

Sucrose Octanoate Toxicity to Brown Citrus Aphid (Homoptera: Aphididae) and the parasitoid *Lysiphlebus testaceipes* (Hymenoptera: Aphidiidae)

C. L. MCKENZIE,¹ A. A. WEATHERSBEE III,¹ WAYNE B. HUNTER,¹ AND GARY J. PUTERKA²

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ABSTRACT We report the toxicological effects of a new biorational, synthetic sucrose octanoate (AVA Chemical Ventures L.L.C., Portsmouth, NH), on brown citrus aphid, *Toxoptera citricida* (Kirkaldy), nymphs and adults and to its native parasitoid *Lysiphlebus testaceipes* (Cresson). Sucrose octanoate topically applied was equally toxic to brown citrus aphid adults and nymphs with LC₅₀ and LC₉₀ values ranging from 356 to 514 and 1029 to 1420 ppm, respectively. Mortalities of both stages did not differ significantly over time during the 3–24-h sampling period. Dry residues of sucrose octanoate exhibited similar levels of toxicity to both nymphs and adults. Mortality ranged from 60 to 70% at 6,000 ppm 4 h after exposure. *L. testaceipes* was not harmed by treatments as high as 4,000 ppm of sucrose octanoate as long as the parasitoid had mummified before treatment. Based on these results, sucrose octanoate would be a useful biorational in citrus integrated pest management programs.

KEY WORDS sugar ester, biorational, *Toxoptera citricida*

BROWN CITRUS APHID, *Toxoptera citricida* (Kirkaldy), causes serious economic damage to citrus crops throughout the world, primarily as a vector of citrus tristeza closterovirus (CTV) (Bar-Joseph et al. 1989). Brown citrus aphid is an efficient vector of CTV (Yokomi et al. 1994), and although aphids can be killed with insecticides, virus transmission may occur before death. As a result, large quantities of insecticides are currently used that are expensive to apply, and whose use raises concern over negative impacts to the crop ecosystem and human health. Brown citrus aphids feed on citrus and its close relatives. Once established, these aphids affect the same trees year after year, causing severe leaf curl during high populations and potentially spreading CTV to new plantings of citrus in the absence of any efficacious control measures. The heavy use of a single insecticide often leads to the rapid development of insecticide resistance, a major concern to growers. Imidacloprid, a systemic insecticide, is currently used against brown citrus aphid and whiteflies; however, whitefly tolerance to imidacloprid has already been observed in Arizona and Spain after only 4 yr of use in the field (Cahill et al. 1996) and more recently in Guatemala (Byrne et al. 2003). The potential to develop resistance has motivated our

group to develop biorational control products for the management of brown citrus aphid.

Plant compounds from glandular trichomes and their exudates have been shown to contain toxicants, repellents, and adherents for killing, repelling, and trapping insect pests (Johnson and Severson 1982, Dimock and Kennedy 1983, Duffey 1986, Walters et al. 1990). Severson et al. (1985) demonstrated that materials secreted by plant trichomes contained sugar esters, including sucrose esters and glucose esters, that provide wild tobacco, *Nicotiana* species, with resistance to aphids and that are toxic to the tobacco aphid, *Myzus nicotianae* Blackman (Severson et al. 1991, Xia et al. 1997); whiteflies (Buta et al. 1993); pear psylla, *Cacopsylla pyricola* Foerster (Puterka and Severson 1995); and other horticultural insect pests (Neal et al. 1994). For these reasons, we evaluated a synthetic analog of sucrose octanoate found in leaf trichomes of wild tobacco to determine its efficacy as a potential compound for use in an integrated pest management (IPM) program aimed at controlling brown citrus aphid in citrus, and to describe its potentially negative effects on *Lysiphlebus testaceipes* (Cresson), a native parasitoid of brown citrus aphid.

Materials and Methods

Mention of a trademark or proprietary product does not constitute a guarantee or warranty of the product by the U.S. Department of Agriculture and does not imply its approval to the exclusion of other products that also may be suitable.

