Effects of Insecticides on Behavior of Adult *Bactericera cockerelli* (Hemiptera: Triozidae) and Transmission of *Candidatus* Liberibacter psyllaurous

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ABSTRACT The potato psyllid, *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae), is a serious pest of potatoes (*Solanum tuberosum* L.) that can cause yield loss by direct feeding on crop plants and by vectoring a bacterial pathogen, *Candidatus* Liberibacer psyllaurous. Current pest management practices rely on the use of insecticides to control the potato psyllid to lower disease incidences and increase yields. Although many studies have focused on the mortality that insecticides can cause on potato psyllid populations, little is known regarding the behavioral responses of the potato psyllid to insecticides or whether insecticides can decrease pathogen transmission. Thus, the objectives of this study were to determine the effects of insecticides on adult potato psyllid behaviors, the residual effects of insecticides on potato psyllid behaviors over time, and effects of these insecticides on *Ca.* L. psyllaurous transmission. Insecticides tested included imidacloprid, kaolin particle film, horticultural spray oil, abamectin, and pymetrozine. All insecticides significantly reduced probing durations and increased the amount of time adult psyllids spent off the leaflets, suggesting that these chemicals may be deterrents to feeding as well as repellents. Nonfeeding behaviors such as tasting, resting, and cleaning showed variable relationships with the different insecticide treatments over time. The insecticides imidacloprid and abamectin significantly lowered transmission of *Ca.* L. psyllaurous compared with untreated controls. The implications of our results for the selection of insecticides useful for an integrated pest management program for potato psyllid control are discussed.

KEY WORDS potato psyllid, potato, insecticides, IPM, "zebra chip"

The potato psyllid, *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae), is a major pest of solanaceous crops in Central and North America (Cranshaw 1994, Jackson et al. 2009). Damaging outbreaks of this pest have been reported across vast geographic areas such as California; Texas; Washington; the central United States; Ontario Canada; and Baja, Mexico (Cranshaw 1994, Zink 1998, Al-Jabr 1999, Ferguson et al. 2002, McGuire 2002, Liu 2006, Munyaneza et al. 2007). In addition, the potato psyllid has recently become established in New Zealand as a pest of solanaceous greenhouse crops, and outdoor potatoes (*Solanum tuberosum* L.) and tomatoes (*Solanum lycopersicum* L.) (Gill 2006, Davidson et al. 2008). The potato psyllid causes significant reduction in quality and crop longevity by feeding on crop plants (Richards and Blood 1933). Yield losses in potatoes of up to 93% can occur when plants are exposed to potato psyllids (Munyaneza et al. 2008). Thus, the potato psyllid seems to be causing greater economic losses and is occurring across a wider geographic range.

There are at least three factors that contribute to making the potato psyllid a severe pest. First, this psyllid has a wide host range of >20 plant families and is able to oviposit and complete development on >40 host species (Knowlton and Thomas 1934). Second, this pest can develop and reproduce rapidly, allowing populations to build quickly. Each of the first four instars takes an average of 2 d to complete, and the fifth instar is completed in 4 d (Knowlton and Janes 1931). The average total number of eggs a female may oviposit in her lifetime varies from 75 to 406 eggs (Lehman 1930, Knowlton and Janes 1931, Davis 1937, Abdullah 2008), whereas the average number of eggs laid per day can vary from 6.4 to 14.1 (Davis 1937, Casteel et al. 2006). Third, this pest plays an important role in plant disease transmission. The potato psyllid can transmit *Ca.* L. psyllaurous (a.k.a. *Candidatus* Liberibacter solanacearum) to potatoes, which is associated with "zebra chip" (ZC) disease (Hansen et al. 2008, Crosslin et al. 2010). This disease results in lower yields and decreased quality and is characterized by a distinctive pattern of necrosis that is evident when infected tubers are fried (Munyaneza et al. 2007, Hansen et al. 2008, Crosslin et al. 2010).

In recent years, much research has been done on ZC, because of its economic impact on the potato industry. ZC has been documented in commercial

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potato fields in the United States. (e.g., Texas, Nebraska, Colorado, Kansas, New Mexico, Arizona, Nevada, and California), New Zealand, Mexico, Guatemala, and Honduras (Munyaneza et al. 2007, Crosslin et al. 2010, http://www.biosecurity.govt.nz/pests/potato-tomato-psyllid). ZC was sporadic until the 2004–2006 growing seasons when it caused economic losses to both potato producers and processors in numerous locations in the United States and Mexico, often causing the abandonment of entire potato fields and losses in the millions of dollars (Munyaneza et al. 2007). ZC not only lowers yields of the potato crop but also increases the rejection of chips processed from infected tubers (Goolsby et al. 2007a). Thus, there is a need for effective control methods to reduce ZC incidence in potato fields through the development of efficient control of the potato psyllid (Gharalari et al. 2009).

