Journal of Chemical Ecology, Vol. 15, No. 7, 1989

APHID DETERRENCE BY GLUCOSE ESTERS IN GLANDULAR TRICHOME EXUDATE OF THE WILD TOMATO, *Lycopersicon pennellii*

JOSEPH C. GOFFREDA,[1] MARTHA A. MUTSCHLER,[1] DIRK A. AVÉ,[1,3] WARD M. TINGEY,[2] and JOHN C. STEFFENS[1]

[1]*Department of Plant Breeding and Biometry*
[2]*Department of Entomology*
Cornell University
Ithaca, New York 14853

(Received December 28, 1987; accepted November 14, 1988)

Abstract—Settling of the potato aphid, *Macrosiphum euphorbiae*, on feeding membranes was deterred by methanolic leaf rinses of *Lycopersicon pennellii*, or of its F_1 with tomato, *L. esculentum*. The active compounds in the *L. pennellii* rinsates were identified as 2,3,4-tri-*O*-acylglucoses bearing short to medium chain length fatty acids. These compounds are localized in the glandular exudate of the type IV trichomes and may accumulate to levels in excess of 400 $\mu g/cm^2$. In choice assays, purified glucose esters from *L. pennellii* reduced aphid settling at concentrations as low as 25 $\mu g/cm^2$; at concentrations of 150 $\mu g/cm^2$ or more, all aphids avoided treated areas. Glucose esters were also active in deterring aphid settling in no-choice assays. At 100 $\mu g/cm^2$, these esters resulted in increased levels of mortality after 48 hr.

Key Words—Aphid resistance, fatty acids, glucose ester, insect resistance, *Lycopersicon esculentum*, *Macrosiphum euphorbiae*, potato aphid, Homoptera, aphididae.

INTRODUCTION

Genetic diversity within the cultivated tomato has been seriously depleted by intensive selection pressure for agronomic traits. Wild germplasm is a potential source of resistance to 30 different diseases and 16 known arthropod pests of tomato (Rick, 1982). Currently, resistance to at least 15 different diseases has

[3]Present address: Ecogen Inc. 2005 Cabot Blvd, Langhorne, Pennsylvania 19047.

0098-0331/89/0700-2135$06.00/0

been incorporated into adapted cultivars utilizing this exotic germplasm (Rick, 1984). Incorporation of insect resistance into tomato has not been as successful because of the complex nature of resistance and a lack of understanding of its biochemical and genetic basis.

Lycopersicon pennellii Corr. (D'Arcy), a wild relative of the cultivated tomato, *L. esculentum* Mill, is resistant to many arthropod pests of tomato including the potato aphid, *Macrosiphum euphorbiae* Thomas; carmine spider mite, *Tetranychus cinnabarinus* Boisduval; two-spotted spider mite, *T. urticae* Koch; glasshouse whitefly, *Trialeurodes vaporariorum* Westw.; cotton bollworm, *Heliothis armigera* Hübner; and potato tuberworm, *Phthorimaea operculella,* Zell. (De Ponti *et al.,* 1975; Gentile and Stoner, 1968; Gentile *et al.,* 1968, 1969; Juvik *et al.,* 1982). These authors have suggested that the resistance in *L. pennellii* is due to the entrapment of these pests in the viscous glandular exudate of the type IV trichomes, which are not present on the cultivated tomato (Luckwill, 1943).

However, aphid resistance in *L. pennellii* cannot be completely attributed to entrapment in the sticky glandular exudate. Although potato aphid mortality in leaf cages is significantly higher on *L. pennellii* and its F_1 than on *L. esculentum,* few adult aphids become entrapped in the glandular exudate (Goffreda *et al.,* 1988). Aphid settling is dramatically reduced on *L. pennellii,* suggesting that starvation may contribute to the high aphid mortality.

We recently characterized aphid feeding behavior on *L. pennellii, L. esculentum,* and F_1 plants using electronic monitoring techniques (Goffreda *et al.,* 1988). Feeding behavior on *L. pennellii* and F_1 plants is characterized by an increase in preprobe time, a reduction in the number of probes per unit time, and a decrease in the total time spent probing, relative to tomato. The transfer of *L. pennellii*'s glandular exudate to *L. esculentum* results in feeding behavior resembling that on *L. pennellii* and F_1 plants. Conversely, removal of the type IV glandular exudate from *L. pennellii* and the F_1 with various solvents decreases preprobe time and increases the number of probes and total time spent probing. These results suggest that the chemistry of the glandular exudate of *L. pennellii* also deters aphid feeding.