¹ USDA-ARS, U.S. Horticultural Research Laboratory, 2001 South Rock Rd., Fort Pierce, FL 34945.

² USDA-ARS, Appalachian Fruit Research Station, 45 Wiltshire Rd., Kearneysville, WV 25430.

Insect Source and Rearing. Brown citrus aphids were collected in 1996 from field populations infesting citrus near the USDA-ARS Research Laboratory at Orlando, FL, and used to start a laboratory colony. Insects used in the experiments were obtained from this original colony of brown citrus aphid that has been

maintained by serial transfer. All stages of brown citrus aphid were reared on a combination of citrus seedlings 'Carrizo' citrange, *Poncirus trifoliate* (L.) Raf. \times *Citrus sinensis* (L.) Osbeck and 'Pineapple sweet orange', *C. sinensis* and the ornamental plant orange jasmine, *Murraya paniculata* (L.) Jack. Aphid colonies were housed in large screened cages located in an air-conditioned insectary glasshouse with ambient light and humidity. Temperatures fluctuated between day and night highs of 29.4 to 26.7°C, respectively, with an overall low of 23.9°C.

Laboratory colonies of *L. testaceipes* were established from specimens initially collected in November 1999 from brown citrus aphid infesting a potted citrus plant at the U.S. Horticultural Research Laboratory, Orlando, FL. Since then, the parasitoids have been propagated on brown citrus aphid reared on young foliage of potted sour orange, *Citrus aurantium* L., or 'Carrizo' citrange. The plants and insects were re-tained in screened cages measuring 45 by 45 by 70 cm in the insectary glasshouse described above.

Biorationals. Sucrose octanoate (SO), a synthetic analog of natural sugar esters, was provided by AVACHEM (AVA Chemical Ventures, L.L.C., Portsmouth, NH) and was used in all bioassays.

Puterka and Severson Petri Dish Spray Bioassay. Sucrose octanoate was initially screened at a wide range of concentrations from 125 to 8,000 ppm (0.03125–2.0% formulated product) to determine the response range. Serial dilutions of sucrose octanoate were prepared in double distilled (dd)H₂O plus a ddH₂O control. Orange jasmine leaves infested with brown citrus aphid (minimum of 20 per leaf) were collected immediately before treatment. Concentrations were applied to mixed populations of brown citrus aphid nymphs and apterous adults on the detached leaf by using a petri dish spray device as described previously (Puterka and Severson 1995). Plastic petri dishes (50 mm in diameter) with tight fitting lids were used to prevent aphid emigration and no filter paper was used. Brown citrus aphid nymph and apterous adults were scored separately and mortality was assessed at 3, 6, and 24 h after treatment. Each concentration was replicated five times, and the bioassays were repeated three times.

McKenzie and Cartwright Petri Dish Residue Bioassay. Commercially formulated sucrose octanoate was dissolved in denatured proprietary ethanol (95%) to make desired stock solutions. Mixed populations of nymph and adult aphids were tested with a wide range (375–12,000 ppm) of sucrose octanoate concentrations to determine whether there was a mortality response to residues following procedures described by McKenzie and Cartwright (1994). Plastic petri dishes (50 mm in diameter) with tight fitting lids were used to prevent aphid emigration. Dishes were treated with 500 μ l of each concentration of sucrose octanoate applied to the inside of both the lid and dish bottom (1 ml total per dish). After treatment, petri dishes were gently rotated to deposit residue evenly over all surfaces and then placed on an orbital shaker under a fume hood for \approx 2 h to allow the ethanol to evaporate completely. Treated dishes were immediately used for aphid bioassays. Nymph and apterous adult brown citrus aphids (20–50) were transferred with a soft camel's-hair brush from colony plants to petri dishes. When all dishes had been loaded, any aphids killed by handling were removed. Each concentration was replicated five times, bioassays were repeated four times, and mortality was assessed at 2, 3, and 4 h after treatment exposure.