Insecticidal control of the potato psyllid has been the subject of extensive research (List 1917, 1935, 1938; List and Daniels 1934; Pletsch 1942; Tate and Hill 1944; Gerhardt and Turley 1961; Harding 1962; Gerhardt 1966; Cranshaw 1985a,b,c, 1989a,b,c; Liu and Trumble 2004, 2005; Goolsby et al. 2007a; Vega-Gutierrez et al. 2008; Gharalari et al. 2009). Current pest management practices for potatoes in the United States use insecticides to control the potato psyllid to lower ZC incidences and increase yields. In Texas, in-furrow applications of phorate followed by several in-season applications of foliar insecticides including imidacloprid+cyfluthrin, endosulfan, and methamidophos reduced ZC incidence in fried tubers to 12.9–20.4% (Goolsby et al. 2007b). Insecticides also were used as a management tool to further lower ZC incidence in tubers to 0.4–2.3% in a pest management plan that included an in-furrow application of imidacloprid, and weekly applications of dinotefuran and spiromesifen used in rotation applied at weekly intervals until the 2-wk preharvest interval (Goolsby et al. 2007a). This pest management plan kept potato psyllid nymphal densities below one per leaf, which is a threshold level that Goolsby et al. (2007a) reported as "a benchmark for further refinement."

In California, existing University of California (UC) Pest Management Guidelines recommend treating potato plants with imidacloprid at planting, and additional treatments with either abamectin, spiromesifen, or spinosad if monitoring indicates that psyllid populations are at one to two per leaf or 10 per plant during the growing season (UC IPM Online 2008). Further research by Gharalari et al. (2009) evaluated the knockdown effect for a variety of insecticides on potato psyllid adults with thiamethoxam and abamectin being the most effective. The dosage and exposure time of abamectin also can significantly increase the mortality rates of potato psyllid adults; however, after 24 h under field conditions the mortality rates on abamectin-treated potato plants are not significantly different from controls (Gharalari et al. 2009). Although these studies focused on the mortality caused by insecticides on the potato psyllid, little is known regarding the behavioral responses of the potato psyllid to insecticides or whether insecticides can prevent or lower transmission of pathogens. This information would be useful for the selection of insecticides for potato psyllid control (Liu and Trumble 2004).

Behavioral responses of insects to insecticides often provide important contributions to chemical control efforts because insecticides can interfere with the normal behavior patterns and might therefore contribute to management of populations (Pluthero and Singh 1984, Haynes 1988). Previous research by Liu and Trumble (2004) documented the behavioral responses of the potato psyllid to insecticides and tomato plant lines. Their results indicated that there can be interactions between potato psyllid behavioral responses to insecticides and tomato lines (Liu and Trumble 2004). Behavioral assays on potato plants are now needed to assess the impact of insecticides, given the significance of the potato psyllid both as a pest of potatoes as well as the vector of the ZC associated pathogen. Thus, the objectives of this study were to 1) determine the effects of insecticides on adult potato psyllid behaviors, 2) determine the residual effects of insecticides on potato psyllid behaviors over time on potato plants, and 3) determine whether these insecticides can decrease transmission of *Ca.* L. psyllaurous. Analysis of behavioral responses can be used to evaluate insecticides that have the potential to impact psyllid population development and decrease the incidence of ZC. The long-term goal of this research is to maximize the effectiveness and use of insecticide selection and to increase options for future management of potato psyllid both as a pest and a vector.

Materials and Methods

Insects. *Bactericera cockerelli* were originally obtained from field collections in Texas. The colony was maintained at ambient conditions of 21–26°C and 40–60% RH in a greenhouse on tomatoes (*Solanum lycopersicum* L. 'Yellow Pear') at the University of California, Riverside, Agricultural Operations facility. A host plant other than potato was chosen as the rearing host to avoid having the insects develop a preference for their natal host plant (Tavormina 1982). Selections of adults used in all tests were based on the protocols of Liu and Trumble (2004). In brief, unsexed adults were standardized by the selection of insects with teneral coloration (light or pale green), indicative of emergence within the previous 2–3 d (Knowlton and Janes 1931).

Plants. Potato (*Solanum tuberosum* L. 'Atlantic') plants used in all tests were grown in 4.9-l pots with UC mix (Matkin and Chandler 1957) and fertilized three times per week with the label rate of Miracle Gro nutrient solution (Scotts Company, Marysville, OH). All plants used were between 3 and 6 wk of age. Plants were treated with insecticides once the potato reached the "vegetative growth" stage (growth stage II), which is marked by the plant producing 8–12 leaves (Strand 2006). Plant leaves used as substrates for the behavioral assays were standardized by selecting the uppermost fully expanded leaf.

Insecticides. We evaluated five insecticides: one soil-applied systemic material and four that were applied to foliage. Chemicals and rates included in this study were imidacloprid (Admire Pro, Bayer Corporation, Kansas City, MO; 0.54 ml Admire/liter, 100 ml applied to the soil), kaolin clay particle film (Surround WP, Engelhard Corporation, Iselin, NJ; 50 g/liter, 15 ml applied with a pressurized sprayer), horticultural spray oil (Pure Spray Oil, Petro-Canada, Mississauga, ON, Canada; 10 ml/liter, 15 ml applied with a pressurized sprayer), abamectin (Agri-Mek 0.15 EC, Syngenta Corporation, Greensboro, NC; 1.25 ml/liter, 15 ml applied with a pressurized sprayer), and pymetrozine (Fulfill, Syngenta Corporation; 0.42 g/liter, 15 ml applied with a pressurized sprayer). Controls were treated with distilled water. Plants treated with imidacloprid were tested weekly for 6 wk postapplication. With foliar-applied insecticides, leaves were used 24 h after treatment and were further examined 1 and 2 wk postapplication.

