

Response of Potato Aphid (Homoptera: Aphididae) to Synthetic Potato-Derived Colorado Potato Beetle (Coleoptera: Chrysomelidae) Attractant and Natural Potato Odor

GIRISH K. NARAYANDAS, ANDREI V. ALYOKHIN,¹ RANDY ALFORD, DONALD WEBER,²
AND JOSEPH C. DICKENS³

Department of Biological Sciences, 5722 Deering Hall, University of Maine, Orono, ME 04473

J. Econ. Entomol. 99(4): 1203–1208 (2006)

ABSTRACT A recently synthesized kairomone blend, based on the volatiles produced by potato (*Solanum* spp.) plants, has been demonstrated to be attractive to both adult and larval stages of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae). It was subsequently formulated in a viscous inert carrier for field applications and showed potential for aggregating beetles in treated areas of the field. We investigated effects of this kairomone formulation on the potato aphid, *Macrosiphum euphorbiae* (Thomas) (Homoptera: Aphididae). The response of both winged and wingless adults to natural potato foliage and synthetic kairomone was tested in a Y-tube olfactometer. Aphid response to untreated potato foliage, foliage treated with the kairomone blend, and foliage treated with blank inert carrier also was tested in petri dishes. In addition, aphid densities on field plots treated with kairomone and blank inert carrier were compared with the control plots. The untreated potato foliage was found to be attractive to wingless, but not winged, potato aphids. In the olfactometer, the foliage treated with synthetic Colorado potato beetle kairomone was not attractive to either winged or wingless aphids. In petri dishes, aphids avoided leaflets treated with both kairomone formulation and its blank carrier. There was no statistical difference between any treatments compared in the field.

KEY WORDS *Macrosiphum euphorbiae*, olfactometer, kairomone, host odor

Several synthetic kairomone blends, based on the volatiles produced by potato (*Solanum* spp.) plants, have recently been demonstrated to be attractive to both adult and larval stages of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae) (Dickens 1999, 2000, 2002). The most promising blend consists of three components: (Z)-3-hexenyl acetate, (±)-linalool, and methyl salicylate. It was combined with a proprietary inert blank carrier by Trécé, Inc. (Salinas, CA) to produce a viscous formulation suitable for field applications. Composition of the resulting formulation and volatilization rates of individual kairomone components are provided by Martel et al. (2005a). Availability of this kairomone formulation potentially opens a means to improve crop protection by manipulating beetle movement in the field (Martel et al. 2005a,b). In small-plot field studies conducted by Martel et al. (2005a), kairomone-treated potato trap crops contained more

colonizing adults, egg masses, and small larvae than untreated trap crops. Although yields on plots bordered by the treated trap crops did not differ from that on conventionally managed plots, 44% less insecticide was applied.

All components of the Colorado potato beetle kairomone are general plant volatiles (Dickens 1999, 2000, 2002). At least some aphid species are known to respond to plant odors (Nottingham et al. 1991, Nottingham and Hardie 1993, Isaacs et al. 1993, Hardie et al. 1994, Hori 1999, Eigenbrode et al. 2002), including methyl salicylate (Hardie et al. 1994, Petterson et al. 1994), linalool (Chapman et al. 1981), and (Z)-3-hexenyl acetate (Visser et al. 1996). Therefore, it is possible that field applications of kairomone may enhance aphid movement by attracting or repelling them to or from the treated foliage. This, in turn, can result in increased transmission of potato leaf roll virus (PLRV) and potato virus Y (PVY). Both of these viruses may cause substantial crop losses (Radcliffe et al. 1993).

Aphid response to host plant volatiles is still not completely understood, and the existing information is largely limited to winged forms. After testing several species in an olfactometer, Hori (1999) suggested that winged polyphagous aphids such as potato aphid *Macrosiphum euphorbiae* (Thomas) (Homoptera: Aphidi-

¹ Corresponding author, e-mail: andrei.alyokhin@umit.maine.edu.

² USDA-ARS, Beltsville Agricultural Research Center, Plant Sciences Institute, Insect Biocontrol Laboratory, BARC-West 011A Room 214, Beltsville, MD 20705.

