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Feeding disruption of potato psyllid, *Bactericera cockerelli*, by imidacloprid as measured by electrical penetration graphs

Casey D. Butler*, Gregory P. Walker & John T. Trumble

Department of Entomology, University of California, Riverside, 900 University Ave., Riverside, CA 92521, USA

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Abstract

The potato psyllid, *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae), is a serious pest of potatoes that can cause yield loss by direct feeding and by transmitting a bacterial pathogen, *Candidatus* Liberibacter psyllaurous (also known as *Candidatus* L. solanacearum), which is associated with zebra chip disease of this crop. Current pest management practices rely on the use of insecticides for control of potato psyllid to lower disease incidences and increase yields. Imidacloprid is typically applied at potato planting, and it remains unknown if imidacloprid has any effect on potato psyllid feeding behavior. Thus, our specific objectives of this study were to determine and characterize the effects of imidacloprid treatment (0.11 ml l^{-1}) to potato plants on adult potato psyllid feeding behavior 1, 2, and 4 weeks post-application. Electrical penetration graph (EPG) recordings of potato psyllid feeding revealed six EPG waveforms, which include non-probing (NP), intercellular stylet penetration (C), initial contact with phloem tissue (D), salivation into phloem sieve elements (E1), phloem sap ingestion (E2), and ingestion of xylem sap (G). The number of NP events and the duration of individual NP events significantly increased on plants treated with imidacloprid compared with untreated controls. Potato psyllids exhibited significant decreases in the number of phloem salivation events on plants treated with imidacloprid. Waveform durations and waveform durations per event for E2 and G were significantly decreased for psyllids on plants treated with imidacloprid compared with untreated controls. These data suggest that the effective use of imidacloprid to reduce transmission of *Ca.* Liberibacter psyllaurous is related to the negative effects of imidacloprid on psyllid feeding.

Introduction

The potato psyllid, *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae), is a severe pest of potatoes in Central and North America, and most recently in New Zealand (Cranshaw, 1994; Liu & Trumble, 2007; Teulon et al., 2009; Crosslin et al., 2010). The potato psyllid feeds directly on potato plants causing significant reductions in commercial potato tuber yields by up to 93% (Munyaneza et al., 2008). In addition, the potato psyllid can transmit a bacterial pathogen, *Candidatus* Liberibacter psyllaurous (also known as *Candidatus* L. solanacearum), and is an unculturable Gram-negative α-proteobacterium that is associated with the phloem tissue of plants (Hansen et al., 2008; Lin et al., 2009). Munyaneza (2010) has reported that as few as one *B. cockerelli* can transmit *Ca.* L. psyllaurous within 2 h of colonizing the plant; however, little is known regarding the mode of transmission of this bacterial pathogen. *Candidatus* L. psyllaurous is associated with 'zebra chip' (ZC) disease in potatoes (Munyaneza et al., 2007; Hansen et al., 2008; Crosslin et al., 2010). Aboveground potato plant symptoms of ZC include stunting, yellowing or purpling of leaves and shoots, swollen internodes of the upper growth, proliferation of axillary buds, aerial tubers, and plant death (Munyaneza et al., 2008; Sengoda et al., 2010). Tuber symptoms of ZC include enlarged lenticels, collapsed stolons, browning of the vascular tissue, necrotic flecking of the internal tissues, and streaking of the medullary ray tissues, all of which affects the entire tuber (Munyaneza et al., 2008; Munyaneza, 2010). Chips processed from these tubers often show pro-

*Correspondence: E-mail: cbutl001@ucr.edu

nounced symptoms with dark blotches, stripes or streaks, making them unacceptable for commercial purposes (Munyaneza et al., 2008; Munyaneza, 2010).