Although previous work associated *L. pennellii*'s type IV trichome exudate with resistance to aphids and other insects, relatively little is known about the chemical basis of this resistance. In this study we show that application of *L. pennellii* type IV glandular exudate to artificial feeding surfaces deters aphid settling, and we identify the chemical constituents responsible for this activity.

METHODS AND MATERIALS

Plant and Aphid Culture. Plants of *L. esculentum* cv. New Yorker, *L. pennellii* (LA 716), and their F_1 were grown from seed in soilless media, a modification of Cornell mix (Boodley and Sheldrake, 1973), supplemented with

a slow-release fertilizer. Plants were not treated with pesticides. All plants used for chemical extraction were grown to maturity (*ca.* 3 months old) in a growth chamber maintained at 29°C day and 27°C night with a relative humidity of *ca.* 65%. The chamber was illuminated with *ca.* 1300 $\mu E/m^2/s$ of fluorescent and incandescent light for a 16-hr photophase.

Aphids were obtained from a colony established from a single apterous potato aphid (*Macrosiphum euphorbiae*) collected from tomato in Ithaca, New York, in September 1985 and maintained on tomato plants cv. New Yorker in a growth chamber at 20°C. The chamber was illuminated with diffuse fluorescent light of *ca.* 55 $\mu E/m^2/s$ intensity. Apterae were gently shaken from the foliage and starved for *ca.* 3 hr prior to bioassays.

Aphid Settling Assays. Potato aphid settling behavior was assayed using a modification of the procedure described by Avé *et al.* (1987). Each feeding chamber was constructed by cutting two 1-cm^2 feeding ports in a hollow polyethylene stopper (Nalgene No. 7). A circular disk of unstretched Parafilm (American Can Company) was placed on top of the stopper and secured with another layer of Parafilm (Figure 1). A 0.9-ml volume of 20% sucrose was supported atop the feeding apparatus with another layer of stretched Parafilm, and yellow transparent disks of cellulose acetate were placed over each of the feeding ports. Tested compounds and extracts were applied to the exposed surface of the unstretched Parafilm, which was directly encountered by the aphids.

Choice Bioassays. A solution of the test material was applied to the surface of one of the two feeding ports, designated as the test port, and an equivalent volume of solvent was applied to the other feeding area (control port). Control feeding chambers were constructed by applying solvent alone to both the test and control feeding ports. Four aphids were placed in each chamber, and the distribution of aphids between the test and control ports was recorded at 2, 6, and 24 hr.

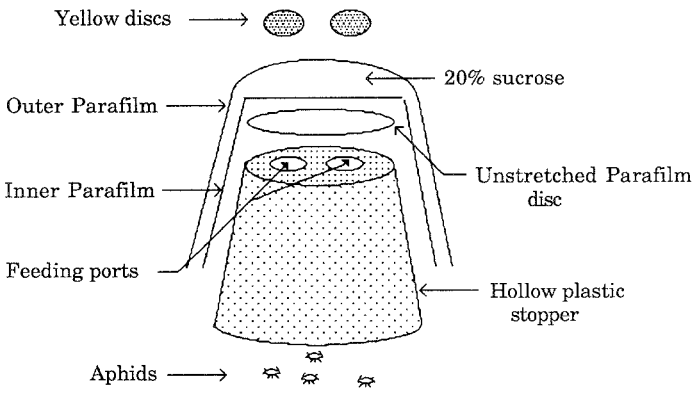

FIG. 1. Schematic diagram of aphid feeding chamber utilized in choice and no-choice assays.

Since aphids are gregarious (Dixon, 1973), each chamber was analyzed as a single experimental unit. Chambers in which there was either an equal aphid distribution between both ports or more aphids settled on the test port were scored as showing no response (NR). Chambers in which there were more aphids settled on the control port were scored as showing a response (R). Since chambers with equal aphid distributions were scored NR, the proportion of control chambers scored NR was expected to be greater than 50% on average. If a compound or extract strongly deters aphid settling, the proportion of chambers scored NR will be significantly lower than that of the control.

No-Choice Bioassays. A solution of the test material was applied to both feeding ports, and only a single aphid was placed in each chamber. Aphid settling was recorded at 2, 6, and 24 hr in short-term no-choice assays. In long-term no-choice studies each chamber was scored for whether or not the aphid was alive, and, for those still living, whether it was settled on a feeding port at 24, 48, and 72 hr.