³ USDA-ARS, Beltsville Agricultural Research Center, Plant Sciences Institute, Chemicals Affecting Insect Behavior Laboratory, Beltsville, MD 20705.

dae); green peach aphid, *Myzus persicae* (Sulzer); and cotton aphid, *Aphis gossypii* Glover, find their hosts mainly by visual cues, whereas monophagous and oligophagous aphids such as *Uroleucon* spp. tend to find their host plants by both visual and olfactory cues. However, in another polyphagous species, bean aphid *Aphis fabae* Scopoli, winged adults were attracted to its host plant odor in a number of olfactometer studies (Nottingham et al. 1991, Nottingham and Hardie 1993, Isaacs et al. 1993). The same species was repelled by the plant-derived compounds methyl salicylate and (-)-(1R,5S)-myrtenal, possibly because they are used by *A. fabae* as indicators of nutritionally unsuitable or nonhost plants (Hardie et al. 1994). Similarly, methyl salicylate reduced attractiveness of oat leaves to the bird cherry-oat aphid, *Rhopalosiphum padi* (L.), in the olfactometer tests and significantly reduced colonization of cereal fields by that species (Pettersson et al. 1994).

Little is currently known about reaction of wingless aphids to plant volatiles, even though there is significant evidence that dispersal of wingless aphids can be important for transmission of plant viruses (Ribbands 1963, Hanafi et al. 1989, Flanders et al. 1991, Hodgson 1991). The few existing studies indicate that host odors may affect aphid behavior. Eigenbrode et al. (2002) observed that volatiles from potato plants infected with PLRV attract and arrest wingless green peach aphids. Similarly, in an electroantennogram study conducted by Visser et al. (1996) on a mixture of winged and wingless forms, (Z)-3-hexenyl acetate elicited highly significant electrophysiological responses in the same species.

In Maine, the aphid community on potatoes is heavily dominated by the potato aphid, with 90–95% of all aphids found in potato crops belonging to this species (A.V.A., unpublished data). Although not as efficient a vector as the green peach aphid, potato aphid is capable of transmitting both PLRV and PVY between potato plants (Radcliffe et al. 1993). It is also highly mobile in a potato crop (Boiteau 1997, Alyokhin and Sewell 2003). Any treatment that enhances aphid movement would be likely to contribute to virus transmission; therefore, knowledge of the effect of the Colorado potato beetle kairomone on aphid movement is essential to an evaluation of its use in the potato system. In the current study, we tested response of potato aphids to its host plant volatiles, synthetic Colorado potato beetle kairomone blend, and its blank carrier.

Materials and Methods

Insects and Foliage. For all of the petri dish and olfactometer experiments, potato aphids were obtained from laboratory colonies that were reared in an environmental chamber (Percival, model I-33VL) at 20°C with a photoperiod of 18:6 (L:D) h. The aphids were fed foliage from 'Kennebec' potato grown in pots with Fafard planting mixture. The plants were maintained in the University of Maine greenhouse at 20–

25°C and natural daylength. Both winged and wingless aphids were reared and used in the experiments.

Aphid Response to Potato Foliage. Aphid responses to foliage were tested in an olfactometer (Analytical Research Systems Inc., Gainesville, FL). The olfactometer consisted of a Y-shaped glass body, a pair of odor source adapters, an insect inlet adapter, and a regulated air delivery system supplying humidified air. The dimensions of the olfactometer were 2.8 cm, uniform tube diameter; 15.24 cm, main body length; and 8.89 cm, branch length. The ends of all adapters were covered with a mesh that allows free air movement while preventing insect escape. The airflow was maintained at 0.8 liters/min throughout the experiment (Hori 1999). All experiments were 2 h and were conducted in a dark room at 22–24°C. The experiment was carried out in the dark to eliminate visual cues in identifying the host plant material. This approach was originally developed by Eigenbrode et al. (2002) for the green peach aphid, and our observations confirmed its applicability for potato aphids (Narayandas and Alyokhin 2006).

