insecticides (Butler et al. 1993). As a result of these problems and other health and environmental concerns, alternative methods of insect control will be needed, including development of insect-resistant crop varieties (Eigenbrode & Trumble 1994).

Wild relatives of cultivated species have often been used for crop improvement (Rick 1976). Certain ecotypes of *Lycopersicon pennellii* (Corr.) D'Arcy (formerly *Solanum pennellii* Correll) have been identified as possessing a very high degree of resistance to whiteflies (de Ponti et al. 1975, Berlinger et al. 1984) and a number of other insect pests (Gentile & Stoner 1968; Gentile et al. 1968, 1969; Juvik et al. 1982). Originally, the resistance mechanism was thought to involve trapping insects in the sticky residue of the glandular trichomes (Gentile et al. 1969). The leaves, stem, and fruit of most accessions of *L. pennellii* are covered with type IV glandular hairs, which exudes a sticky exudate primarily (90%) composed of acylsugars in *L. pennellii* LA716 (Burke et al. 1987, Goffreda et al. 1989, Steffens & Walters 1991). Removal of this exudate from *L. pennellii* increased feeding by the potato aphid, *Macrosiphum euphorbiae* (Thomas), and transfer of the exudate to *L. esculentum* reduced feeding as measured by electronic feeding monitoring (Goffreda et al. 1988). Purified acylsugars applied on synthetic feeding membranes also exhibited a feeding deterrence for *M. euphorbiae* (Goffreda et al. 1989). Moreover, acylsugars have been found to act as feeding deterrents for the greenpeach aphid, *Myzus persicae* (Sulzer), as a feeding/oviposition deterrent for leafminer species, *Liriomyza trifolii* (Burgess), and reduces growth and development in larvae of *Helicoverpa zea* (Boddie) and *Spodoptera exigua* (Hübner) (Hawthorne et al. 1992, Rodriguez et al. 1993, Ju-

---

[1] Department of Plant Breeding and Biometry, Cornell University, 252 Emerson Hall, Ithaca, NY 14853.

[2] Department of Entomology, University of California–Riverside, Riverside, CA 92521.

[3] Current address: BHN Research, 16750 Bonita Beach Road, Bonita Springs, FL 33923.

[4] To whom correspondence should be addressed.

vik et al. 1994). The amount of acylsugars needed for control of potato and green peach aphid, fruitworm, armyworm and leaf miner under laboratory conditions is ≈50–70 μg acylsugars per square centimeter.

The objectives of this study were to determine whether the acylsugars of *L. pennellii* LA716 were responsible for the previously observed resistance of this species to *B. argentifolii* and to determine a minimum level for the effective concentration of acylsugars that offers significant resistance to *B. argentifolii.*

Materials and Methods

Purification of Acylsugars. Samples of partially purified acylsugars, extracted from foliage of field-grown *L. pennellii* accession LA716, were provided by B. A. Burke (ARCO Plant Cell Research, Dublin, CA). Concentrated extract was further purified and assayed according to the method in Juvik et al. (1994).

Application and Quantification of Acylsugars. Purified acylsugars were applied to leaflets with a hobbyist's airbrush (Model H with H-3 color adjusting part, Paasche Airbrush, Harwood Heights, IL). In each experiment, a treatment of 95% ethanol (the carrier solution) was used as the control. Previous studies using this method of application showed this method to be superior to application by dipping (Hawthorne et al. 1992). The highest amount of acylsugars applied was based on the levels found for *L. pennellii* LA716 (250–600 μg/cm^2) (J.A.S., unpublished data). The amount of spray volume used in the experiments varied with the plant species to account for the differences in leaf area; however, the concentration of the solutions applied were the same. The total volume per surface used in experiments with lima beans, *Phaseolus lunatus* L. 'Henderson bush', was 0.75 ml, which was applied as two treatments of 0.375 ml. Experiments with tomatoes, *Lycopersicon esculentum* Mill., had two applications of 0.25 ml to give the final volume of 0.5 ml per surface. Because of differences in the types of chambers used, only the adaxial surface of the leaf or leaflet was treated in experiment 1 and both the abaxial and adaxial surface of each leaflet were treated in experiment 2. Two bean leaves or two leaflets per tomato leaf were treated with the same amount to approximate the amount of acylsugars applied in experiment 1 and three leaflets per tomato leaf in experiment 2. Recovery tests were made in all of the experiments except the preliminary test within experiment 1 to quantitate the amount of acylsugars applied, compared with the target levels. To do this, one leaf or leaflets from each plant or leaf was dipped into a vial of methylene chloride to remove the acylsugars which were then quantitated by a modified Nelson's assay for reducing sugars, as described by Goffreda et al. (1990). The surface area of assayed leaves or leaflets was measured with a leaf area meter (Model LI 3000, LI-COR, Lincoln, NE).