Behavioral Bioassays. All assays were based on the protocols of Liu and Trumble (2004). Assays were monitored in arenas made by layering the following components: a Plexiglas rectangle (9 by 11.5 cm) serving as the base, a 9-cm-diameter Whatman filter paper on the Plexiglas, the test leaflet (psyllid was placed on abaxial surface), foam (0.5 by 8 by 9 cm) with a 2.5-cm^2 hole, and an additional 12.5-cm-diameter glass plate that covered the arena. A newly emerged adult was placed into the arena and allowed to adjust for 5 min before initiating behavioral recording. An observation period lasted 15 min. Preliminary studies (D. G. Liu and J.T.T., unpublished data) indicated that the 15-min observation period was sufficient for the psyllids to exhibit most of the behaviors. The observations were recorded using the Noldus Observer program (Noldus, Wageningen, The Netherlands).

Specific behaviors recorded included cleaning (using legs to cleanse or wipe antennae, appendages or abdomen), probing (stylets inserting into the leaflet, based on electrical penetration graphs; C.D.B. et al. unpublished), jumping (leaping from one point to another on the leaflet), off-leaflet (exiting or abandoning the leaf surface), tasting (tapping the mouthparts on the leaf surface sporadically), resting (no activity on the leaflet and mouthparts not in contact with the leaflet), and walking (walking on the leaf surface). Jumping occurs so rapidly that accurately recording duration time was not possible, so only numbers of occurrences were recorded. The behavioral observations were replicated 20 times with different psyllids for each of the insecticides and for each of the time periods.

Imidacloprid Analysis in Potato Leaves. Imidacloprid residues in potato leaf tissue were measured by enzyme-linked immunosorbent assay ([ELISA]; QuantiPlate kit for imidacloprid available from EnviroLogix, Portland, ME). At 3 and 6 wk after treatments, leaves were sampled ($N = 12$) from the plants. A disc was cut from each leaf using a 0.39-cm^2 cork borer. Individual discs were placed in vials containing 200 μl of 100% methanol, macerated using a Teflon pestle, and then shaken for 12 h at 25°C. An aliquot of each extract was dried completely in a TurboVap LV evaporator (Caliper Life Sciences, Hopkinton, MA) and then reconstituted in a 0.05% aqueous solution of Triton X-100 before analysis by ELISA.

Purification of imidacloprid was conducted to determine whether there was any contamination of extracts with imidacloprid metabolites (Nauen et al. 1998b, 1999) that could potentially cross-react with the ELISA kit antibody (Byrne et al. 2005). Aliquots from composite samples for each sampling date were spotted directly on the concentrating zone of LK6 DF silica gel 60 TLC plates (Whatman Inc., Florham Park, NJ) and then chromatographed in a mobile phase of methylene chloride:methanol:ammonium hydroxide (45:5:1) (after Byrne et al. 2005). The position of imidacloprid was determined by co-chromatographing an imidacloprid standard with the potato extracts. The imidacloprid bands were cut from the plate, washed from the silica with 100% methanol, and then quantified by ELISA.

Transmission Assays. Ten psyllids (subsequently determined to be infected, see below) were caged on a 7- by 7.5-cm cage on the terminal leaflet of one of the fully expanded potato leaves on 10 replicated plants for a 24-h inoculation access period for each of the foliar-applied insecticides treatments 24 h postapplication, and for the plants treated with imidacloprid 1 and 4 wk postapplication. After 24 h, the psyllids were removed from the leaflet and placed in 100% ethanol and stored at −20°C until real-time polymerase chain reaction (PCR) analysis. The plants were held for 2 wk after potato psyllid exposure to allow disease development. The potato leaf was then removed from the plant and placed in a Ziploc bag and stored at −80°C until real-time PCR analysis.

Real-Time PCR Analysis. Psyllids were tested in aliquots of three adults per extraction by using a procedure modified from Manjunath et al. (2008) for the presence of *Ca.* L. psyllaurous. Psyllids were placed on Whatman filter paper #1 by using disposable Pasteur pipets, air-dried for ≈10 min, and further processed using a Fast DNA spin kit (MP Biomedicals Ltd., Solon, OH). The air-dried psyllids were homogenized in 1 ml of extraction buffer in lysing matrix A by using a beadbeater (Bispec Inc., Bartlesville, OK) at maximum speed for 4 min. Final elution of DNA was done in a volume of 100 μl of elution buffer per extraction. Possible cross-contamination during the extraction process was monitored by using at least on negative extraction control for a batch of 12 samples. A Taqman-based real-time PCR assay was used in the detection of LPS by using a protocol modified from Li et al. (2006) and Manjunath et al. (2008). DNA concentrations were estimated using NanoDrop spectrophotometer (Thermo Fisher Scientific, Wilmington, DE). The forward primer HLBf was replaced by LPSf (5′-TCGAGCGCTTATTTTTAATAGG-3′) and used along with HLBp and HLBr primers. The primer concentrations and the reaction conditions were same as published previously (Manjunath et al. 2008). Samples with a cycle threshold (ct) value of 32 and below for the bacterial probe were considered positive for *Ca.* L.