Two or three fresh potato leaves collectively weighing 1.1–1.2 g were placed in an odor source adapter designated as the treatment chamber on top of a double-layered sheet (3 by 4 cm) of paper towel moistened with distilled water. Similar moistened paper towel alone was placed inside the other odor source adapter that was designated as the control chamber.

The experiment was initiated by inserting the insect inlet adapter containing 10 potato aphids into the body of the olfactometer. The numbers of aphids in the treatment and control sides of the olfactometer were recorded. The experiment was repeated 10 times for wingless and winged aphids, with a total of 100 individuals of each morphotype tested. Treatment and control arms of the olfactometer were alternated between the trials to avoid directional bias. The apparatus was washed in acetone and air-dried after each trial.

Data normality was determined using Wilk–Shapiro test at $\alpha = 0.05$ (PROC UNIVARIATE, SAS Institute 2002) and found to be normal for both wingless ($W = 0.9606$, $P = 0.5563$) and winged aphids ($W = 0.9313$, $P = 0.1639$). A one-sample *t*-test (PROC TTEST, SAS Institute 2002) was performed to test the null hypothesis that an equal proportion of aphids would move toward each side.

Aphid Response to Synthetic Colorado Potato Beetle Attractant. The protocol was very similar to the previous experiment, but a clean piece of glass (2 by 2 cm) smeared with 0.01928 g of kairomone formulation was used instead of a potato leaflet. Formulation amount was deduced based on field application rate of 0.3415 ml per plant of 15–20-cm height with an average of 18 leaflets (Martel et al. 2005a,b). Data were found to be normal for both wingless ($W = 0.9413$, $P = 0.2545$) and winged ($W = 0.9764$, $P = 0.8812$) aphids, as determined by Wilk–Shapiro test (PROC UNIVARIATE, SAS Institute 2002).

Aphid Response to Attractant Droplets on Potato Leaflets. Glass Pyrex petri dishes (15 cm in diameter) were used as experimental arenas. The petri dishes contained a 5-mm layer of field soil that was collected from Aroostook Research Farm, Presque Isle, ME. The soil was moistened at the beginning of each trial. Two potato leaflets of similar shape and size were placed on the opposite sides of the experimental arena. Of the two leaflets, one was left untreated and other was treated with kairomone formulation. There were three different application rates: 0.00964, 0.01928, and 0.03857 g per leaflet. These rates correspond, respectively, to half, full, or twice the field application rate of 0.3415 ml per plant of 15–20-cm height with an average of 18 leaflets (Martel et al. 2005a,b).

The experiment was initiated by releasing 10 wingless potato aphids in the center of each petri dish with their heads facing in the direction perpendicular to the imaginary line connecting the centers of the leaflets. We limited tests to wingless aphids only because olfactometer experiments showed them to be more responsive to olfactory stimuli (see below). The same procedure was replicated with 12 petri dishes for each treatment. After the aphid release, the experimental arenas were placed in a growth chamber at 20°C for 2 h. The numbers of aphids on treated and untreated leaflets were then recorded. The data were found to be normal ($W = 0.9706$, $P = 0.0905$) by using Wilk-Shapiro test (PROC UNIVARIATE, SAS Institute 2002) and analyzed with split-plot analysis of variance (ANOVA) (PROC GLM, SAS Institute 2002). Kairomone application rates were considered to be main plot effects, and treated and untreated leaflets were considered to be subplot effects.

Aphid Response to Blank Carrier Droplets on Potato Leaflets. This experiment was conducted to test whether the effect observed in the previous experiment was because of the kairomone or blank carrier used for field kairomone applications. We followed the same procedure as described above except that the three leaflets were placed equidistant within the petri dish. One leaflet was treated with the kairomone formulation (kairomone plus blank inert carrier), the second leaflet was treated with the blank inert carrier, and the third leaflet was left untreated and used as control. The experiment was initiated by releasing the aphids. Application rates were 0.01928 g per leaflet for both kairomone formulation and blank carrier. The data were found to be normal ($W = 0.9661$, $P = 0.4390$) using Wilk-Shapiro test (PROC UNIVARIATE, SAS Institute 2002) and analyzed using ANOVA (PROC GLM, SAS Institute 2002).