Insecticides are the only tools to date that have effectively managed the potato psyllid and ZC for the protection of potato yields (Goolsby et al., 2007; Vega-Gutierrez et al., 2008; Gharalari et al., 2009). In particular, imidacloprid is used extensively for potato psyllid pest management (Goolsby et al., 2007; UC IPM Online, 2008). Imidacloprid is a systemic, neonicotinoid insecticide that is an agonist of acetylcholine and binds to the post-synaptic nicotinic acetylcholine receptors resulting in the disruption of feeding, tremors, convulsions, and death of insects (Nauen, 1995; Oliveira et al., 2011). Relatively little is known regarding potato psyllid feeding behavior, and most studies regarding insecticides have focused on mortality caused by these compounds on the potato psyllid. The potato psyllid is a piercing–sucking insect, which is ideal for utilizing the electrical penetration graph (EPG) technique to characterize feeding behavior and understand the effects of imidacloprid on psyllid feeding behavior. The EPG technique has been a mainstay for studies on hemipteran feeding behavior, hemipteran–plant interactions, and the influence of insecticides on hemipteran feeding behavior (Harrewijn & Kayser, 1997; Walker, 2000; Daniels et al., 2009; Ameline et al., 2010; Cui et al., 2010; Serikawa et al., 2010; Costa et al., 2011; He et al., 2011).

Current practices to manage the potato psyllid recommend the use of an in-furrow application of imidacloprid at the time of planting as well as foliar-applied applications of imidacloprid during the growing season (Goolsby et al., 2007; UC IPM Online, 2008). Our previous research found that soil-applied applications of imidacloprid can be both a feeding deterrent as well as a repellent to the potato psyllid, and that the effects of imidacloprid can last for up to 6 weeks in the laboratory (Butler et al., 2011). On the basis of these results, we initiated studies to further elucidate the effects of imidacloprid on potato psyllid feeding behavior using a direct current (DC) EPG technique.

Materials and methods

Insects and plants

Potato psyllids and potato plants were reared and maintained following the methods described by Butler et al. (2011). Briefly, potato psyllids were originally attained from field collections in Weslaco, TX, USA (26°09′33″N, 97°59′15″W). The colony was maintained at 21–26 °C, 40–60% r.h., and L14:D10 h photoperiod (light provided by 40-W fluorescent bulbs; Osram Sylvania, Danvers, MA, USA) at the University of California, Riverside, Insectary and Quarantine facility. Potato psyllids were reared on tomatoes [*Solanum lycopersicum* L. cv. 'Yellow Pear' (Solanaceae)] to avoid any particular preference for potato. Post-teneral adult females were selected for all EPG experiments. Potato (*Solanum tuberosum* L. cv. 'Atlantic') plants were grown in the greenhouse in 4.9-l pots with UC soil mix (Matkin & Chandler, 1957) and fertilized three times per week with the label rate of Miracle Gro nutrient solution (Scotts, Marysville, OH, USA).

Experimental treatments

Imidacloprid (Admire; Bayer, Kansas City, MO, USA) was applied to the soil in 100 ml of distilled water at the recommended field rate of 0.54 ml l^{-1}. Controls were treated with 100 ml of distilled water. Potato plants were treated once the potato reached the 'vegetative growth' stage (growth stage II), which is characterized by the plant possessing 8–12 leaves (Strand, 2006). Potato plants treated with imidacloprid were tested 1, 2, and 4 weeks post-application.

Electrical penetration graph recordings

Two Giga-4 DC-EPG systems (WF Tjallingii, Wageningen University, Wageningen, The Netherlands) with a 1 giga ohm input resistance were used to record EPGs in a Faraday cage and a gain of 100× as in Stafford & Walker (2009). Output from the EPG was digitized at a rate of 100 samples per second per channel using a DI-720 analog-to-digital (A-D) board and recorded using Windaq software (both from Dataq Instruments, Akron, OH, USA). Electrical penetration graph recordings were performed on whole plants under ambient laboratory conditions with the abaxial surface of leaves used as substrates, and standardized by selecting the uppermost fully expanded leaf. The substrate voltage probe was inserted into the soil, the initial substrate voltage was set to 30 mV, and adjustments were made so that the output would fit the +5 to −5 V window provided by the Windaq software.