Table 1. Number of occurrences ($N = 20$ adults) of selected behaviors of the potato psyllid in response to imidacloprid

Time (wk)	Treatment	Tasting		P	Probing		P	Cleaning		P	Jumping		P	Resting		P	Walking		P	Off-leaflet		P
		N	Y		N	Y		N	Y		N	Y		N	Y		N	Y		N	Y	
1	Imidacloprid	18	2	1.0000	19	1	<0.0001	17	3	1.0000	20	0		2	18	0.0138	7	13	0.0240	10	10	0.0958
	Control	19	1		6	14		18	2		20	0		10	10		15	5		16	4	
2	Imidacloprid	14	6	0.7164	15	5	<0.0001	15	5	0.1818	20	0		6	14	0.0036	12	8	1.0000	9	11	0.2003
	Control	16	4		2	18		19	1		20	0		16	4		12	8		14	6	
3	Imidacloprid	19	1	0.3416	15	5	<0.0001	17	3	0.2308	18	2	0.4872	5	15	0.0104	11	9	0.7475	11	9	0.5145
	Control	16	4		2	18		20	0		20	0		14	6		13	7		14	6	
4	Imidacloprid	20	0	1.0000	13	7	0.0562	15	5	0.4075	18	2	0.4872	7	13	0.5231	13	7	0.7311	11	9	0.1760
	Control	19	1		6	14		18	2		20	0		10	10		15	5		16	4	
5	Imidacloprid	18	2	0.6614	12	8	0.0022	18	2	1.0000	19	1	1.0000	6	14	0.0036	14	6	0.7411	14	6	1.0000
	Control	16	4		2	18		19	1		20	0		16	4		12	8		14	6	
6	Imidacloprid	16	4	1.0000	12	8	0.0022	15	5	0.0471	19	1	1.0000	10	10	0.3332	13	7	1.0000	10	10	0.3332
	Control	16	4		2	18		20	0		20	0		14	6		13	7		14	6	

psyllaurous. A ct value of 33–34 was counted as a "suspect," and a ct value of 35 and above indicated the absence of *Ca.* L. psyllaurous.

Potato leaflets were tested for the presence of *Ca.* L. psyllaurous as follows. Leaf samples were collected from test plants and stored frozen at −80°C in Ziploc bags. DNA extraction was conducted using a Plant DNeasy kit (QIAGEN, Valencia, CA) according to manufacturer's recommendations. Individual 100-mg samples of leaf midrib were finely chopped and extracted in 600 μl of extraction buffer and one 2.5-mm steel bead in a 2-ml screw-cap tubes by using bead-beater as described above. The final elution of DNA was done in a volume of 100 μl per extraction. Real-time PCR assay was conducted essentially as described by Li et al. (2006) except for the forward primer (LPSf) as described above. The primer-probe set for mitochondrial cytochrome oxidase gene (COX) served as internal control for detection of potato DNA. The results of the PCR tests for *Ca.* L. psyllaurous were analyzed as described above.

Statistical Analysis. The soil-applied imidacloprid experiment was conducted as a randomized complete block design with four blocks. Each block consisted of five replicates of the six time treatments. The foliar-applied insecticide experiment was conducted as randomized complete block design with five blocks. Each block consisted of four replicates of the five treatments. For each insecticide postapplication period, the treatments were rerandomized within each block before observations. Treatment differences in the number of occurrences of each behavior exhibited over each time period for both experiments were analyzed using chi-square analysis with a Fisher exact test (PROC FREQ, SAS Institute 2008). For the soil-applied imidacloprid experiment, the durations of the probing and resting behaviors were log transformed to homogenize variances. Durations of behaviors were analyzed using analysis of variance (ANOVA) in a general linear models procedure of SAS version 9.2 (PROC GLM, SAS Institute 2008). When effects were significant ($P < 0.05$), multiple comparisons tests using the LSMEANS/PDIFF option were accomplished to discriminate differences among treatment means. A nonparametric Kruskal–Wallis test (PROC NPAR1WAY, SAS Institute 2008) was used to test the differences between the mean amounts of imidacloprid in the potato leaf disc samples because these data were not normally distributed and showed nonconstant variance. Post hoc separations used the Mann–Whitney U test with a Bonferroni adjustment ($\alpha = 0.01$). For the foliar-applied insecticide experiments, various transformations were used to homogenize variances. For the 24 h postapplication time period, durations of the probing behavior were reciprocal square root transformed, and times spent off the potato leaflet were log transformed. For 1 and 2 wk postapplication time periods, durations of the probing behavior were log transformed. Durations of behaviors were analyzed separately for each time period by using ANOVA in a general linear models procedure of SAS version 9.2 (PROC GLM, SAS Institute 2008). When treatment effect was significant ($P < 0.05$) a least significant difference (LSD) test was used to discriminate significant differences among treatment means. Treatment differences in the number of potato plants infected with *Ca.* L. psyllaurous were compared using chi-square analysis with a Fisher exact test (PROC FREQ, SAS Institute 2008).

Results

Behavioral Responses to Imidacloprid. There were significant differences in the number of occurrences for probing, cleaning, resting, and walking (Table 1). Imidacloprid significantly reduced the number of psyllids that fed during the first ($\chi^2 = 18.03$, df = 1, $P < 0.0001$), second ($\chi^2 = 17.29$, df = 1, $P < 0.0001$), third ($\chi^2 = 17.29$, df = 1, $P < 0.0001$), fifth ($\chi^2 = 10.99$, df = 1, $P = 0.0022$), and sixth ($\chi^2 = 10.99$, df = 1, $P = 0.0022$) weeks postapplication. After the first week of the imidacloprid application, only one of the 20 psyllids fed, whereas 70% of the psyllids fed on the control potatoes during the first week. For weeks 2, 3, 5, and 6, 25, 25, 40, and 40% of the psyllids exhibited probing behavior in the imidacloprid treatments, respectively, whereas in the control 90% of the psyllids exhibited probing behavior for week 2, 3, 5, and 6. Psyllids rested significantly more in the imidacloprid treatments in the first ($\chi^2 = 7.62$, df = 1, $P = 0.0138$), second ($\chi^2 = 10.10$, df = 1, $P = 0.0036$), third ($\chi^2 = 8.12$, df = 1, $P = 0.0104$), and fifth ($\chi^2 = 10.10$, df = 1, $P = 0.0036$) week