Effect of Attractant Applications on Peak Aphid Densities during 2003 Field Season. We compared aphid densities on control plots, plots treated with kairomone formulation, and plots treated with blank carrier. For each treatment, five 15.6-m-long and four-row-wide experimental plots were planted with certified seed potatoes, providing six replications per treatment. Plots were arranged in a randomized complete block design. 'Kennebec' seed tubers were cut into 75–80 g pieces before planting. The distance be-

tween the rows was ≈ 90 cm, and seed spacing was ≈ 35 cm. Approximately 1.8 m was left between the plots within each block, and blocks were spaced at ≈ 3 m. All plots were fertilized with 14–14–14 (N–P–K) fertilizer at planting at the rate of 200 kg N ha⁻¹ and sprayed weekly with 1.2–4.9 liters ha⁻¹ mancozeb to control fungal diseases. Potatoes were grown in a 3-yr rotation with small grains and clover.

Kairomone formulation was applied twice during the season at a rate of 0.9 ml per 1 row meter. That rate was shown to aggregate Colorado potato beetles on small field plots in the study by Martel et al. (2005a). The first application was directed against overwintering adults and was made at 80% plant emergence from the soil. It was made using a CO₂-powered syringe applicator supplied by Trécé, Inc. The second application was directed against summer generation adults and was made at the peak of their eclosion from pupae. It was made using commercially available paint sprayers (model 120, HomeRight, Minneapolis, MN). The switch in application mode was made for operational reasons. Later comparison (see below) did not find any difference in aphid densities on plots treated using syringes and paint sprayers.

Aphid populations were sampled four times (4, 6, 8, and 14 August) during the period of their peak abundance as determined from weekly sampling of adjacent insecticide trial plots. Twenty plants were randomly selected from each experimental plot, and the number of potato aphids was recorded for one top, middle, and bottom leaf of each selected plant. The data were analyzed using repeated measures ANOVA (PROC GLM, SAS Institute 2002).

Effect of Attractant and Carrier Applications on Aphid Densities and Virus Spread during 2004 Field Season. We compared aphid densities on control plots, plots treated with kairomone formulation, and plots treated with blank carrier. Experimental design and plot maintenance were very similar to the 2003 growing season, except that six plots were set up for each treatment. Kairomone and blank carrier were applied twice during the season at a rate of 0.9 ml per 1 row meter (Martel et al. 2005a). The first spray was directed against overwintering adults and was applied at 80% plant emergence from the soil. The second spray was directed against small larvae and applied at $\approx 70\%$ egg hatch. Applications of kairomone formulation and blank carrier on three plots at each treatment were made using commercially available paint sprayers (model 120, HomeRight). Applications on the other three plots were made using disposable plastic syringes.

Before furrow closure, 10 certified seed pieces in control plots and kairomone-treated plots were manually replaced with seed pieces deliberately infected with PLRV. Another 10 seed pieces were replaced with the seed pieces infected with PVY. This provided an overall incidence of 5% for each of the two viruses. Infected pieces were marked at planting so that the tubers produced by infected plants would not be sampled at harvest. Unmarked plants developing from accidentally infected seed pieces and showing viral

symptoms after emergence from the soil were rogued out to maintain 5% inoculum level within the experimental plots. Fifty-two tubers (13 tubers selected at random from each row) were harvested and stored over the winter at 4°C. The following spring, collected tubers were planted in the field and emerging plants were visually examined for the symptoms of PLRV and PVY infections. Results of visual inspections were confirmed with enzyme-linked immunosorbent assay (ELISA) (Pathoscreen, Agdia Company, Elkhart, IN). ELISA protocol followed a standard procedure according to the instructions supplied by Agdia with the ELISA kit.

Twenty plants were randomly selected at weekly intervals from each plot, and the number of potato aphids was recorded for one top, middle, and bottom leaf of each selected plant. The data were analyzed using repeated measures ANOVA. Because application method did not affect larval densities ($F = 1.46$; $df = 1, 2$; $P = 0.3499$) and its interaction with treatment was not significant ($F = 2.68$; $df = 1, 2$; $P = 0.2430$), the data from plots treated using paint sprayers and syringes were pooled.