Bioassay of Leaf Rinses. Since previous work (Goffreda *et al.*, 1988) has demonstrated that the feeding deterrent activity of *L. pennellii* can be removed by washing the leaf in alcohols, leaf rinses were assayed for activity in choice bioassays. Approximately 200 cm^2 of leaflets of *L. esculentum* cv. New Yorker, *L. pennellii* (LA 716), or their F_1 were briefly (1–3 sec) dipped in two 15-ml volumes of methanol (Fisher HPLC Grade). Microscopic examination of treated leaves revealed that the methanolic dip effectively removed the type IV trichome exudate droplets with no apparent damage to the membrane-enclosed type VI trichomes. A number of solvents are capable of efficient removal of type IV trichome exudate droplets. Alcohols such as methanol cause the least disruption of leaf and trichome metabolism; within 48 hr, leaflets treated with methanol regenerate exudate droplets. However, halogenated solvents cause wilting and death of the leaflet within a few hours after exposure.

The first and second rinses were combined and concentrated so that 10 μl of this extract represented half the exudate obtained from 1 cm^2 of leaf surface. In choice bioassays, 10 μl of the concentrated rinse was applied to the test port and allowed to dry as described above. There were 24 replicates per genotype arranged in a completely randomized design. Data were analyzed by partitioning of the likelihood ratio chi-square (G statistic) as described by Shaffer (1973).

Identification of Feeding Deterrents in L. pennellii Type IV Trichome Exudate. The glandular exudates of several hundred type IV trichomes were individually collected with a finely drawn capillary tube and injected into a Varian 3740 gas chromatograph equipped with a flame-ionization detector and a 25-m BP-5 fused silica narrow-bore capillary column (5% phenyl, methyl silicone, bonded phase, 0.25 μm) (SGE, Australia). The injection port temperature was maintained at 260°C, and the column was held at 50°C for 5 min and programmed to 250°C at 4°C/min. Identity of fatty acids in the exudate was con-

firmed by comparison of retention times and by coinjection with both free and methyl esters of fatty acid standards. Methyl ester derivatives were prepared by treatment with BF_3–methanol (Pierce Chemical Co). GC-MS of fatty acids was carried out on a Finnigan 3300 gas chromatograph–mass spectrometer in electron impact and chemical ionization modes.

Thin-layer chromatography (TLC) analysis of sugars in hydrolyzed and untreated trichome exudates was carried out on silica gel TLC plates (DC Fertigplatten Plate-Kieselgel 60 F-254) eluted twice with *n*-butanol, glacial acetic acid, ether, and distilled water (9:6:3:1) (Harborne, 1973). The plate was stained by heating with aniline–diphenylamine–phosphoric acid (Schwimmer and Bevenue, 1956).

Preparative isolation of *L. pennellii* glucose esters was achieved by a brief (1–3 sec) dip of 300 leaves in 1 liter of methanol to collect the polar epicuticular lipids; 12.5 ml of water was added to a 37.5-ml subsample of the leaf rinse and partitioned against hexane. The aqueous fraction was concentrated to a yellowish oil using a rotory evaporator equipped with a vacuum pump. The sample was taken up in a minimal volume of chloroform and purified over a Florisil column (30 × 2.5 cm) eluted with a 1.2-liter gradient of 100% chloroform to 50% chloroform–acetone. Glucose esters eluted as a clear viscous oil at approximately 20% acetone. Individual glucose esters were purified for characterization by reverse-phase HPLC (210 nm, Waters 5-micron C18 radial compression column). Authentic *L. pennellii* glucose ester standards were graciously provided by Dr. Basil Burke of Plant Cell Research Institute Inc. (Dublin, California).

Fatty acid compositions were identified as described above. Positions of esterification on the glucose esters were established by [^{1}H]NMR spectra recorded in $CDCl_3$ using a Varian XL-400 spectrometer. Spectra were referenced to $CDCl_3$ at δ7.26. High-resolution positive ion desorption chemical ionization MS spectra of purified glucose esters were recorded on a Kratos MS 890 spectrometer.

Bioassay of Purified Glucose Esters. Biological activity of purified glucose esters was assayed using choice and both short- and long-term no-choice assays as described. To ensure even coverage of glucose esters on the Parafilm, 2.5 μl of a solution of glucose esters dissolved in a mixture of acetone, chloroform, and paraffin oil (15:3:1) was applied onto the feeding membrane surface and allowed to dry. All treatments were arranged in a completely randomized design. In choice assays, glucose esters were tested at 0, 25, 50, 100, 150, and 200 $\mu g/cm^2$, with 22 replicates per concentration. In short-term no-choice assays, glucose esters were tested at 0, 50, 100, and 200 $\mu g/cm^2$, with 20 replicates per concentration. To determine if there was a relationship between the concentration of sugar esters applied and aphid settling, data were analyzed for homogeneity and tested for linearity by regression of the arcsine square root of the

proportion on the concentration of purified total glucose esters (Snedecor and Cochran, 1980). Long-term no-choice assays were conducted at two levels, 0 and 100 $\mu g/cm^2$, and analyzed by partitioning of the likelihood ratio chi square (Shaffer, 1973).