Table 2. Duration (in seconds) ± SE (N = 20 adults) of selected behaviors of the potato psyllid in response to imidacloprid

Time (wk)	Treatment	Tasting[a]	Probing	Cleaning	Resting	Walking	Off-leaflet
1	Imidacloprid	0.57 ± 0.41a	5.39 ± 5.39a	2.67 ± 1.81a	611.28 ± 78.40a	27.15 ± 9.29a	252.95 ± 74.86a
	Control	0.13 ± 0.13a	549.37 ± 87.30c	17.32 ± 13.66b	173.94 ± 69.67b	4.02 ± 2.11a	155.23 ± 73.78b
2	Imidacloprid	1.82 ± 0.93a	67.88 ± 34.76ab	44.64 ± 31.51a	422.44 ± 87.05a	43.03 ± 25.51a	320.19 ± 96.92a
	Control	0.41 ± 0.19a	664.80 ± 70.51c	4.85 ± 4.85b	96.35 ± 53.39b	14.00 ± 6.87a	119.58 ± 55.98b
3	Imidacloprid	0.34 ± 0.34a	168.20 ± 72.69ab	46.69 ± 38.52a	428.38 ± 81.25a	16.14 ± 5.67a	240.26 ± 76.00a
	Control	0.66 ± 0.33a	654.62 ± 76.83c	0.00 ± 0.00b	99.56 ± 51.16b	11.99 ± 6.13a	133.16 ± 59.26b
4	Imidacloprid	0.00 ± 0.00a	198.92 ± 75.92b	28.32 ± 21.40a	386.31 ± 87.24a	12.20 ± 4.40a	274.26 ± 86.22a
	Control	0.13 ± 0.13a	549.37 ± 87.30c	17.32 ± 13.66b	173.94 ± 69.67b	4.02 ± 2.11a	155.23 ± 73.78b
5	Imidacloprid	0.37 ± 0.26a	258.92 ± 85.78b	8.80 ± 6.06a	476.65 ± 91.41a	8.54 ± 3.89a	146.71 ± 72.98a
	Control	0.41 ± 0.19a	664.80 ± 70.51c	4.85 ± 4.85b	96.35 ± 53.39b	14.00 ± 6.87a	119.58 ± 55.98b
6	Imidacloprid	0.67 ± 0.35a	201.29 ± 76.31b	61.32 ± 35.94a	338.60 ± 85.57a	12.14 ± 4.25a	285.99 ± 86.15a
	Control	0.66 ± 0.33a	654.62 ± 76.83c	0.00 ± 0.00b	99.56 ± 51.16b	11.99 ± 6.13a	133.16 ± 59.26b

[a] Means within a column for the respective time periods followed by different letters are significantly different using the LSMEANS/PDIFF option.

compared with controls. Eighteen of the 20 psyllids rested during the first week in the imidacloprid treatment, and only 10 of the 20 (50%) in the controls. For weeks 2, 3, and 5, 70, 75, and 70% of the psyllids rested in the imidacloprid treatments, respectively, even as 20, 30, and 20% exhibited resting behavior in the controls during weeks 2, 3, and 5. Less consistent were the cleaning and walking behaviors. Significantly more psyllids exhibited cleaning behavior in the imidacloprid treatment only during the sixth week ($\chi^2 = 5.71$, df = 1, $P = 0.0471$), whereas significantly more psyllids displayed walking behavior in the imidacloprid treatment only during the first week ($\chi^2 = 6.46$, df = 1, $P = 0.0240$). Five of the 20 (25%) psyllids exhibited cleaning at week 6 in the imidacloprid treatment whereas none (0%, 0/20) in the controls. Thirteen of the 20 (65%) psyllids walked in the imidacloprid treatments during the first week but only five of the 20 (25%) in the controls.

Psyllids spent significantly less time probing on potato plants treated with imidacloprid compared with the controls ($F = 131.60$; df = 1, 225; $P < 0.0001$) and there were significant differences in probing durations of psyllids over the 6-wk experimental period ($F = 2.40$; df = 5, 225; $P = 0.0383$) (Table 2). Durations of time probing averaged 5.39 ± 5.39 s for psyllids probing on imidacloprid-treated plants 1 wk postapplication, which was significantly less than the time spent probing for psyllids exposed to plants 4 wk (198.92 ± 75.92 s), 5 wk (258.92 ± 85.78 s), and 6 wk (201.29 ± 76.31 s) postapplication. Psyllids spent more time cleaning (except for week 1) when exposed to plants treated with imidacloprid compared with controls ($F = 4.69$; df = 1, 225; $P = 0.0314$) (Table 2). On average psyllids spent 32.07 ± 10.83 s cleaning on plants treated with imidacloprid versus 7.39 ± 3.41 s on control plants. Psyllids consistently spent significantly more time resting ($F = 54.47$; df = 1, 225; $P < 0.0001$) and more time off the potato leaflet ($F = 7.81$; df = 1, 225; $P = 0.0056$) on potato plants treated with imidacloprid compared with controls (Table 2). On average psyllids spent 443.94 ± 34.96 s resting on plants treated with imidacloprid versus 123.28 ± 23.67 s resting on control plants. Psyllids spent on average 253.39 ± 33.38 s off the potato leaflet on plants treated with imidacloprid, whereas psyllids spent 135.99 ± 25.40 s off the potato leaflet on control plants.