Experiment 1. Plants of *P. lunata* 'Fordhook' (seeds obtained from Burpee Seed, Warminster, PA) were grown in the greenhouses of the Department of Entomology, University of California–Riverside. Plants were used 10–14 days after planting in a UC soil mix (Matkin & Chandler 1957) under greenhouse conditions. Natural light, supplemented with metal halide lamps, provided a photoperiod of 16:8 (L:D) h, while temperatures were maintained at 80°C. Plants were watered daily and fertilized weekly with one-half strength Hoagland's solution (Downs & Helmers 1975). No pesticides were applied to the plants throughout their growth.

Field grown plants of *L. esculentum* 'Sunny' (seeds obtained from Asgrow Seed, Kalamazoo, MI) were grown with standard cultural practices and drip irrigation at the University of California South Coast Research and Education Center, Santa Ana. Leaves were cut from the stem from plants 9–10 wk after transplanting and were not treated with any pesticides. The petiole of the excised leaf was inserted into a florist water-pik (Cleveland Plant and Flower, Binghamton, NY) filled with water. All leaflets, except for the distal pair of lateral leaflets, were removed from the leaf before application of acylsugars.

Adult *B. argentifolii* were acquired from a laboratory colony maintained on a mixed culture of common bean and mustard plants maintained by T. Perring and C. Farrar (Department of Entomology, University of California–Riverside). Whiteflies were collected from the colony in a random manner to obtain a cross section of the population.

Petri dish chambers were constructed from two plastic petri dishes. The port consisted of a 1-cm diameter hole in the lid of one dish. Two small holes were made in the lids of both dishes to aspirate the whiteflies into the chamber. An organdy window was also added to the bottom of the petri dish for ventilation. The entire chamber then consisted of the bottom of one dish with an organdy window, a lid with the port and aspiration hole, and an inverted lid with an aspiration hole. The treated leaflet was placed between the two lids exposing the adaxial side of the leaflet through the port. Rubber bands were used to keep the chamber together and a ringstand was used to support the chamber clamped to the leaf (or leaflet) of the plant.

In a preliminary experiment with *P. lunatus*, plants (or leaves) were assigned randomly and sprayed with a target amounts consisting of 0, 145, and 290 μg acylsugar per square centimeter. A petri dish chamber was positioned on the treated leaf and ≈20 adult insects were placed in the chamber. Eight chambers were used for each treatment. The experiment was conducted in a growth chamber where temperatures were maintained at 23 ± 3°C and a photoperiod of 16:8 (L:D) h. Plants were watered daily and no pesticides were applied to the plants throughout their growth. Data were taken at 2, 4, 8, and 24 h by recording the number of live insects at the port. All data was analyzed by analysis of variance (ANOVA), with treatments as the main effect and separation of the treatment means was determined by subjecting the data to Fisher's protected least significant difference (LSD) test (Abacus Concepts 1989).

In the no-choice feeding assay on both *P. lunatus* and *L. esculentum*, plants (or leaves) were assigned randomly and sprayed with a target amount. Acylsugar level applied consisted of 0, 18.6, 37.3, 72.5, 145, and 290 μg acylsugar per square centimeter. A petri dish chamber was positioned on the treated leaf (or leaflet) and ≈20 adult insects were placed in the chamber. Ten chambers were used for each treatment. The final number of replicates per treatment varied because of problems in treating the plant material and constructing the experiment. The experiment was conducted in greenhouse conditions, where natural light was supplemented to provide a 16:8 (L:D) h and the plants were watered daily. Data were taken at 16 and 24 h by recording the number of live insects at the port. All data was analyzed by ANOVA with treatments as the main effect. Treatment means were separated by subjecting the data to Fisher's protected LSD test (Abacus Concepts 1989).