RESULTS

Leaf Rinse Bioassays. Leaf rinses from both *L. pennellii* and its F_1 with *L. esculentum* strongly deterred aphid settling on treated feeding ports in choice assays (Figure 2). Aphid response to the *L. esculentum* rinse did not differ significantly from the control chambers (Table 1). Aphid response to *L. pennellii* and F_1 leaf rinses also did not differ significantly. The chi square from the pooled data (*L. esculentum* and control vs. *L. pennellii* and F_1) was highly significant and accounted for over 90% of the total variation at each time period (Table 1).

Identification of Deterrents in Type IV Glandular Exudate and Leaf Rinses. TLC and HPLC analyses of both type IV trichome exudate and methanolic leaf rinses showed that the primary constituents of *L. pennellii* trichome exudate are glucose esters of branched short and medium chain length (C_4 to C_{12}) fatty acids. TLC analysis showed that *L. pennellii* leaf rinses, hydrolyzed by treatment with weak base, contained free glucose, which was not present in unhydrolyzed samples, suggesting esterification. Similarly, fatty acids were also not detected by GC unless injection port temperatures exceeded 150°C. The predominant fatty acids, identified by GC and GC-MS of the free acids and methyl

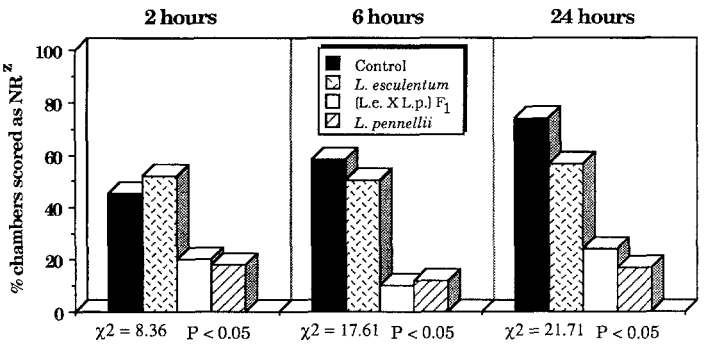

FIG. 2. Aphid settling response to leaf dip rinsate from *L. esculentum*, *L. pennellii*, and their F_1 hybrid in choice assays at 2, 6, and 24 hr. [z]Expressed as percent of the chambers scored as NR. Chambers in which there was either an equal distribution of aphids between both ports or more aphids settled on the test port were scored as showing no response (NR).

TABLE 1. APHID SETTLING RESPONSE TO LEAF DIP RINSATES OF *L. pennellii* (L.p.), *L. esculentum* (L.e.), AND F_1 AS ANALYZED BY ORTHOGONAL PARTITIONING OF LIKELIHOOD RATIO CHI SQUARE FROM CHOICE STUDIES

	Likelihood ratio chi square[a]			
Time (hr)	Total ($df = 3$)	L.p. vs. F_1 ($df = 1$)	Control (C) vs. L.e. ($df = 1$)	(L.p. and F_1) vs. (C and L.e.) ($df = 1$)
2	8.36[b]	0.03	0.22	8.11**
6	17.62***	0.03	0.26	17.33***
24	21.72***	0.36	1.55	19.81***

[a] Likelihood ratio chi square was obtained from analysis of frequency tables of chambers scored as NR and R for the different treatments.
[b] *, **, ***: $P < 0.05$, 0.01, and 0.001, respectively.

esters, include 2-methylpropanoic, 3-methylbutanoic, 8-methylnonanoic, *n*-decanoic, and *n*-dodecanoic acids. GC analysis of individually collected, type IV droplets possessed high levels of these esterified fatty acids in the same proportions as they occur in the glucose esters from the leaf rinses. Individually collected type VI trichomes did not contain detectable quantities of the esterified fatty acids.