There were significant differences in the mean amounts of imidacloprid in the potato leaf disc samples ($\chi^2 = 32.33$, df = 2, $P < 0.0001$). The average amount of imidacloprid in the controls (0.00 ± 0.00 μg/g, N = 12) was significantly less than the amounts in the plant sampled 3 wk (129.65 ± 6.44 μg/g, N = 12) and 6 wk (78.26 ± 4.60 μg/g, N = 12) after application. The average amounts in the plants at weeks 3 and 6 also differed significantly from each other with the amount in week 3 significantly greater than week 6.

Behavioral Responses to Foliar-Applied Insecticides. There were significant differences in the number of occurrences for tasting and probing (Table 3). The foliar-applied insecticides significantly reduced the number of psyllids that exhibited tasting behavior 24 h after application ($\chi^2 = 11.25$, df = 4, $P = 0.0239$). Nine of the 20 (45%) psyllids exhibited tasting behavior in the controls, whereas only one (5%), three (15%), three (15%), and four (20%) psyllids exhibited tasting behavior for the treatments of kaolin clay particle film, horticultural spray oil, abamectin, and pymetrozine, respectively, 24 h after application. The foliar-applied insecticides significantly reduced the number of psyllids that fed 1 wk ($\chi^2 = 13.37$, df = 4, $P = 0.0096$) and 2 wk ($\chi^2 = 19.89$, df = 4, $P = 0.0005$) after application. Seventeen of the 20 (85.0%) psyllids fed in the controls, whereas eight (40%), eight (40%), nine (45%), and seven (35%) exhibited probing behavior for the treatments of kaolin clay particle film, horticultural spray oil, abamectin, and pymetrozine, respectively, 1 wk after application. For psyllids in the 2 wk postapplication treatments, seven (35%), six (30%), eight (40%), and seven (35%) fed in the treatments of kaolin clay particle film, horticultural spray oil, abamectin, and pymetrozine, respectively. In contrast, eighteen of the 20 (90%) psyllids in the control treatment during the 2-wk time period exhibited probing behavior.

The durations of probing and abandonment of leaflets were significantly different by treatment (Table 4). Durations of probing were significantly less for psyllids exposed to insecticides 24 h ($F = 2.60$; df = 4, 91; $P = 0.0414$), 1 wk ($F = 5.08$; df = 4, 91; $P = 0.0010$), and 2 wk ($F = 5.27$; df = 4, 91; $P = 0.0007$) after application as compared with controls. Durations of time probing averaged 243.33 ± 72.71 s for psyllids

Table 3. Number of occurrences ($N = 20$ adults) of selected behaviors of the potato psyllid in response to insecticide treatment

Time	Treatment	Tasting		P	Probing		P	Cleaning		P	Jumping		P	Resting		P	Walking		P	Off-leaflet		P
		N	Y		N	Y		N	Y		N	Y		N	Y		N	Y		N	Y	
24 h	Surround WP	19	1	0.0229	14	6	0.1444	16	4	0.7153	19	1	0.1621	9	11	0.0951	12	8	0.0556	9	11	0.0640
	Pure Spray Oil	17	3		17	3		16	4		19	1		9	11		15	5		8	12	
	Abamectin	17	3		16	4		17	3		19	1		7	13		12	8		9	11	
	Pymetrozine	16	4		13	7		13	7		15	5		5	15		9	11		8	12	
	Control	11	9		10	10		15	5		18	2		2	18		6	14		16	4	
1 wk	Surround WP	15	5	0.7262	12	8	0.0101	13	7	0.7153	17	3	0.6719	7	13	0.6486	12	8	0.9895	12	8	0.0579
	Pure Spray Oil	15	5		12	8		17	3		19	1		6	14		11	9		8	12	
	Abamectin	14	6		11	9		16	4		17	3		6	14		11	9		12	8	
	Pymetrozine	17	3		13	7		15	5		19	1		6	14		13	7		10	10	
	Control	13	7		3	17		16	4		19	1		10	10		12	8		17	3	
2 wk	Surround WP	15	5	0.1054	13	7	0.0004	17	3	0.2572	19	1	1.0000	10	10	0.3328	16	4	0.2487	11	9	0.1681
	Pure Spray Oil	19	1		14	6		18	2		19	1		9	11		16	4		11	9	
	Abamectin	18	2		12	8		18	2		19	1		11	9		13	7		8	12	
	Pymetrozine	17	3		13	7		16	4		20	0		5	15		11	9		12	8	
	Control	13	7		2	18		13	7		19	1		7	13		11	9		16	4	

probing on control plants, which was significantly more than the time spent probing for psyllids treated with horticultural spray oil (83.45 ± 52.36 s) and abamectin (41.49 ± 23.97 s) 24 h postapplication. Probing time durations were all significantly less for all insecticides tested 1 and 2 wk after application compared with the controls (Table 4). Time spent off the potato leaflet was significantly greater for psyllids exposed to insecticides 24 h ($F = 2.47$; df = 4, 91; $P = 0.0499$) and 2 wk ($F = 2.93$; df = 4, 91; $P = 0.0250$) postapplication compared with controls (Table 4).