Parasitoid Leaf Dip Bioassays. Fresh citrus seedlings infested with all stages of brown citrus aphid were exposed to a newly emerging (<48-h-old) laboratory colony of adult *L. testaceipes* for 24 h. Seedlings were removed and aphids monitored for mummy formation. Citrus seedlings were cut into 7.62-cm sections containing >100 aphids per cutting. Treatments were applied 8.5 d after infestation and 2 d after mummy formation was initiated, at which time sufficient mummy formation had occurred. Each section was completely submerged in a 4,000 ppm (1%) solution of sucrose octanoate until thoroughly wetted. Untreated controls were submerged in water only. Sections were placed individually into magenta boxes (66 by 99 by 68 mm) lined with a filter paper to absorb moisture and facilitate counting. Magenta box lids were equipped with a small filter for air exchange. Treatments were evaluated after 10 d for numbers of parasitoids emerged, mummies on the plant, exit holes from mum-

Table 1. Toxicity of sucrose octanoate to nymphs and apterous brown citrus aphids by using a spray petri dish bioassay system with a detached leaf substrate

Bioassay time (h)	n	Life stage	Slope \pm SE	LC ₅₀ ^a (95% FL)	LC ₉₀ ^a (95% FL)
3	1,398	Nymph	3.12 \pm 0.16	514 (403–643)	1,325 (992–2,184)
	220	Adult	2.54 \pm 0.35	444 (363–541)	1,420 (1,057–2,277)
	1,618	Total ^b	3.01 \pm 0.14	503 (398–625)	1,340 (1,005–2,178)
6	1,398	Nymph	2.89 \pm 0.15	450 (279–641)	1,247 (830–3,357)
	220	Adult	2.70 \pm 0.39	361 (297–436)	1,077 (813–1,704)
	1,618	Total ^b	2.79 \pm 0.14	435 (308–576)	1,254 (881–2,523)
24	1,398	Nymph	3.26 \pm 0.16	444 (213–684)	1,097 (708–4,102)
	220	Adult	2.78 \pm 0.39	356 (293–427)	1,029 (786–1,590)
	1,618	Total ^b	3.07 \pm 0.14	428 (253–615)	1,117 (749–2,928)

^a LC values expressed in ppm active ingredient of commercially formulated sucrose octanoate.

^b Mixed populations of nymphal and apterous adult brown citrus aphid.

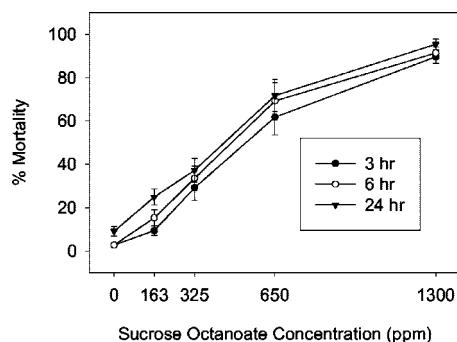


Fig. 1. Mean percentage of mortality (\pm SE) of sucrose octanoate to brown citrus aphid by using a petri dish bioassay with a detached leaf substrate.

mies on the plant, mummies off the plant, and exit holes from mummies off the plant.

Statistics. Relationships between mortality and concentration of sucrose octanoate were evaluated by probit analysis (Sparks and Sparks 1987). Differences between LC values among life stages of brown citrus aphid were determined by overlapping fiducial limits. Regression analysis was used to determine relationships between percentage of mortality and concentration of sucrose octanoate. Data were analyzed by the General Linear Models (GLM) procedure, and differences among treatment means were determined by Ryan-Einot-Gabriel-Welsch multiple-range test (REGWQ) at $\alpha = 0.05$ or pairwise *t*-tests where appropriate (SAS Institute 2000).