Experiment 2. The *L. esculentum* 'E6203' (seed obtained from J. DeVerna, Campbell Research and Technology, Davis, CA) plants were provided by E. D. Cobb (Department of Plant Breeding and Biometry, Cornell University, Ithaca, NY) and were used 3 wk after planting. All plants were grown in peat–vermiculite mix (Boodley & Sheldrake 1982) supplemented with Osmocote (Serra, Milpitas, CA); provided with a photoperiod of 16:8 (L:D) h, and temperatures were maintained at 23 ± 3°C. Plants were watered daily and fertilized weekly with Peters 9:14:15 (W. R. Grace, Fogelsville, PA). No pesticides were applied to the plants throughout their growth. The insects used for this experiment were *B. argentifolii* acquired from a laboratory colony raised on poinsettia supplied by J. Sanderson, Department of Entomology, Cornell University, Ithaca, NY.

This bioassay was performed on plant material exposed to insects in 3-liter bottle cages described in Hawthorne et al. (1992). Each bottle cage consisted of a 3-wk-old seedling trimmed to three leaflets. The apical meristem was removed, so untreated leaves did not expand during the experiment. Five treatment levels were made using 95% ethanol as the carrier solution. A control using the carrier solution was also included. All three leaflets on a plant were sprayed on both the abaxial and adaxial side with the same treatment. One of the three leaflets was removed randomly to quantify the amount of acylsugar applied. Plants were then placed in the bottle cages. Fifty adult insects collected in scintillation vials were added to the cages through the port. Bottle cages were arranged randomly in a growth chamber (23 ± 3°C and a photoperiod 16:8 [L:D] h). Numbers of live insects per bottle cage were recorded at 2 and 24 h. Adults were removed from the bottle cages at 48 h to prevent additional oviposition. After 1 wk, one leaflet was removed from each bottle cage to determine the number of eggs and a second leaflet was removed after 12 d to determine the number of nymphs per leaflet. Data was normalized by the square-root transformation and subjected to analysis by ANOVA with treatments as the main effect, treatment means were separated by Fisher's protected LSD test (Abacus Concepts 1989).

Results

Application of Acylsugars. For all experiments performed, the actual levels of acylsugars detected after application were less than the target levels. Differences between the target and actual levels may be attributed to the loss of material (overspray) in airbrush application. Because a constant volume of acylsugar solution was applied to each leaf or leaflet, variation in leaf or leaflet size may also account for some of the difference. The greatest differences between the target and actual amounts tended to occur at the lower application levels. Given the relatively small absolute difference between the target and actual amounts at these levels, we feel that the larger percentages or error may be caused primarily by error in measurement of low concentrations of the acylsugars on the leaf surfaces and variation in the size of the leaflets. An alternative method of dipping the leaf in the solution was attempted in a study by Hawthorne et al. (1992), but the coverage was patchy and left many areas bare.

Experiment 1. A preliminary test was performed on *P. lunatus* with acylsugars applied at levels found on *L. pennellii* LA 716 and the interspecific F_1 (*L. esculentum* 'New Yorker' × *L. pennellii* LA716) (Table 1). Acylsugars were significant in deterring settling of silverleaf whiteflies; most of the insects in the cage settled on leaves treated with the carrier solution and few if any were found on the port treated with acylsugars at either level. The same response was found for all four time points (2, 4, 8, and 24 h), suggesting the effect is rapid and persistent. Use of additional observation times was not practical becuase most of the insects in the treated cages were dead by 24 h, probably because of an inability to settle and, therefore, feed in the presence of acylsugars. Because, acylsugars deterred the whiteflies in this limited assay, this test was broadened to include more levels of acylsugars to be tested on both *P. lunatus* and *L. esculentum*.

Application of acylsugars were effective in reducing settling of *B. argentifolii* on leaves of *P. lunatus* (Table 2). Reduced settling occurred as great-

Table 1. Mean number ± SEM of *B. argentifolii* on *P. lunatas* treated with two levels of acylsugars after 2, 4, 8, and 24 h

Acylsugars (μg/cm^2)[a]	No. chambers	*B. argentifolii* settled			
		2 h	4 h	8 h	24 h
0.0	8	11.63 ± 1.92a	11.00 ± 2.22a	9.13 ± 1.43a	8.75 ± 1.85a
145.0	8	3.13 ± 0.83b	2.50 ± 0.78b	0.38 ± 0.38b	2.38 ± 0.87b
290.0	8	1.63 ± 0.63b	0.88 ± 0.30b	0.00b	0.63 ± 0.50b

Data are displayed as the number of silverleaf whiteflies settling. Within a column means followed by the same letter are not significantly different ($P > 0.05$; Fisher's protected LSD test [Abacus Concepts 1989]).