The [^{1}H]NMR spectrum of total glucose esters from *L. pennellii* showed, in agreement with Burke *et al.* (1987), that fatty acid esterification was at positions 2, 3, and 4 of glucose for all members of the complex: δ 4.92, *dd*, J = 9.8, 3.7 Hz; δ 5.69, *t*, J = 9.8 Hz; and δ 4.95, *t*, J = 9.8 Hz for H-2, H-3, and H-4, respectively, of the α anomer. As the glucose esters are hygroscopic, and in the field are constantly exposed to moisture, it is likely that the esters exist as an anomeric mixture both on the plant as well as *in vitro*. We were unable to assign precise positions of each fatty acid on individual glucose esters by either NMR or MS. High-resolution MS of a purified ester identified by GC as composed of di-2-methylpropanoic, *n*-decanoic fatty acids gave a mass of 457.2799, satisfying the formula for $C_{24}H_{41}O_8$ (M + H − H_2O; calc. 457.2801).

Activity of L. pennellii Total Glucose Esters. In choice assays, there were highly significant deviations ($P < 0.001$) in the proportion of chambers scored as showing no response (NR) at different levels of glucose ester application for the 2-, 6-, and 24-hr time periods (Table 2). The test for linear trend was also highly significant at each time period ($P < 0.001$), indicating that there was an increase in aphid deterrence with increasing levels of glucose ester application. Aphids completely avoided the test port at concentrations of 150 $\mu g/cm^2$ and higher.

TABLE 2. APHID SETTLING RESPONSE TO *L. pennellii* TOTAL GLUCOSE ESTERS IN CHOICE ASSAYS[a]

Concentration ($\mu g/cm^2$)	Time					
	2 hours		6 hours		24 hours	
	NR (%)	*N*	NR (%)	*N*	NR (%)	*N*
Control (0)	70	20	50	20	55	20
25	44	18	44	18	21	19
50	17	18	12	16	32	19
100	16	19	9	22	15	20
150	0	19	0	19	0	21
200	0	21	0	21	0	19
Homogeneity χ^2	40.78 ($P < 0.001$)		31.33 ($P < 0.001$)		26.88 ($P < 0.001$)	
Test for linear trend ($b = 0$)	$P < 0.001$		$P < 0.001$		$P < 0.001$	

[a] Expressed as percent of chambers scored as exhibiting no response (NR).
[b] Test for linear trend in proportions is calculated by regression of the arcsine square root of the proportion NR on the concentration of purified total glucose ester applied to the feeding membrane.

In short-term no-choice assays, there was a highly significant shift ($P < 0.005$) in the proportion of aphids settled at each time period (Figure 3). There was also a highly significant linear trend ($P < 0.001$) in aphid settling with increasing levels of glucose ester application to the feeding areas. In long-term

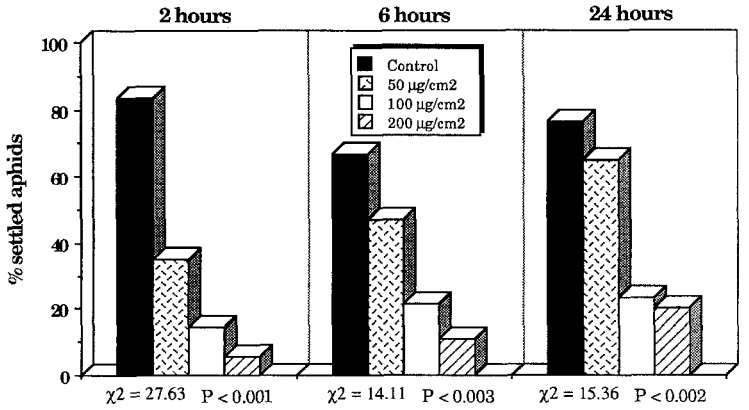

FIG. 3. Aphid settling response to *L. pennellii* total glucose esters in no-choice assays at 2, 6, and 24 hr.

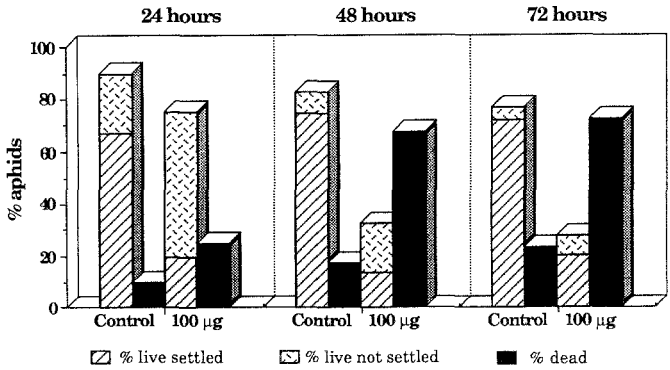

FIG. 4. Effect of *L. pennellii* total glucose esters (100 $\mu g/cm^2$) on aphid settling and mortality in long-term no-choice assays.