Results

Puterka and Severson Petri Dish Spray Bioassay. Sucrose octanoate was extremely toxic to both nymphal and apterous adult brown citrus aphid when sprayed directly on aphids by using a petri dish bioassay spray device with a detached leaf substrate (Table 1). LC₅₀ and LC₉₀ values ranged from 356 to 514 and 1,029 to 1,420 ppm, respectively, for all time points and developmental stages evaluated. Sucrose octanoate was not significantly more toxic to nymphs compared with apterous adults as indicated by overlapping LC₅₀ and LC₉₀ fiducial limits (FL), so data were combined to reflect mortality of sucrose octanoate to the total mixed population of brown citrus aphid tested (Fig. 1). Toxicity did not increase significantly over

time as indicated by overlapping LC₅₀ and LC₉₀ FL for all time points evaluated. Aphids seemed swollen immediately after being sprayed and death occurred almost instantaneously. Hour ($F = 0.78$; $df = 1, 125$; $P < 0.3793$) hour*dose ($F = 0.10$; $df = 4, 125$; $P < 0.9816$), hour*rep ($F = 0.13$; $df = 4, 125$; $P < 0.9692$), and hour*replication*dose interactions ($F = 0.14$; $df = 16, 125$; $P < 1.000$) were not significant, so data were combined for regression analysis (Table 2) and comparison to 4-h residue bioassay mortality (Fig. 3). Regression analysis of mortality data for the spray bioassay combined (all time points and life stages) provided the best line fit, with lower coefficient of variation (46.9) and higher R^2 (0.71) values compared with the residual bioassay.

McKenzie and Cartwright Petri Dish Residue Bioassay. Sucrose octanoate was not significantly more toxic to nymphs compared with apterous adults as indicated by overlapping fiducial limits for both LC values within a time point evaluation (Table 3), so data were combined by time point to reflect temporal mortality of sucrose octanoate to the total mixed population of brown citrus aphid tested (Fig. 2). Mortality reached a plateau by using the residue bioassay method, which peaked at 79% for the total mixed population of brown citrus aphid (nymph, 85%; adult, 74%). Although 100% mortality was not achieved during the times evaluated, longer times resulted in unacceptable, high levels of mortality in the controls. Concentrations $> 12,000$ ppm (3%) could not be evaluated because the residue became tacky and trapped aphids, which undoubtedly contributed to mortality not directly related to toxicity. Regression analysis for mortality data for 2-, 3-, and 4-h evaluations revealed that coefficient of variation values declined and R^2 values generally increased as time elapsed in the residual bioassay. Therefore, for this product and bioassay method, 4-h evaluations were the most consistent and thus were chosen for comparison with the spray bioassay.

Brown citrus aphids were more tolerant to sucrose octanoate when exposed to a residue compared with a directed spray bioassay (Fig. 3). Mortalities were significantly different among sucrose octanoate concentrations by using either a residue ($F = 117.0$; $df = 6, 108$; $P < 0.0001$) or spray ($F = 233.54$; $df = 4, 141$; $P < 0.0001$) bioassay and ranged from 12 to 79% and 25 to 95%, respectively. Slopes for the spray bioassay (2.70–3.26) were steeper compared with slopes for

Table 2. Regression of percentage of mortality calculated by hour for the residual bioassay or combined (3, 6, and 24 h) for the spray bioassay and dose of sucrose octanoate

Regression equation	CV	R ²	F ^a	df
Residual bioassay				
2 h % mortality = 2.37 + 0.003 (\pm 0.0003) * dose	101.55	0.49	121.16	1,124
3 h % mortality = 15.92 + 0.005 (\pm 0.0004) * dose	51.67	0.60	183.13	1,124
4 h % mortality = 21.72 + 0.006 (\pm 0.0004) * dose	47.01	0.59	181.10	1,124
Spray bioassay				
Combined % mortality = 10.49 + 0.069 (\pm 0.0033) * dose	46.86	0.71	424.54	1,177

^a *F* values calculated for each regression were significant at $P < 0.0001$ level.