[a] Estimated level of acylsugars on sprayed leaflets.

er amounts of acylsugars were applied to the leaves. The target levels of acylsugars applied in the larger *P. lunatus* test ranged from 18.6 to 290 μg/cm^2; however, the actual levels of acylsugars applied were lower (8–239 μg/cm^2). The threshold of the effect of the acylsugars on *B. argentifolii* in this assay was at 29.06 μg/cm^2, because additional resistance was not gained by increasing the acylsugar concentration above this level. As observed in the preliminary study, use of additional time points past 24 h was not practical, because most of the insects in the treated chambers were dead.

Acylsugars were also effective in reducing settling of *B. argentifolii* on leaflets of *L. esculentum* (Table 3). The same target levels of acylsugars were applied as in the test on *P. lunatus*, but the actual levels of acylsugars detected were lower than the target levels (27–101 μg/cm^2) as was also observed in the test on *P. lunatus*. The effect of acylsugars was the same as in the test on *P. lunatus;* increased levels of applied acylsugars resulted in reduced settling of *B. argentifolii* on treated *L. esculentum* leaflets. The threshold of the effect of acylsugars on *B. argentifolii* in this assay was at 16.31 μg/cm^2. As in the previous test, the system becomes saturated very rapidly; we observed no difference in the effect of acylsugars on settling of *B. argentifolii* on *L. esculentum* at 24 h at acylsugar levels between 16 and 101 μg per square centimeter. The results of acylsugars on settling of *B. argentifolii* were similar at 16 h, except that the reduction in settling at acylsugar level of 101 μg/cm^2 was significantly lower than that observed at 16 or 43 μg/cm^2. Again, use of observation times beyond 24 h were not practical, because most of the insects in the treated chambers were dead.

Table 2. Mean number ± SEM of *B. argentifolii* on *P. lunatas* treated with various levels of acylsugars after 24 h

Acylsugars (μg/cm^2)[a]		No. chambers	*B. argentifolii* settled
Target	Actual		
0.0	5.47[b]	10	7.4 ± 2.06a
18.6	8.27	10	4.8 ± 0.98ab
37.3	23.30	10	3.4 ± 1.64ab
72.5	29.06	10	3.3 ± 1.02b
145.0	61.70	10	1.6 ± 1.07b
290.0	238.88	10	1.4 ± 1.40b

Data are displayed as the number of silverleaf whiteflies settling. Within a column means followed by the same letter are not significantly different ($P > 0.05$; Fisher's protected LSD test [Abacus Concepts 1989]).

[a] Estimated level of acylsugars on sprayed leaflets.

[b] This value represents the background level of acylsugar measured in a sample with only the carrier solution.

Experiment 2. Acylsugars had a significant effect in reducing the number of silverleaf whitefly eggs oviposited in 48 h and nymphs present after 12 d (Table 4). The target levels of acylsugars applied ranged from 72–290 μg/cm^2. However, as we had previously observed, the actual levels of acylsugars detected were lower (27–114 μg/cm^2). The number of *B. argentifolii* eggs oviposited decreased as the levels of acylsugar increased, with a threshold level of 27 μg/cm^2 required to observe a significant reduction of *B. argentifolii* eggs as a result of the presence of acylsugars. No acylsugar levels were tested between the control and the threshold level; therefore, lower levels of acylsugars may also have been effective. This level, however, is similar to the threshold level found for reduction in settling of *B. argentifolii* on treated tomato leaves in experiment 1. Above the threshold level, increased amounts of acylsugars elicited an additional significant reduction in the number of *B. argentifolii* eggs oviposited. However, the system rapidly became saturated and no additional reduction in the number of *B. argentifolii* eggs oviposited was observed at application levels between 42 and 114 μg/cm^2.