TABLE 3. ORTHOGONAL PARTITIONING OF LIKELIHOOD RATIO CHI SQUARE CALCULATED FROM APHID SETTLING AND MORTALITY DATA IN LONG-TERM NO-CHOICE STUDIES ON EFFECT OF TOTAL GLUCOSE ESTERS (100 $\mu g/cm^2$)

	Likelihood ratio chi square[a]		
Time (hr)	Total ($df = 2$)	Dead vs. alive ($df = 1$)	Settled vs. not settled ($df = 1$)
24	19.17***[b]	3.20	15.97***
48	31.67***	21.55***	10.12***
72	23.03***	20.21***	2.82

[a] Likelihood ratio chi square was obtained from analysis of frequency tables of chambers scored as dead, settled, and not settled for the 100 $\mu g/cm^2$ and control treatments.
[b] ***, $P < 0.001$.

no-choice assays, the proportion of living aphids settled at 24 and 48 hr was significantly lower in chambers in which 100 $\mu g/cm^2$ of total glucose esters were applied to the feeding area than in control chambers (Figure 4; Table 3). At 48 and 72 hr, the proportion of dead aphids in treated chambers was significantly higher than in control chambers ($P < 0.001$).

DISCUSSION

Settling of the potato aphid, *Macrosiphum euphorbiae,* is deterred in artificial feeding chambers by methanolic leaf rinses of *L. pennellii* and its F_1 with *L. esculentum.* In contrast, *L. esculentum* methanolic leaf rinses have no effect on aphid settling behavior.

Active compounds in the *L. pennellii* leaf rinses are 2,3,4-tri-*O*-acyl glucoses comprised of short to medium chain length fatty acids (C_4 to C_{12}). Individual collection of type IV trichome exudates confirms that these compounds are localized in the glandular exudate of this trichome. Sugar esters of short and medium chain length fatty acids are the predominant compounds in the leaf rinses of *L. pennellii* and the F_1. Few other components are detectable in either the leaf rinses or the type IV trichome exudate of these plants.

Our structural identification of these glucose esters in the trichome exudate of *L. pennellii* is in agreement with that published by Burke *et al.* (1987) and with the properties of authentic *L. pennellii* glucose ester standards (kindly supplied by B.A. Burke). Sucrose esters of similar fatty acids have been isolated from the trichomes of other insect-resistant species within the family Solanaceae, including *Nicotiana tabacum, Solanum berthaultii,* and *Lycopersicon hirsutum* (Severson *et al.*, 1985; King *et al.*, 1986, 1987).

Insecticidal properties of free decanoic and dodecanoic acids and their derivatives have been known for over 50 years (Siegler and Popenoe, 1925; Shepard, 1951). The biological effects of endogenous fatty acid esters have only recently been studied within the family Solanaceae. Johnson and Severson (1984) characterized the leaf surface chemistry of nearly 30 tobacco accessions and found one accession with high sucrose ester levels and low docosanol levels that was resistant to damage from the tobacco budworm, *Heliothis virescens.* Other research indicates that 3-methylvalerate-substituted sucrose esters of tobacco also inhibit gram-positive bacteria, including *Bacillus subtilis, B. cereus,* and *Mycobacterium theromosphactum* (Cutler *et al.*, 1986). Recent work with *Solanum berthaultii* also implicates the involvement of sucrose esters in this species' resistance to aphids (Neal *et al.*, in press) and potato late blight, *Phytphtora infestans* (Holley *et al.*, 1987).

L. pennellii glucose esters are perceived by aphids at concentrations of 25 $\mu g/cm^2$ in choice bioassays (Table 2). It is unlikely that the aphid is responding to the viscous properties of the glucose ester since these compounds only form a microscopic film at this low concentration. It is possible that abiotic or biotic conditions may hydrolyze the ester linkage, thereby liberating free short and medium chain fatty acids. Fatty acids with chain lengths of C_9 to C_{13} are disruptive to settling of the green peach aphid, *Myzus persicae* Sulzer, at concentrations of 1–100 $\mu g/cm^2$ (Greenway *et al.*, 1978). In our assays, *n*-decanoic or *n*-dodecanoic acids repel potato aphid settling at concentration of 50 $\mu g/cm^2$ (unpublished data).