Table 3. Temporal toxicity of sucrose octanoate to nymphs and apterous brown citrus aphid adults by using a residual petri dish bioassay system

Bioassay time (h)	n	Life stage	Slope \pm SE	LC ₅₀ ^a (95% FL)	LC ₉₀ ^a (95% FL)
2	2,156	Nymph	1.42 \pm 0.09	14,006 (11,692–17,479)	112,660 (76,146–185,831)
	1,917	Adult	1.56 \pm 0.11	17,390 (14,444–21,902)	115,737 (78,589–191,166)
	4,073	Total ^b	1.73 \pm 0.06	13,799 (9,408–24,671)	76,079 (38,248–247,206)
3	2,156	Nymph	1.36 \pm 0.07	4,489 (4,014–5,066)	39,344 (30,283–53,989)
	1,917	Adult	1.24 \pm 0.06	4,554 (2,892–8,734)	49,466 (20,921–331,561)
	4,073	Total ^b	1.27 \pm 0.05	4,528 (3,562–6,032)	45,903 (26,960–100,958)
4	2,156	Nymph	1.41 \pm 0.07	2,705 (2,444–2,998)	21,821 (17,686–27,979)
	1,917	Adult	1.37 \pm 0.07	2,648 (2,373–2,965)	22,696 (18,083–29,698)
	4,073	Total ^b	1.38 \pm 0.05	2,686 (2,183–3,340)	22,896 (15,283–40,259)

^a LC values expressed in ppm active ingredient of commercially formulated sucrose octanoate.

^b Mixed populations of nymphal and apterous adult brown citrus aphids.

the residual bioassay (1.24–1.73). Biologically, the slope of a probit regression line estimates the changes in activity per unit change in concentration. Use of insecticide bioassays that elicit a flat slope (>2) severely limit the validity of the results because FL of LC values are inversely related to slope (low slope equals wide FL and broad response range). For example, although the LC₅₀ FLs for 2, 3, and 4 h total mixed populations do not overlap, the LC₉₀ FLs (15,283–247,206 ppm) are so wide that they do overlap which diminishes the ability of the bioassay to predict accurate lethal concentrations for higher mortalities. Because higher sucrose octanoate concentrations could not be evaluated with this method, accurate predictions at the higher mortalities are compromised with this bioassay.

Parasitoid Leaf Dip Bioassays. Significantly more mummies were formed both on and off plants dipped in water compared with those dipped in sucrose octanoate (Table 4). However, no significant differences could be detected between treatments for percentage of adult emergence, either on or off the plant, indicating that if the aphid formed the mummy before exposure to sucrose octanoate, then that parasitoid was protected and would emerge. Aphids that had been parasitized by *L. testaceipes* but not yet mummified were susceptible to sucrose octanoate and were rapidly killed, which would account for the differences in the total numbers of mummies formed. We

speculate that after the citrus seedlings were cut and dipped, aphids began moving off the plant. This behavior has been noted previously for parasitized brown citrus aphid (A.A.W., personal observation). Aphids dipped in water continued to mummify and those dipped in sucrose octanoate died immediately, with very few making it off the plant.

Discussion

Selection and breeding of tobacco for resistance to the green peach aphid, *Myzus persicae* (Sulzer), lead to the discovery of toxic secretions from leaf trichomes of some *Nicotiana* species that confer resistance (Thurston 1961). Further screening revealed that many aphid species, including the corn leaf aphid, *Rhopalosiphum maidis* (Fitch); pea aphid, *Macrosiphum pisi* (Harris); bird cherry-oat aphid, *Rhopalosiphum padi* (L.); and yellow clover aphid, *Therioaphis trifolii* (Monell), also were susceptible to *Nicotiana* species (Thurston and Webster 1962). Chemical analysis of the constituents of the trichome exudates determined that the primary active compound was a sugar ester fraction comprised of two sucrose esters (Buta et al. 1993) and two glucose esters (Severson et al. 1994). When applied as a direct spray, our results demonstrated that brown citrus aphid is very suscep-

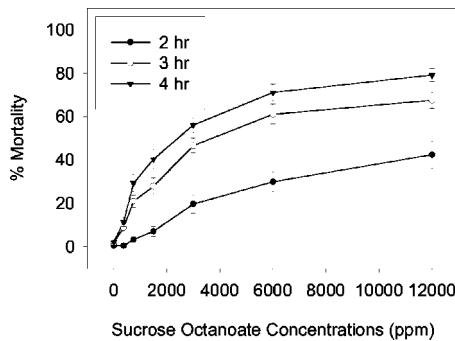


Fig. 2. Temporal mean percentage of mortality (\pm SE) of sucrose octanoate to brown citrus aphid by using a residual petri dish bioassay system.