Acylsugar treatment also resulted in a reduction of the *B. argentifolii* nymphs present, a result which parallels the results for the number of *B. argentifolii* eggs oviposited. The threshold level (27 μg/cm^2) required for effect of acylsugars on numbers of nymphs present was the same as that required for effects on either numbers of eggs oviposited or settling of silverleaf whiteflies. Because acylsugar levels between the control and the threshold were applied, levels of acylsugar lower than the threshold may also have been effective. Above the threshold level, increased amounts of acylsugars elicited an additional significant reduction in the presence of *B. argentifolii* nymphs. Presence of nymphs requires oviposition of eggs by the female, thus, the similarity of the effects of acylsugars on the presence of *B. argentifolii* eggs and nymphs, and the fact that the average number

Table 3. Mean number ± SEM of *B. argentifolii* on *L. esculentum* treated with various levels of acylsugars after 16 and 24 h

Acylsugars (µg/cm^2)[a]		No. chambers	Whiteflies			
			16 h		24 h	
Expected	Observed		Untransformed	Transformed	Untransformed	Transformed
0.0	12.04[b]	10	12.60 ± 2.21	3.44 ± 0.30a	12.00 ± 2.19	3.33 ± 0.32a
18.6	10.55	10	7.50 ± 2.29	2.48 ± 0.39ab	8.60 ± 2.44	2.70 ± 0.39ab
37.3	9.42	11	8.82 ± 2.57	2.51 ± 0.50ab	12.09 ± 2.55	3.25 ± 0.39a
72.5	16.31	9	4.33 ± 1.14	1.79 ± 0.38b	6.22 ± 2.17	2.17 ± 0.43b
145.0	42.96	10	4.00 ± 1.35	1.67 ± 0.37b	5.1 ± 1.26	2.04 ± 0.32b
290.0	101.08	10	1.2 ± 0.73	0.57 ± 0.31c	3.8 ± 1.44	1.03 ± 0.33b

Data are displayed as the number of silverleaf whiteflies settling. Within a column means followed by the same letter are not significantly different ($P > 0.05$; Fisher's protected LSD test [Abacus Concepts 1989]). Data were analyzed using square-root transformation for statistical test.

[a] Estimated level of acylsugars on sprayed leaflets.

[b] This value represents the background level of acylsugar measured in a sample with only the carrier solution.

of nymphs emerged is roughly equivalent to the number of eggs laid per treatment, suggests that acylsugars do not affect nymph emergence.

Discussion

Substrate selection is a critical phase in the life of the silverleaf whitefly, because most silverleaf whiteflies feed and oviposit on the same leaf (van Lenteren & Noldus 1990). This selection may be based on visual, olfactory, and gustatory stimuli. Previous work suggested whiteflies distinguish between species of host plants for feeding and oviposition primarily by probing the apoplast of the mesophyll just below the epidermis, rather than by probing the phloem or olfactory cues (van Lenteren & Noldus 1990). In the case of *B. argentifolii*, oviposition usually occurs within a minute of the beginning of a penetration and terminates within 30 s, suggesting that penetration was specifically made for oviposition (Walker & Perring 1994). Host choice during oviposition is, therefore, critical for survival of the progeny, because the nymph stage is sessile and the range of movement of crawlers is extremely small effectively restricting the progeny to the leaf on which they were oviposited (Lloyd 1922, Dowell et al. 1978). Thus, oviposition is a better indicator of host-plant acceptance than feeding for *B. argentifolii* (Walker & Perring 1994).

Other researchers identified *L. pennellii* as a source of resistance for the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Gentile et al. 1968) and *B. tabaci* (Berlinger et al. 1984). Recently, *B. argentifolii* was designated a separate species rather than a strain or biotype of *B. tabaci* (Bellows et al. 1994). Because these two species are very similar morphologically, we cannot verify whether previous research was with the new species (*B. argentifolii*) or the old species (*B. tabaci*).

Our investigation showed that acylsugars from *L. pennellii* reduced both settling and oviposition of *B. argentifolii* on treated tomato leaflets and settling on lima bean leaves. We observed a significant reduction in the number of eggs oviposited on leaves treated with acylsugars suggesting that the acylsugars of *L. pennellii* LA716 reduce the acceptance of *L. esculentum* as a host plant for *B. argentifolii*. Acylsugars are effective in reducing the number of settling and ovipositing silverleaf whiteflies. Thus, acylsugars could account for at least for part of the means of resistance for silverleaf whitefly and may also be the mechanism for resistance *L. pennellii* LA716 contains to the other whitefly species.