Results

Aphid Response to Potato Foliage. The proportions of wingless aphids that moved (either to the treatment chamber or to the control chamber) and the proportions that did not respond in the olfactometer were 79 and 21%, respectively. Of those aphids that moved, $70 \pm 5.5\%$ moved to the treatment chamber. Effect of potato foliage was statistically significant ($T = 3.59$, $df = 9$, $P = 0.0058$). The proportion of winged aphids that moved and the proportions that remained stationary were 73 and 27%, respectively. The trend was similar for the winged aphids, with $63 \pm 8\%$ arriving to the treatment chamber. However, percentage of aphids moving toward potato leaflet was not significantly different from 50% ($T = 1.58$, $df = 9$, $P = 0.1478$).

Aphid Response to the Synthetic Colorado Potato Beetle Attractant. Fifty-four percent of wingless aphids and 64% of winged aphids moved either to the treatment chamber or the control chamber. On average, $61 \pm 7.5\%$ of moving wingless aphids and $44 \pm 7.4\%$ of moving winged aphids arrived to the treatment side of the olfactometer. Kairomone was neither attractive nor repellent for either wingless ($T = 1.49$, $df = 9$, $P = 0.1701$) or winged ($T = 0.79$, $df = 9$, $P = 0.4509$) morphotype.

Aphid Response to Kairomone Droplets on Potato Leaflets. Aphid density was lower for attractant treated than for untreated leaflets (Fig. 1). The difference between aphid densities on treated and untreated leaflets was highly significant ($F = 10.24$; $df = 1, 11$; $P = 0.0085$). There was no difference found in aphid response to the varying rates of kairomone applications used in this experiment ($F = 0.01$; $df = 2, 44$; $P = 0.9869$).

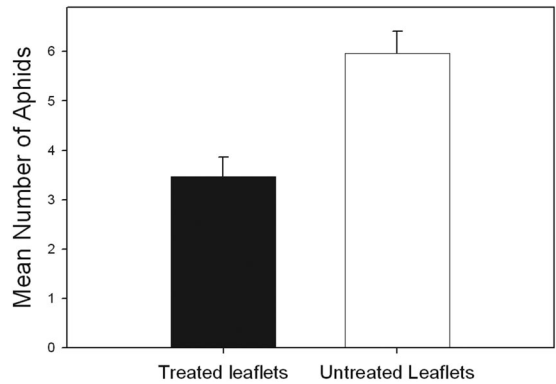


Fig. 1. Mean number of aphids on leaflets treated with the synthetic Colorado potato beetle attractant and untreated control leaflets in petri dish arenas ($n = 12$). Error bars indicate standard errors. The differences between the treatments were statistically significant (ANOVA; $P < 0.01$).

Aphid Response to Blank Carrier Droplets on Potato Leaflets. The mean aphid densities found on kairomone-treated and carrier-treated leaflets were substantially lower than on untreated leaflets (Fig. 2). Treatment had a highly significant effect on aphid colonization of the leaflets ($F = 12.6$; $df = 2, 27$; $P = 0.0002$). Results of the Tukey's mean separation test (SAS Institute 2002) revealed a significant difference between untreated leaflets and treated leaflets but not between kairomone and blank carrier ($P < 0.05$).

Effect of Attractant and Carrier Applications on Aphid Densities and Virus Spread in the Field. In 2003, peak aphid densities were, on average, 284.85 ± 56.72 on the plots treated with kairomone formulation and 252.10 ± 53.00 on the untreated control plots. The difference was not statistically significant ($F = 0.21$; $df = 1, 4$; $P = 0.6739$). In 2004, attractant-treated plots