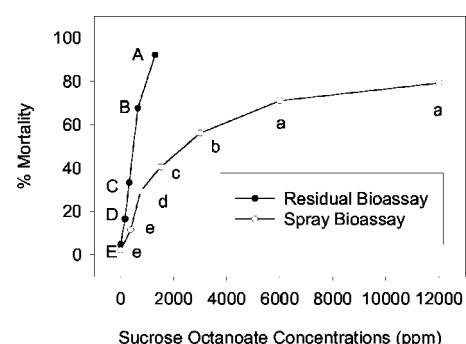


Fig. 3. Comparison of sucrose octanoate toxicity to brown citrus aphid by using spray or residual bioassays. Means within bioassay type followed by the same uppercase (spray) or lowercase (residual) letter are not significantly different ($P > 0.05$, REGWQ).

Table 4. Effect of sucrose octanoate on mummy formation and adult emergence of *L. testaceipes* from brown citrus aphid

Conc. (ppm) ^a	No. of mummies formed ^b			% Adult emergence ^b		
	On plant	Off plant	Total	On plant	Off plant	Total
0	17.6 ± 2.0a	42.4 ± 4.2a	59.9 ± 4.7a	96.6 ± 1.2a	81.2 ± 2.9a	84.9 ± 2.5a
4000	9.6 ± 1.3b	0.5 ± 0.2b	10.1 ± 1.3b	92.3 ± 3.0a	86.7 ± 13.3a	88.4 ± 3.1a

Each treatment was replicated 16 times and consisted of young citrus shoots with >100 brown citrus aphids previously exposed to *L. testaceipes* parasitoids. Treatments were applied 2 d after mummy formation was initiated.

^a Concentrations expressed in ppm active ingredient of commercially formulated sucrose octanoate.

^b Means within a column sharing the same letter were not significantly different ($P > 0.05$) by pairwise *t*-tests.

tible to sucrose octanoate (Table 1; Figs. 1 and 3), a synthetic analog of natural sugar esters found in the leaf trichomes of wild tobacco, *Nicotiana gossei* Domin. Nymphal and adult brown citrus aphids were equally susceptible regardless of the type of exposure (spray or residue) as determined by overlapping fiducial limits. Xia and Johnson (1997) reported similar sugar ester toxicity for the tobacco aphid, *Myzus nicotianae* Blackman. Puterka et al. (2003) also reported comparable sucrose octanoate toxicity levels for the tobacco aphid under similar testing procedures.

Although the exact mode of action is not known, sugar esters have been shown to have contact toxicity and very rapid knockdown ability to many soft-bodied arthropods, including aphids, mites, psyllids, and whiteflies (Neal et al. 1994, Puterka and Severson 1995, Liu et al. 1996, McKenzie and Puterka 2004). Dead nymphal and apterous adult brown citrus aphid seemed swollen immediately after being sprayed with sucrose octanoate and then rapidly desiccate after death, supporting the theory for disruption of the cuticle or cellular membranes (Thurston and Webster 1962, Puterka and Severson 1995). In contrast, brown citrus aphid exposed to residues of sucrose octanoate showed paralysis in the legs followed by the inability of the aphid to keep its balance or right itself, rapid erratic twitching of the legs, and finally death and rapid desiccation. Regardless of the type of exposure, it seems that the insect cuticle is penetrated by sucrose octanoate (Thurston and Webster 1962, Severson et al. 1994, Puterka and Severson 1995).