L. pennellii glucose esters are also active in no-choice assays, although the threshold level of activity is higher than in choice assays; between 50 and 100 $\mu g/cm^2$ was required to detect a deterrent response at 24 hr (Figure 3). In long-term no-choice assays, there was significantly higher mortality in chambers treated with 100 $\mu g/cm^2$ than control chambers at 48 hr and 72 hr, probably

because the aphids died from starvation since they would not settle and feed (Table 3; Figure 4). There was no evidence of aphid habituation to glucose esters because the proportion of aphids that were settled on the treated feeding area remained constant through the course of the experiment. This high level of aphid deterrence possessed by glucose esters may be of practical significance in reducing the rate of virus transmission because, in many cases, aphids cease to be viruliferous minutes after acquiring a nonpersistent virus (Bradley, 1959; Harris, 1977).

The activity of individual glucose esters is not different from that of the total glucose esters, suggesting the absence of either synergistic or antagonistic interaction between individual glucose esters. Furthermore, there was little variation in deterrent activity among individual glucose ester fractions, suggesting that fatty acid chain length is not critical for deterrence (data not shown).

Polar epicuticular lipids can accumulate to concentrations exceeding 400 $\mu g/cm^2$ on *L. pennellii* foliage (Fobes *et al.*, 1985). Data presented here suggest that glucose esters may be active deterrents of aphid settling at concentrations far lower than those reported on mature *L. pennellii* plants: total avoidance was observed at concentrations as low as 150 $\mu g/cm^2$.

This high level of deterrent activity of glucose esters at relatively low concentrations should facilitate the transfer of aphid resistance into the cultivated tomato in an applied breeding program. Our research has determined that the presence of the type IV trichome is relatively simply inherited (Lemke and Mutschler, 1984), but we have had difficulty in retaining high densities of type IV trichomes bearing large exudate droplets in hybrid populations. Since fatty acid chain length on *L. pennellii* glucose esters may not be critical to the activity of these compounds in choice assays, screening plants for total epicuticular glucose esters should be effective in the development of resistant hybrids. We have developed a rapid colorimetric assay to evaluate sugar ester accumulation in large segregating populations. We are in the process of evaluating this assay as a selection technique for the development of insect-resistant tomato cultivars.

Acknowledgments—The authors are especially grateful to Dr. Basil Burke who provided us with preparative quantities of HPLC-purified glucose esters and Dr. T. Wachs for acquiring G.C./M.S. spectra. This research was supported through Hatch project numbers 149484 and 149411, U.S.D.A. and by U.S.D.A. competitive grant number 8800683.

REFERENCES

AVÉ, D.A., GREGORY, P., and TINGEY, W.M. 1987. Aphid repellent sesquiterpenes in glandular trichomes of *Solanum berthaultii* and *S. tuberosum*. *Entomol. Exp. Appl.* 44:131–138.

BOODLEY, J.W., and SHELDRAKE, R., JR. 1973. Cornell peat-like mixes for commercial plant growing. New York Agricultural Experiment Station Agricultural Information Bulletin 43.

BRADLEY, R.H.E. 1959. Loss of virus from the stylets of aphids. *Virology* 8:308–318.

BURKE, B.A., GOLDSBY, G., and MUDD, J.B. 1987. Polar epicuticular lipids of *Lycopersicon pennellii. Phytochemistry* 26:2567–2571.

CUTLER, H.G., SEVERSON, R.F., COLE, P.D., JACKSON, D.M., and JOHNSON, A.W. 1986. Secondary metabolites from plants: Their possible role as biological control agents, pp. 178–196, *in* M.B. Green and P.A. Hedin, (eds.). Natural Resistance of Plants to Pests: Role of Allelochemicals, ACS Symposium Series 296. American Chemical Society, Washington, D.C.

DE PONTI, O.M.B., PET, G., and HOGENBOOM, N.G. 1975. Resistance to the glasshouse whitefly (*Trialeurodes vaporariorum* Westw.) in tomato (*Lycopersicon esculentum* Mill.) and related species. *Euphytica* 24:645–649.

DIXON, A.F.G. 1973. Biology of Aphids. (Institute of Biology: Studies in Biology No. 44.) Edward Arnold, London. 58 pp.

FOBES, J.F., MUDD, J., and MARSDEN, M. 1985. Epicuticular lipids on the leaves of *Lycopersicon pennellii* and *L. esculentum. Plant Physiol.* 77:567–570.

GENTILE, A.G., and STONER, A.K. 1968. Resistance in *Lycopersicon* and *Solanum* to greenhouse whiteflies. *J. Econ. Entomol.* 61:1355–1357.

GENTILE, A.G., WEBB, R.E., and STONER, A.K. 1968. Resistance in *Lycopersicon* and *Solanum* to the potato aphid. *J. Econ. Entomol.* 61:1152–1154.