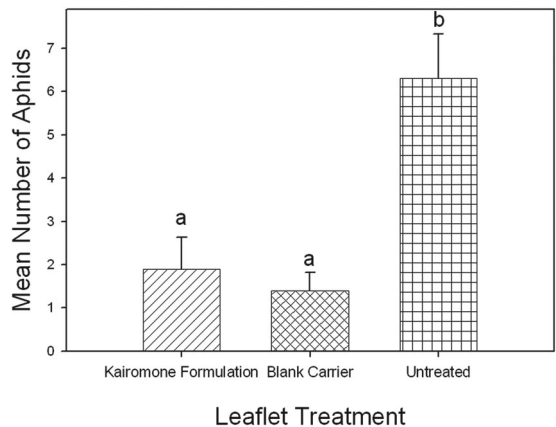


Fig. 2. Mean number of aphids on leaflets treated with the synthetic Colorado potato beetle attractant, blank inert carrier, and untreated control leaflets in petri dish arenas ($n = 10$). Bars followed by the same letter were not significantly different from each other (Tukey test; $P > 0.05$). Error bars indicate standard errors.

had, on average, 2.83 ± 0.81 potato aphids per sampling date, carrier-treated plots had 4.67 ± 1.21 aphids per sampling date, and untreated control plots had 4.52 ± 1.13 aphids per sampling date. The difference between the treatments was not statistically significant ($F = 1.00$; $df = 2, 10$; $P = 0.4019$). Only a single tuber collected from the control plots and two tubers collected from the plots treated with the kairomone formulation tested positive for PLRV. No PVY spread was detected. Dramatic difference in mean aphid densities in 2003 and 2004 were due to our sampling the plots throughout the 2004 growing season. Densities of potato aphids on potatoes in northern Maine are generally low until mid- to late August, when they produce a short but often considerable outbreak.

Discussion

Wingless potato aphids were strongly attracted to the potato foliage in the current study. Winged potato aphids did not show such a response. This is consistent with several previous studies. Wingless green peach aphids were attracted by potato odor in the experiments of Eigenbrode et al. (2002), whereas Hori (1999) did not find such a response for the winged form. Also, similar to our findings, Hori (1999) did not detect statistically significant differences in the number of winged potato aphids moving toward the odor of excised potato leaves in an olfactometer (although it is worth noting that in both studies, more winged aphids moved toward the odor source). In the field, potato odor is likely to consist of a mixture of chemicals emitted by intact potato plants as well as by mechanically damaged potato plants and plants damaged by insect herbivores. In our experiment, the aphids were exposed only to the odor of mechanically damaged leaves. Therefore, our experiment did not quantify the extent to which potato aphids use chemical cues for finding their hosts. However, it did show statistically significant response to leaf volatiles. Therefore, lack of aphid reaction toward Colorado potato beetle attractant observed in the subsequent experiments could not be attributed to the general lack of response to olfactory stimuli.

The synthetic Colorado potato beetle attractant did not have a significant effect on the movement of either wingless or winged potato aphids in the olfactometer (although, again, the numerical trend was toward higher proportion of aphids moving toward the odor source). Also, when the kairomone formulation and blank carrier were applied to leaflets, aphids tended to avoid the treated leaflets. Avoidance response was similar regardless of whether the carrier was impregnated with the kairomone to form the attractant formulation or left blank. We suggest that the observed effect was due to the change in physical appearance and texture of the leaflets, with part of each treated leaflet coated with a layer of black and sticky carrier substance. Two of the kairomone components, methyl salicylate and linalool, have been shown to interfere with host finding by black bean aphid and carrot aphid (Chapman et al. 1981, Hardie et al. 1994). However,

very similar aphid reaction to the kairomone formulation and odorless blank carrier in the petri dish assay as well as the lack of repellency in the olfactometer indicates that this was probably not the case in the current study. However, it is possible that the presence of blank carrier somehow masked or altered the odor of potato leaflets, making them unattractive to potato aphids.