Transmission Assays. The mean percentage and number of psyllids and potato plants that were infected with *Ca.* L. psyllaurous are shown in Table 5. All of the psyllids tested were infected with *Ca.* L. psyllaurous. There were significant decreases in the number of potato plants that were infected with *Ca.* L. psyllaurous based on treatment compared with controls (imidacloprid, 1 wk posttreatment: $\chi^2 = 4.46$, df = 1, $P = 0.0412$; imidacloprid, 4 wk posttreatment: $\chi^2 = 4.89$, df = 1, $P = 0.0341$; abamectin, 24 h posttreatment: $\chi^2 = 4.29$, df = 1, $P = 0.0433$). None of the other foliar-applied insecticides were significantly different from the control. The insecticide treatments of imidacloprid at 1 and 4 wk postapplication and abamectin at 24 h postapplication decreased infection by 59, 64, and 64%, respectively.

Discussion

The occurrences and durations of potato psyllid behavioral responses to insecticides varied by compound and over time, which impacted transmission of *Ca.* L. psyllaurous. Specifically, our results indicate that the use of these insecticides reduced probing times, increased abandonment of potato leaflets, and applications of imidacloprid and abamectin decreased disease transmission of *Ca.* L. psyllaurous compared with controls. Psyllid adults infected with *Ca.* L. psyllaurous can inoculate a potato plant after 1 h of feeding (Munyaneza 2009). Thus, for imidacloprid and abamectin, the behavioral modifications resulting from antifeedant effects, repellency, toxicity, or a combination of these activities on psyllid adults are sufficient to lower disease transmission.

Systemic imidacloprid application can significantly lower the number of adults that feed, reduce the durations of probing times, and increase the amount of time spent off the potato leaflet for up to 6 wk posttreatment. This effect was most profound 1 wk after

Table 4. Duration (in seconds) ± SE ($N = 20$ adults) of selected behaviors of the potato psyllid in response to insecticide treatment over time

Time	Treatment	Tasting[a]	Probing	Cleaning	Resting	Walking	Off-leaflet
24 h	Surround WP	0.18 ± 0.18a	210.75 ± 82.76ab	52.87 ± 37.00a	230.50 ± 80.37a	48.93 ± 31.32a	356.77 ± 95.92a
	Pure Spray Oil	1.94 ± 1.14a	83.45 ± 52.36a	12.19 ± 6.37a	389.61 ± 90.20a	16.54 ± 9.46a	396.27 ± 95.64a
	Abamectin	6.38 ± 4.57a	41.49 ± 23.97a	5.11 ± 3.36a	426.23 ± 88.10a	15.60 ± 8.16a	405.19 ± 96.87a
	Pymetrozine	1.02 ± 0.58a	205.35 ± 73.37ab	64.10 ± 38.44a	270.00 ± 68.72a	37.27 ± 9.36a	322.26 ± 76.91a
	Control	7.36 ± 3.04a	243.33 ± 72.71b	27.20 ± 13.82a	493.36 ± 84.99a	28.40 ± 10.45a	100.36 ± 60.31b
1 wk	Surround WP	1.65 ± 0.86a	231.38 ± 75.27a	39.09 ± 23.70a	358.55 ± 82.59a	21.55 ± 12.08a	247.79 ± 82.80a
	Pure Spray Oil	3.93 ± 2.44a	234.15 ± 78.30a	46.18 ± 34.15a	286.22 ± 75.17a	29.18 ± 17.49a	300.33 ± 84.70a
	Abamectin	1.71 ± 0.77a	230.30 ± 76.85a	31.94 ± 26.03a	339.25 ± 83.47a	13.56 ± 6.74a	283.24 ± 87.18a
	Pymetrozine	2.27 ± 1.44a	167.46 ± 70.04a	24.51 ± 15.39a	349.00 ± 86.16a	17.44 ± 7.60a	339.32 ± 92.10a
	Control	1.75 ± 0.84a	597.03 ± 77.94b	19.98 ± 11.21a	190.97 ± 67.89a	13.73 ± 6.20a	76.54 ± 51.41a
2 wk	Surround WP	1.03 ± 0.55a	260.66 ± 85.77a	32.81 ± 24.42a	256.71 ± 82.26a	6.68 ± 4.09a	342.11 ± 96.05a
	Pure Spray Oil	0.14 ± 0.14a	166.50 ± 70.67a	13.45 ± 12.36a	358.56 ± 91.08a	9.46 ± 5.10a	351.89 ± 99.03a
	Abamectin	0.46 ± 0.36a	262.36 ± 82.47a	5.96 ± 4.77a	231.18 ± 75.10a	6.48 ± 3.09a	393.56 ± 90.26a
	Pymetrozine	0.81 ± 0.52a	202.81 ± 74.13a	19.32 ± 10.41a	391.90 ± 81.31a	8.60 ± 3.64a	276.56 ± 87.46a
	Control	2.33 ± 1.05a	504.18 ± 81.17b	37.14 ± 24.20a	302.90 ± 76.69a	22.59 ± 13.55a	30.86 ± 25.99b

[a] Means within a column for the respective time periods followed by different letters are significantly different using the LSD test.