GENTILE, A.G., WEBB, R.E., and STONER, A.K. 1969. *Lycopersicon* and *Solanum* spp. resistant to the carmine and two-spotted spider mite. *J. Econ. Entomol.* 62:834–836.

GOFFREDA, J.C., MUTSCHLER, M.A., and TINGEY, W.M. 1988. Feeding behavior of potato aphid affected by glandular trichomes of wild tomato. *Entomol. Exp. Appl.* 48:101–107.

GREENWAY, A.R., GRIFFITHS, D.C., and LLOYD, S.L. 1978. Response of *Myzus persicae* to components of aphid extracts and to carboxylic acids. *Entomol. Exp. Appl.* 24:169–174.

HARBORNE, J.B. 1973. Phytochemical Methods: A Guide to Modern Techniques of Plant Analysis. Halsted Press, a division of John Wiley & Sons, New York.

HARRIS, K.F. 1977. An ingestion-egestion hypothesis of noncirculative virus transmission, pp. 165–220, *in* K.F. Harris and K. Maramorosch (eds.). Aphids as Virus Vectors. Academic Press, New York.

HOLLEY, J.D., KING, R.R., and SINGH, R.P. 1987. Glandular trichomes and the resistance of *Solanum berthaultii* (PI 473340) to infection from *Phytophtora infestans. Can. J. Plant Pathol.* 9:291–294.

JOHNSON, A.W., and SEVERSON, R.F. 1984. Leaf surface chemistry of tobacco budworm resistant tobacco. *J. Agric. Entomol.* 1:23–32.

JUVIK, J.A., BERLINGER, M.J., BEN-DAVID, T., and RUDICH, J. 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.

KING, R.R., PELLETIER, Y., SINGH, R.P., and CALHOUN, L.A. 1986. 3,4-Di-*O*-isobutryl-6-*O*-caprylsucrose: The major component of a novel sucrose ester complex from the type B glandular trichomes of *Solanum berthaultii* Hawkes (PI 473340). *J. Chem. Soc., Chem. Commun.* 14:1078–1079.

KING, R.R., SINGH, R.P., and BOUCHER, A. 1987. Variation in sucrose esters from the type B glandular trichomes of certain wild potato species. *Am. Potato J.* 64:529–534.

LEMKE, C.A., and MUTSCHLER, M.A. 1984. Inheritance of glandular trichomes in crosses between *Lycopersicon esculentum* and *L. pennellii. J. Am. Soc. Hortic. Sci.* 109:592–596.

LUCKWILL, L.C. 1943. The genus *Lycopersicon:* An historical, biological, and taxonomic survey of the wild and cultivated tomatoes. Aberdeen University Studies No. 120. Aberdeen Univ. Press, Scotland. 44 pp.

NEAL, J.J., TINGEY, W.M. and STEFFENS, J.C. 1989. Sucrose esters of carboxylic acids in glandular trichomes of *Solanum berthaultii* deter settling and probing by the green peach aphid. *J. Chem. Ecol.* In press.

RICK, C.M. 1982. The potential of exotic germplasm for tomato improvement, pp. 1–28, *in* I.K. Vasil, W.R. Scowcroft, and K.J. Frey (eds.). Plant Improvement and Somatic Cell Genetics. Academic Press, New York.

RICK, C.M. 1984. Conservation and use of exotic germplasm, pp. 119–144, *in* Conservation and Utilization of Exotic Germplasm to Improve Varieties, Report of the 1983 Plant Breeding Research Forum. Pioneer Hi-Bred International, Inc., Des Moines, Iowa.

SCHWIMMER, S., and BEVENUE, A. 1956. Reagent for differentiation of 1,4- and 1,6-linked glucosaccharides. *Science* 123:543–544.

SEVERSON, R.F., ARRENDALE, R.F., CHORTYK, O.T., GREEN, C.R., THOME, F.A., STEWART, J.L., and JOHNSON, A.W. 1985. Isolation and characterization of the sucrose esters of the cuticular waxes of green tobacco leaf. *J. Agric. Food Chem.* 33:870–875.

SIEGLER, E.H., and POPENOE, C.H. 1925. The fatty acids as contact insecticides. *J. Econ. Entomol.* 18:292–299.

SHAFFER, J.E. 1973. Testing specific hypotheses in contingency tables: Chi-square partitioning and other methods. *Psychol. Rep.* 33:343–348.

SHEPARD, H.H. 1951. The Chemistry and Action of Insecticides. McGraw-Hill, New York.

SNEDECOR, G.W., and COCHRAN, W.G. 1980. Statistical Methods. Iowa State University Press, Ames, Iowa.