Table 4. Mean number ± SEM of *B. argentifolii* eggs and nymphs deposited in 48 hours on *L. esculentum* leaves treated with acylsugars

Acylsugars (µg/cm^2)[a]		No. cages	Eggs		Nymphs	
Target	Actual		Untransformed data	Transformed data	Untransformed data	Transformed data
0.0	7.9 ± 4.3[b]	8	195.38 ± 17.09	13.90 ± 0.60a	159.75 ± 19.60	12.48 ± 0.77a
72.5	27.3 ± 13.3	8	13.50 ± 1.95	3.60 ± 0.30b	14.38 ± 3.28	3.44 ± 0.61b
145.0	42.4 ± 21.1	8	2.25 ± 1.86	0.70 ± 0.50c	1.38 ± 0.78	0.70 ± 0.36c
217.5	114.6 ± 40.6	8	1.00 ± 0.57	0.60 ± 0.31c	0.00	0.00c
290.0	101.1 ± 36.6	8	0.38 ± 0.38	0.22 ± 0.22c	0.00	0.00c

Data are displayed as the number of silverleaf whitefly eggs or nymphs per leaflet. Within a column means followed by the same letter are not significantly different ($P > 0.05$; Fisher's protected LSD test [Abacus Concepts 1989]).

[a] Estimated level of acylsugars on sprayed leaflets.

[b] This value represents the background level of acylsugar measured in a sample with only the carrier solution.

A similar degree in the reduction was observed for the numbers of eggs oviposited and the number of nymphs present with increasing levels of acylsugars in experiment 2, indicating the major effect of acylsugars is on oviposition, and that the effects of acylsugars on the number of nymphs is a result of its effects on the number of eggs oviposited, rather than on hatching or larval survival. Previous work with acylsugars demonstrated their effect on feeding preference or growth of *H. zea* and *S. exigua* nymphs (Juvik et al. 1994). As designed, our experiments could not determine whether acylsugars had any effect of feeding preference or behavior by the nymphs. Therefore, additional studies would be required to ascertain if acylsugars might also be effective in reducing the silverleaf whitefly population by these mechanisms.

Because application of acylsugars to the leaf or leaflet surface was sufficient to reduce settling and oviposition of *B. argentifolii*, acylsugars need not be present in a trichome or other specialized structure for efficacy. This effects of acylsugars on silverleaf whitefly settling and ovipositioning are similar to those on aphid feeding using artificial surfaces treated with acylsugars (Goffreda et al. 1988, Rodriguez et al. 1993), on leafminer oviposition using leaflets treated with acylsugars (Hawthorne et al. 1992), and on feeding, growth, and survival of fruitworm and armyworm larvae using of artificial diets supplemented with acylsugars and leaflets treated with acylsugars (Juvik et al. 1994).

A threshold level of 50–70 μg acylsugars per square centimeter has been identified under laboratory conditions as the amount required to obtain control of potato and greenpeach aphid, armyworm, fruitworm, and leafminer (Goffreda et al. 1988, Hawthorne et al. 1992, Rodriguez et al. 1993, Juvik et al. 1994). Thus, the level of acylsugar required to observe a reduction in oviposition and settling of *B . argentifolii* in our experiments is less than the levels of purified acylsugars effective for the other pests. Including our study, acylsugars have now been shown to mediate the resistance of *L. pennellii* LA716 to all six pests tested.

Transfer of acylsugar-mediated insect resistance to cultivated tomato as a means to control multiple pests could significantly reduce the use of agrochemical sprays (Mutschler et al. 1993). In previous work, concern was expressed that the levels of acylsugars required to control greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood), would create a level of stickiness that would interfere with use of the parasitoid *Encarsia formosa* (Gahan) for control of this pest in greenhouses (Berlinger & Dahan 1987, de Ponti et al. 1990). However, a breeding program currently transferring the ability to produce acylsugars to freshmaket tomatoes has resulted in lines that accumulate acylsugars at levels exceeding that required for pest deterrence in the laboratory studies. This breeding program significantly reduced infestation by *B. argentifolii* and *H. zea* in preliminary field tests (M.A.M., unpublished data), but the tomatoes are much less sticky than *L. pennellii* LA716. Therefore, effective levels of acylsugars may not endanger the concurrent use of biological control of pests. An additional benefit of use of acylsugar-mediated resistance could be the reduction or delay of spread of insect-vectored virus, because some of the insect pests affected by acylsugars have been implicated in the spread of virus. This possibility depends on the interrelationships of the pathogen, pest and host (Kennedy 1976). Detailed field trials of the efficacy of acylsugar-mediated insect resistance in the field and of the possibility for reduction in damage caused by insect-borne virus will be possible after tomato plants producing effective levels of acylsugars are fully developed.