Table 5. Mean percentage ± SE (number of infected/inoculated potato psyllids and potato plants infected with *Ca.* L. psyllaurous) by insecticide treatment

Exp	Treatment	Potato psyllid	Potato[a]
Soil-applied			
	Imidacloprid, 1 wk PA[b]	100 ± 0.00 (18/18)	28.57 ± 12.53 (4/14)a
	Imidacloprid, 4 wk PA	100 ± 0.00 (21/21)	25.00 ± 13.06 (3/12)a
	Control	100 ± 0.00 (20/20)	69.23 ± 13.32 (9/13)b
Foliar-applied			
	Abamectin	100 ± 0.00 (15/15)	20.00 ± 10.69 (3/15)a
	Pymetrozine	100 ± 0.00 (17/17)	52.94 ± 12.48 (9/17)b
	Surround WP	100 ± 0.00 (16/16)	61.54 ± 14.04 (8/13)b
	Horticultural spray oil	100 ± 0.00 (16/16)	62.50 ± 12.50 (10/16)b
	Control	100 ± 0.00 (13/13)	56.25 ± 12.81 (9/16)b

Range of ct values: potato psyllids [19.85–30.42], potato [23.51–40.00].

[a] Within columns, frequencies followed by different letters differ significantly (χ^2 paired comparisons with the control of their respective experiments).

[b] PA, postapplication.

treatment in which the duration of probing averaged 5.39 s, a 99% decrease compared with the control. These results are in accordance with studies on other piercing–sucking insects such as the aphids *Myzus persicae* (Sulzer), *Myzus nicotianae* (Blackman), the leafhopper *Nephotettix cincticeps* (Uhler), the whitefly *Bemisia tabaci* (Gennadius), and the psyllid *Diaphorina citri* Kuwayama that have documented the antifeedant effects of imidacloprid at lethal and sublethal dosages (Nauen 1995, Devine et al. 1996, Nauen and Elbert 1997, Widiarta et al. 1997, Nauen et al. 1998a, Boina et al. 2009). In addition, our experiments documented that imidacloprid significantly increased the time spent resting as well as number of psyllid adults that rested. This result also was found for *M. persicae* in which this aphid rested significantly more when fed sucrose solutions containing 10 mg/liter imidacloprid (Nauen 1995). Imidacloprid consistently increased the amount of time adults abandoned potato leaflets. These results suggest that imidacloprid can act as both a feeding deterrent and as a repellent (i.e., adults orient themselves away from treated surfaces). Amounts of imidacloprid in leaf samples averaged 78.26 ± 4.60 μg/g after 6 wk, which indicate that these levels were high enough to impact behaviors. In other studies, the concentration of imidacloprid in leaves of poinsettas (*Euphorbia pulcherrima* Willdenow ex Klotsch), snap beans (*Phaseolus vulgaris* L.), and rice (*Oryza sativa* L.) reached 1.5–50 μg/g, although higher concentrations of up to ≈120 μg/g have been recorded previously (van Iersel et al. 2000, 2001; Nault et al. 2004, Yu et al. 2007). Thus, the concentrations of imidacloprid in the potato leaflets in our study fall within the range reported for other plant species, even given the variability in application rates and days posttreatment. Imidacloprid also significantly lowered transmission of *Ca.* L. psyllaurous 59–64% compared with the untreated controls. The use of imidacloprid was reportedly successful in preventing plant disease acquisition and inoculation by *M. persicae* and the leafhopper *Macrosteles quadripunctulatus* Kirschbaum (Mowry and Ophus 2002, Saracco et al. 2008). The effectiveness of imidacloprid on potato psyllid behaviors remains to be tested in the field, but the recommendations for imidacloprid application at the time of planting (Goolsby et al. 2007a, UC IPM Online 2008) suggests the strategy has proven useful. This compound seems to have residual activity for at least 6 wk, which may lower the need for additional applications.

Foliar-applied insecticides can decrease the numbers of adults that exhibit behaviors such as tasting (24 h postapplication) and probing (1 and 2 wk postapplication). In our study, the durations of the probing behaviors and the amount of time spent off the potato leaflets were the only behaviors significantly affected by foliar insecticides. Horticultural spray oil and abamectin were the only two compounds to significantly lower probing durations 24 h postapplication compared with controls. Our results are consistent with the recommendation for use of abamectin by UC IPM Online (2008) and add another aspect of control to the knockdown effect on potato psyllid adults reported by Gharalari et al. (2009). Abamectin reduced probing times by 82, 61, and 48% at 24 h, 1 wk, and 2 wk, respectively. Abamectin also significantly decreased *Ca.* L. psyllaurous transmission by 64% compared with the control and was the only foliar-applied compound in this study to achieve a decrease in transmission of the pathogen.

Horticultural spray oil also significantly reduced probing times by 66, 61, and 67% at 24 h, 1 wk, and 2 wk, respectively, and they may be another chemical to consider in potato psyllid management. However, there was no significant difference in infection levels from the control for this compound. Interestingly, the residual activity of all of the foliar-applied compounds sprayed on the plants did decrease probing durations 1 and 2 wk postapplication. In addition, the foliar insecticides increased abandonment of leaflets significantly as compared with the controls at 24 h and 2 wk postapplication (Table 4), although it is uncertain why this trend was not statistically significant 1 wk after application. Furthermore, like imidacloprid, the effectiveness of these compounds for reducing feeding, increasing abandonment of leaflets, and lowering disease transmission remains to be tested in the field. There are many opportunities for future research and may include the effects of insecticides on nymphal potato psyllid behaviors and disease transmission, the use of electrical penetration graphs to further characterize feeding behavior and acquisition or inocula-

tion of *Ca.* L. psyllaurous, influences of insecticides on adult oviposition, combinations of insecticides to lower disease transmission in the field, and the interaction of insecticides with host plants, natural enemies, or a combination on psyllid behaviors and disease transmission to crop plants in the field.

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