The level of toxicity to aphids that we observed from residues was unexpected (Table 2) because sugar esters are considered contact poisons and are mainly active in the liquid state. However, Puterka and Severson (1995) reported mortality rates as high as 67% for newly eclosed pear psylla nymphs 7 d after application to leaves and speculated the moist bodies of the newly eclosed nymphs activated the dry sugar ester residues. Furthermore, Neal et al. (1994) reported dry sugar ester residues caused significant rates of mortality (80%) to female twospotted spider mite, *Tetranychus urticae* Koch. Further testing is needed to determine the length of time residues will cause mortality; but theoretically, sucrose octanoate could provide up to 50% control of brown citrus aphid migrating into a recently sprayed grove at the current recommended field rate of 1% (4,000 ppm) (Fig. 3).

Sucrose octanoate with high monoester content had the broadest insecticidal activity when systematic al-

terations in sugar or fatty acid components of sugar ester compounds were performed to determine their influence on insecticidal properties (Puterka et al. 2003). We found sucrose octanoate to be safe for *L. testaceipes* if the parasitoid had already induced mummy formation in the aphid before exposure to sucrose octanoate (Table 4). Michaud and McKenzie (2004) found sucrose octanoate to be nontoxic to the following beneficial insects representing four orders important in biological control of homopteran pests: *Aphytis melinus* De Bach (Hymenoptera: Aphelinidae); green lacewing, *Chrysoperla rufilabris* Burmeister (Neuroptera: Chrysopidae); insidious flower bug, *Orius insidiosus* (Say) (Hemiptera: Anthocoridae); and four species of lady beetles, i.e., *Curinus coeruleus* Mulsant, *Cycloneda sanguinea* L., *Harmonia axyridis* Pallas, and *Olla v-nigrum* Mulsant (Coleoptera: Coccinellidae). Sucrose octanoate is selectively active against homopteran pests yet is nontoxic to the beneficial insects occupying the same environment and should provide an alternative insecticide for citrus growers that allow them to preserve the natural beneficial complex in their grove.

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References Cited

- Bar-Joseph, M., R. Marcus, and R. F. Lee. 1989. The continuous challenge of citrus tristeza virus control. *Annu. Rev. Phytopathol.* 27: 291–316.
- Buta, J. G., W. R. Lusby, J. W. Neal, Jr., R. M. Waters, and G. W. Pittarelli. 1993. Sucrose esters from *Nicotiana gossei* active against the greenhouse whitefly *Trialeurodes vaporariorum*. *Phytochemistry* 32: 859–864.
- Byrne, F. J., S. Castle, N. Prabhaker, and N. C. Toscano. 2003. Biochemical study of resistance to imidacloprid in B biotype *Bemisia tabaci* from Guatemala. *Pest. Manage. Sci.* 59: 347–352.
- Cahill, M., K. Gorman, S. Day, I. Denholm, A. Elbert, and R. Nauen. 1996. Baseline determination and detection of resistance to imidacloprid in *Bemisia tabaci* (Homoptera: Aleyrodidae). *Bull. Entomol. Res.* 86: 343–349.
- Dimock, M. B., and G. G. Kennedy. 1983. The role of glandular trichomes in the resistance of *Lycopersicon hirsutum*

F. *glabratum* to *Heliothis zea*. *Entomol. Exp. Appl.* 33: 263–268.

Duffey, S. S. 1986. Plant glandular trichomes: their partial role in defense against insects, pp. 151–172. In B. E. Juniper and T. R. Southwood [eds.], *Insects and the plant surface*. Edward Arnold, London, United Kingdom.

Johnson, A. W., and R. F. Severson. 1982. Physical and chemical characteristics of aphid resistant susceptible tobacco. *Tobacco Sci.* 26: 98–102.

Liu, T.-X., P. A. Stansly, and O. T. Chortyk. 1996. Insecticidal activity of natural and synthetic sugar esters against *Bemesia argentifolii* (Homoptera: Aleyrodidae). *J. Econ. Entomol.* 89: 1233–1239.

McKenzie, C. L., and B. Cartwright. 1994. Susceptibility of *Aphis gossypii* (Glover) to insecticides as affected by host plant using a rapid bioassay. *J. Entomol. Sci.* 29: 289–301.