Field results suggested a neutral response of potato aphid to the Colorado potato beetle kairomone. We did not observe aphid buildup in the treated plots compared with the untreated plots. Also, aphid numbers on treated plots did not decline relative to the untreated control, which was different from the findings of Pettersson et al. (1994). They found fewer *R. padi* in the cereal fields treated with methyl salicylate. The avoidance of the carrier component of the kairomone formulation was not strong enough to have a detectable effect on aphid densities in the field. Numerical differences were due to sporadic high aphid populations on several plants within blank carrier-treated and control plots. Even if aphids avoided the kairomone formulation or blank carrier in the field, they had an opportunity to move toward the untreated leaves of the same or adjacent plant. Moreover, there is evidence that potato-infesting aphid species including potato aphid, preferentially colonize lower leaves of potato plants (Shands et al. 1954, Mack and Smilowitz 1981), presumably because of their superior food quality (greater quantities of amino-nitrogen compounds) (Jansson and Smilowitz 1986). Because the kairomone formulation and blank carrier in our experiment were applied to the upper portion of the potato canopy, the majority of aphids probably escaped their effects.

Inert ingredients of pest control formulations are usually assumed to have little or no effects on target or nontarget organisms. Our laboratory experiments suggest that application of the viscous carrier compound (alone or in combination with Colorado potato beetle kairomone) may potentially encourage aphid movement in an attempt to avoid treated leaves. We did not detect increased virus transmission in our field plots. However, virus spread in this study was generally low, and the situation might be different in years, locations, or a combination with the higher disease pressure. Therefore, increased transmission due to avoidance of the carrier cannot be ruled out. Martel et al. (2005a) advocated applying kairomone early in the season to manipulate crop colonization by the overwintered beetles. If the currently available kairomone formulation indeed stimulates virus transmission, early applications also can be recommended because aphid colonization usually starts later in the season.

Acknowledgments

We thank Trécé, Inc. for providing kairomone formulation and blank carrier. Gary Sewell and Caroline Robinson provided technical assistance. William Halteman helped with statistical analyses. This research was supported in part by the USDA-CSREES Northeastern Regional IPM Grant (Coop-

erative Agreement No. 58-1275-3-183). This is Publication No. 2865 of the Maine Agricultural and Forest Experiment Station.