Acknowledgments

We thank E. D. Cobb (Department of Plant Breeding and Biometry, Cornell University), J. Sanderson (Department of Entomology, Cornell University), and H. Yoshida (Department of Entomology, University of California–Riverside) for technical assistance. This research was supported by Hatch Project 149484, USDA Competitive Grant No. 90-37157-5438, California League of Food Processors and California Tomato Research Institute.

References Cited

Abacus Concepts. 1989. SuperANOVA manual, Abacus Concepts, Berkeley, CA.

Bellows, T. S., Jr., T. M. Perring, R. J. Gill & D. H. Headrick. 1994. Description of a species of *Bemisia* (Homoptera: Aleyrodidae). Ann. Entomol. Soc. Am. 87: 195–206.

Berlinger, M. J. & R. Dahan. 1987. Breeding for resistance to virus transmission by whiteflies in tomatoes. Insect. Sci. Applic. 8: 783–784.

Berlinger, M. J., R. Dahan & E. Shevach-Urkin. 1984. Resistance to the tobacco whitefly, *Bemisia tabaci*, in tomato and related species: a quick screening method. Bull. IOBC/WPRS 1984/7/4: 39–40.

Boodley, J. W. & R. Sheldrake, Jr. 1982. Cornell peat-like mixes for commercial plant growing. Cornell Coop. Ext. Inf. Bull. 43: 1–8.

Burke, B. A., G. Goldsby & J. B. Mudd. 1987. Polar epicuticular lipids of *Lycopersicon pennellii*. Phytochemistry 26: 2567–2571.

Butler, G. D., T. J. Henneberry & W. D. Hutchinson. 1986. Biology, sampling, and population dynamics of *Bemisia tabaci*. Agric. Zool. Rev. 1: 167–197.

Butler, G. D., Jr., T. J. Henneberry, P. A. Stansly & D. J. Schuster. 1993. Insecticidal effects of selected soaps oils and detergents on the sweetpotato whitefly (Homoptera: Aleyrodidae). Fla. Entomol. 76: 161–167.

Byrne, D. N., T. S. Bellows, Jr., & M. P. Parrella. 1990. Whiteflies in agricultural systems, pp. 227–261. *In* D. Gerling [ed.], Whiteflies: their bionomics, pest status and management. Intercept, Andover, Hants, UK.

Dowell, R. V., G. E., Fitzpatrick & F. W. Howard. 1978. Activity and dispersal of first instar larvae of the citrus blackfly. J. N.Y. Entomol. Soc. 86: 121–122.

Downs, R. L. & H. Helmers. 1975. Environment and the experimental control of plant growth. Academic, London.

Eigenbrode, S. D. & J. T. Trumble. 1994. Host plant resistance to insects in integrated pest management in vegetable crops. J. Agric. Entomol. 11: 201–224.

Farrar, R. R., Jr., & G. G. Kennedy. 1991. Insect and mite resistance in tomato, pp. 121–142. *In* G. Kalloo [ed.], Genetic improvement of tomato. Springer, Berlin.

Gentile, A. G. & A. K. Stoner. 1968. Resistance in *Lycopersicon* and *Solanum* species to the potato aphid. J. Econ. Entomol. 61: 1152–1154.

Gentile, A. G., R. E. Webb & A. K. Stoner. 1968. Resistance in *Lycopersicon* and *Solanum* to greenhouse whiteflies. J. Econ. Entomol. 61: 1355–1357.

1969. *Lycopersicon* and *Solanum* spp. resistant to the carmine and two-spotted spider mite. J. Econ. Entomol. 62: 834–836.

Goffreda, J. C., M. A. Mutschler & W. M. Tingey. 1988. Feeding behavior of potato aphid affected by glandular trichomes of wild tomato. Entomol. Exp. Appl. 48: 101–107.

Goffreda, J. C., M. A. Mutschler, D. A. Ave, W. M. Tingey & J. C. Steffens. 1989. Aphid deterrence by glucose esters in glandular trichome exudate of the wild tomato, *Lycopersicon pennellii*. J. Chem. Ecol. 15: 2135–2147.

Goffreda, J. C., J. C. Steffens & M. A. Mutschler. 1990. Association of epicuticular sugars with aphid resistance in hybrids with wild tomato. J. Am. Soc. Hortic. Sci. 115: 161–165.