McKenzie, C. L., and G. J. Puterka. 2004. Effect of sucrose octanoate on survival of nymphal and adult *Diaphorina citri* (Homoptera: Psyllidae). *J. Econ. Entomol.* 97: 970–975.

Michaud, J. P., and C. L. McKenzie. 2004. Safety of a novel insecticide, sucrose octanoate, to beneficial insects. *Fla. Entomol.* 87: 6–9.

Neal, J. W., Jr., J. G. Buta, G. W. Pittarelli, W. R. Lusby, and J. A. Bentz. 1994. Novel sucrose esters from *Nicotiana gossei*: effective biorationals against selected horticultural insect pests. *J. Econ. Entomol.* 87: 1600–1607.

Puterka, G. J., and R. F. Severson. 1995. Activity of sugar esters isolated from the trichomes of *Nicotiana gossei* to pear psylla (Homoptera: Psyllidae). *J. Econ. Entomol.* 88: 615–619.

Puterka, G. J., W. Farone, T. Palmer, and A. Barrington. 2003. Structure-function relationships affecting the insecticidal and miticidal activities of sugar esters. *J. Econ. Entomol.* 96: 636–644.

SAS Institute. 2000. *SAS/STAT guide for personal computers*, version 8. SAS Institute, Cary, NC.

Severson, R. F., A. W. Johnson, and D. M. Jackson. 1985. Cuticular constituents of tobacco: factors affecting their production and their role in insect disease resistance and smoke quality. *Recent Adv. Tob. Sci.* 11: 105–174.

Severson, R. F., R.V.W. Eckel, and D. M. Jackson. 1991. Effects of cuticular components from *Nicotiana* spp. on the tobacco aphid, *Myzus nicotianae* Blackman. 201st National Meeting American Chemical Society, 14–19 April 1991, Atlanta, GA. Abstr. No. 60 In Book of abstracts, part 1. Division of Agrochemicals, American Chemical Society, Washington, DC.

Severson, R. F., O. T. Chortyk, M. G. Stephenson, D. H. Akey, J. W. Neal Jr., G. W. Pettereli, D. M. Jackson, and V. A. Sisson. 1994. Characterization of natural pesticides from *Nicotiana gossei*, pp. 109–121. In P. A. Hedin [ed.], *Bio-regulators for crop protection and pest control*. Am. Chem. Soc. Symp. Series No. 557.

Sparks, T. C., and A. Sparks. 1987. *Micro Probit*. DowElanco, Greenfield, IN.

Thurston, R. 1961. Resistance in *Nicotiana* to the green peach aphid and some other tobacco insect pests. *J. Econ. Entomol.* 54: 946–949.

Thurston, R., and J. A. Webster. 1962. Toxicity of *Nicotiana gossei* Domin to *Myzus persicae* (Sulzer). *Entomol. Exp. Appl.* 5: 233–238.

Walters, D. S., R. Craig, and R. O. Mumma. 1990. Effects of tall glandular trichome exudates of geraniums on the mortality and behavior of foxglove aphid. *J. Chem. Ecol.* 16: 877–886.

Xia, Y., and A. W. Johnson. 1997. Effects of leaf surface moisture and relative humidity on the efficacy of sugar esters from *Nicotiana gossei* against the tobacco aphid (Homoptera: Aphididae). *J. Econ. Entomol.* 90: 1010–1014.

Xia, Y., A. W. Johnson, and O. T. Chortyk. 1997. Enhanced toxicity of sugar esters to the tobacco aphid (Homoptera: Aphididae) using humectants. *J. Econ. Entomol.* 90: 1015–1021.

Yokomi, R. K., R. Lastra, M. B. Stoetzel, V. C. Damsteegt, R. F. Lee, S. M. Garnsey, T. R. Gottwald, M. A. Rocha PeAa, and C. L. Niblett. 1994. Establishment of the brown citrus aphid (Homoptera: Aphididae) in Central America and the Caribbean Basin and transmission of citrus tristeza virus. *J. Econ. Entomol.* 87: 1078–1085.

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