References Cited

- Alyokhin, A., and G. Sewell. 2003. On-soil movement and plant colonization by walking wingless morphs of three aphid species (Homoptera: Aphididae) in greenhouse arenas. *Environ. Entomol.* 32: 1393-1398.
- Boiteau, G. 1997. Comparative propensity for dispersal of apterous and alate morphs of three potato-colonizing aphid species. *Can. J. Zool.* 75: 1396-1403.
- Chapman, R. F., E. A. Bernays, and S. J. Simpson. 1981. Attraction and repulsion of the aphid, *Cavariella aegopodii*, by plant odors. *J. Chem. Ecol.* 7: 881-888.
- Dickens, J. C. 1999. Predator-prey interactions: olfactory adaptations of generalist and specialist predators. *Agric. For. Entomol.* 1: 47-54.
- Dickens, J. C. 2000. Orientation of Colorado potato beetle to natural and synthetic blends of volatiles emitted by potato plants. *Agric. For. Entomol.* 2: 167-172.
- Dickens, J. C. 2002. Behavioral response of larvae of the Colorado potato beetle, *Leptinotarsa decemlineata* Say (Coleoptera: Chrysomelidae) to host plant volatile blends attractive to adults. *Agric. For. Entomol.* 4: 309-314.
- Eigenbrode, S. D., H. Ding, P. Shiel, and P. Berger. 2002. Volatiles from potato plants infected with potato leafroll virus attract and arrest the virus vector, *Myzus persicae* (Homoptera: Aphididae). *Proc. R. Soc. Lond. B* 269: 455-460.
- Flanders, K. L., E. B. Radcliffe, and D. W. Ragsdale. 1991. Potato leafroll virus spread in relation to densities of green peach aphid (Homoptera: Aphididae): implications for management thresholds for Minnesota seed potatoes. *J. Econ. Entomol.* 84: 1028-1036.
- Hanafi, A., E. B. Radcliffe, and D. W. Ragsdale. 1989. Spread and control of potato leafroll virus in Minnesota. *J. Econ. Entomol.* 84: 1201-1206.
- Hardie, J., R. Isaacs, J. A. Pickett, L. J. Wadhams, and C. M. Woodcock. 1994. Methyl salicylate and (-)-(1R,5S)-myrtenal are plant-derived repellents for black bean aphid, *Aphis fabae* Scop. (Homoptera: Aphididae). *J. Chem. Ecol.* 20: 2847-2855.
- Hodgson, C. 1991. Dispersal of apterous aphids (Homoptera: Aphididae) from their host plant and its significance. *Bull. Entomol. Res.* 81: 417-427.
- Hori, M. 1999. Role of host plant odors in the host finding behaviors of aphids. *Appl. Entomol. Zool.* 34: 293-298.
- Isaacs, R., J. Hardie, A. J. Hick, B. J. Pye, L. E. Smart, L. J. Wadhams, and C. M. Woodcock. 1993. Behavioral responses of *Aphis fabae* to isothiocyanates in the laboratory and field. *Pestic. Sci.* 39: 349-355.
- Jansson, R. K., and Z. Smilowitz. 1986. Influence of nitrogen on population parameters of potato insects: abundance, population growth, and within-plant distribution of the green peach aphid, *Myzus persicae* (Homoptera: Aphididae). *Environ. Entomol.* 15: 49-55.
- Mack, T. P., and Z. Smilowitz. 1981. The vertical distribution of green peach aphids and its effect on a model quantifying the relationship between green peach aphids and a predator. *Am. Potato J.* 58: 345-353.
- Martel, J. W., A. R. Alford, and J. C. Dickens. 2005a. Synthetic host volatiles increase efficacy of trap cropping for management of Colorado potato beetle, *Leptinotarsa decemlineata* (Say). *Agric. For. Entomol.* 7: 79-86.
- Martel, J. W., A. R. Alford, and J. C. Dickens. 2005b. Laboratory and greenhouse evaluation of a synthetic host volatile attractant for Colorado potato beetle, *Leptinotarsa decemlineata* (Say). *Agric. For. Entomol.* 7: 71-78.
- Narayandas, G., and A. Alyokhin. 2006. Diurnal patterns in host finding by potato aphids, *Macrosiphum euphorbiae* (Homoptera: Aphididae). *J. Insect Behav.* (in press).
- Nottingham, S. F., and J. Hardie. 1993. Flight behaviour of the black bean aphid, *Aphis fabae*, and the cabbage aphid, *Brevicoryne brassicae*, in host and non-host plant odour. *Physiol. Entomol.* 18: 389-394.
- Nottingham, S. F., J. Hardie, G. W. Dawson, A. J. Hick, J. A. Pickett, L. J. Wadhams, and C. M. Woodcock. 1991. Behavioral and electrophysiological responses of aphids to host and non host plant volatiles. *J. Chem. Ecol.* 17: 1231-1242.
- Pettersson, J., J. A. Pickett, B. J. Pye, A. Quiroz, L. E. Smart, L. J. Wadhams, and C. M. Woodcock. 1994. Winter host component reduces colonization by bird-cherry-oat aphid, *Rhopalosiphum padi* (L.) (Homoptera, Aphididae), and other aphids in cereal fields. *J. Chem. Ecol.* 20: 2565-2574.
- Radcliffe, E. B., Flanders, K. L., and Ragsdale, D. W. 1993. Management of aphids and leafhoppers, pp. 103-115. In R. C. Rowe [ed.], *Potato health management*. APS Press, St. Paul, MN.
- Ribbands, C. R. 1963. The spread of apterae of *Myzus persicae* (Sulz.) and of yellow viruses within a sugar-beet crop. *Bull. Entomol. Res.* 54: 267-283.
- SAS Institute. 2002. SAS OnLine Doc, version 8. SAS Institute, Cary, NC.
- Shands, W. A., G. W. Simpson, and L. B. Reed. 1954. Subunits of sample for estimating aphid abundance on potatoes. *J. Econ. Entomol.* 47: 1024-1027.
- Visser, J. H., P.G.M. Piron, and J. Hardie. 1996. The aphids' peripheral perception of plant volatiles. *Entomol. Exp. Appl.* 80: 35-38.

Received 5 October 2005; accepted 22 March 2006.

This article is the copyright property of the Entomological Society of America and may not be used for any commercial or other private purpose without specific written permission of the Entomological Society of America.