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

Juvik, J. A., M. J. Berlinger, T. Ben-David & J. Rudich. 1982. Resistance among accessions of the genera *Lycopersicon* and *Solanum* to four of the main insect pests of tomato in Israel. Phytoparasitica 10: 145–156.

Juvik, J. A., J. A. Shapiro, T. E. Young & M. A. Mutschler. 1994. Acylglucoses from wild tomatoes alter behavior and reduce growth and survival of *Helicoverpa zea* and *Spodoptera exigua* (Lepidoptera: Noctuidae). J. Econ. Entomol. 87: 482–492.

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

Lenteren, J. C. van & L.P.J.J. Noldus. 1990. Whitefly-plant relationships: behavioural and ecological aspects, pp. 47–89. *In* D. Gerling [ed.], Whiteflies: their bionomics, pest status and management. Intercept, Andover, Hants, UK.

Lloyd, L. L. 1922. The control of the greenhouse whitefly (*Asterochiton vaporariorum*) with notes on its biology. Ann. Appl. Biol. 90: 1–32.

Matkin, O. A. & P. A. Chandler. 1957. The U.C.-type of soil mixes, pp. 68–85. *In* K. F. Baker [ed.], The U.C. system for producing healthy container-grown plants. Calif. Agric. Exp. Stn. Manage. 23.

Mutschler, M. A., J. C. Steffens & W. Tingey. 1993. Broad based insect resistance from *L. pennellii*: its nature and potential for pest control in tomato, pp. 285–290. *In* J. I. Yoder [ed.], Molecular biology of tomato: fundamental advances and crop improvement. Technomic, Lancaster, PA.

Perring, T. M., A. D. Cooper, R. J. Rodriquez, C. A. Farrar & T. S. Bellows. 1993. Identification of a whitefly species by genomic and behavioral studies. Science (Washington, DC) 259: 74–77.

Ponti, O.M.B. de, G. Pet & N. G. Hogenboom. 1975. Resistance to the glasshouse whitefly (*Trialeurodes vaporariorum* Westw.) in tomato (*Lycopersicon esculentum* Mill.) and related species. Euphytica 24: 645–649.

Ponti, O.M.B de, L. R. Romanow & M. J. Berlinger. 1990. Whitefly–plant relationships: plant resistance, pp. 91–106. *In* D. Gerling [ed.], Whiteflies: their bionomics, pest status and management. Intercept, Andover, Hants, UK.

Prabhaker, N., N. C. Toscano & D. L. Coudriet. 1989. Susceptibility of the immature and adult stages of the sweetpotato whitefly (Homoptera: Aleyrodidae) to selected insecticides. J. Econ. Entomol. 82: 983–988.

Price, J. F., D. J. Schuster & D. E. Short. 1987. Managing sweetpotato whitefly. Greenhouse Grower (December): 55–57.

Rick, C. M. 1976. Natural variability in wild species of Lycopersicon and its bearing on tomato breeding. Genet. Agric. 30: 249–259.

Rodriguez, A. E., W. M. Tingey & M. A. Mutschler. 1993. Acylsugars of *Lycopersicon pennellii* deter settling and feeding of the greenpeach aphid (Homoptera: Aphididae). J. Econ. Entomol. 86: 34–39.

Schuster, D. J., P. H. Everett, J. F. Price & J. B. Kring. 1989. Suppression of the sweetpotato whitefly on commercial fresh market tomatoes. Proc. Fla. State Hortic. Soc. 102: 374–379.

Schwartz, P. H. & W. Klassen. 1981. Estimate of losses caused by insects and mites to agricultural crops, pp. 15–77. *In* D. Pimentel [ed.], CRC handbook of pest management in agriculture, vol. 1. CRC, Boca Raton, FL.

Steffens, J. C. & D. S. Walters. 1991. Biochemical aspects of glandular trichome-mediated insect resistance in the Solanaceae, pp. 136–149. *In* P. A. Hedin [ed.], Naturally occurring pest bioregulators, ACS Symp. Ser. 449. American Chemical Society, Washington, DC.

Walker, G. P. & T. M. Perring. 1994. Feeding and oviposition behavior of whiteflies (Homoptera: Aleyrodidae) interpreted from AC electronic feeding monitor waveforms. Ann. Entomol. Soc. Am. 87: 363–374.

Received for publication 1 June 1994; accepted 29 December 1994.