Potato psyllids were immobilized on a cold plate and then secured on a vacuum device for the attachment of wires (van Helden & Tjallingi, 2000). A 10-μm diameter gold wire (Sigmund Cohn, Mount Vernon, NY, USA) piece of ca. 1 cm long was attached to the head of 3-mm-diameter nail with Electrodag 503 silver glue (Ladd Research Industries, Williston, VT, USA). Once the glue dried, the unattached end of the gold wire was dipped in fresh silver glue until a small ball was formed. The wet ball of glue was applied to the psyllid's notum and allowed to dry. The psyllid was then allowed access to a potato leaf and acclimated for at least 30 min before being connected, via the nail, to the input of the DC-EPG probe. Each psyllid was monitored for 5 h, and the recordings were replicated 20 times with different psyllids and plants for each of

the treatments (control vs. imidacloprid) and for each of the time periods (1, 2, and 4 weeks post-application).

Statistical analysis

A factorial experiment with two factors, that is, factor 1: treatment with two levels (control vs. imidacloprid) and factor 2: time of application with three levels (i.e., 1, 2, and 4 weeks post-application) was conducted as a randomized complete block design with 21 blocks in time. Each block consisted of three replicates of one of the treatments (control vs. imidacloprid) for a given time period (1, 2, and 4 weeks post-application). Treatment differences within each of the three post-application times for the proportion of potato psyllid adults that produced a specific waveform were analyzed using a Fisher's exact test (Proc FREQ/FISHER; SAS Institute, 2008). For each waveform – non-probing, NP; pathway phase, C; initial contact with phloem tissue, D (after Bonani et al., 2010); salivation into phloem sieve elements, E1; phloem ingestion, E2; and xylem ingestion, G (see definitions in Results) – the following non-sequential parameters (i.e., information irrespective of waveform order within a probe) were calculated based on Backus et al. (2007) and Bonani et al. (2010): the mean number of waveform events per psyllid, waveform duration per psyllid, and waveform duration per individual bout. Sequential parameters (i.e., information inherent in the sequential order of the waveforms within a probe; Backus et al., 2007) were calculated for the mean number of probes in the 1st, 2nd, 3rd, 4th, and 5th hour of the EPG recordings, the number of probes before the first E1, and after the first E1/E2 of potato psyllids on control and imidacloprid-treated plant at weeks 1, 2, and 4 post-application. In addition, sequential parameters were calculated for the mean duration of time elapsed of the (1) first probe from the start of the EPG, (2) first E1 from the start of the EPG recording, (3) first sustained E2 (>10 min) from start of the EPG recording, (4) first probe to first E1, and (5) first probe to first sustained E2 (>10 min) of potato psyllids on control and imidacloprid-treated plant at weeks 1, 2, and 4 post-application. Non-sequential and sequential parameters were analyzed using analysis of variance (ANOVA) in a general linear models procedure of SAS version 9.2 (Proc GLM; SAS Institute, 2008). When treatment or time effect alone was significant ($P<0.05$), a Scheffé test was used to discriminate differences among the means. When there was a significant interaction ($P<0.05$) between time and treatment, multiple comparison tests using the LSMEANS/PDIFF option were conducted to discriminate differences among the means. When necessary, non-sequential and sequential parameters were transformed (i.e., log, √, reciprocal, or reciprocal √) to homogenize variances and normalize the data.

Results

Potato psyllid waveforms appeared similar to aphid and Asian citrus psyllid, *Diaphorina citri* Kuwayama, waveforms; therefore, equivalent waveform labels were used (Reese et al., 2000; Bonani et al., 2010). Electrical penetration graph recordings of potato psyllid feeding revealed six EPG waveforms. These waveforms included the following: NP, baseline voltage (NP); pathway phase or intercellular stylet penetration (C), characterized by high frequency and high amplitude; suggested to be initial contact with phloem tissue (D), based on Bonani et al. (2010) and occurs after waveform C but before E1; salivation into phloem sieve elements (E1); phloem sap ingestion (E2); and ingestion of xylem sap (G) (Figures 1–3).

The number of potato psyllid adults that produced the waveforms NP, C, D, E1, E2, and G per week are listed in Table 1. All psyllids in both treatments and for all weeks

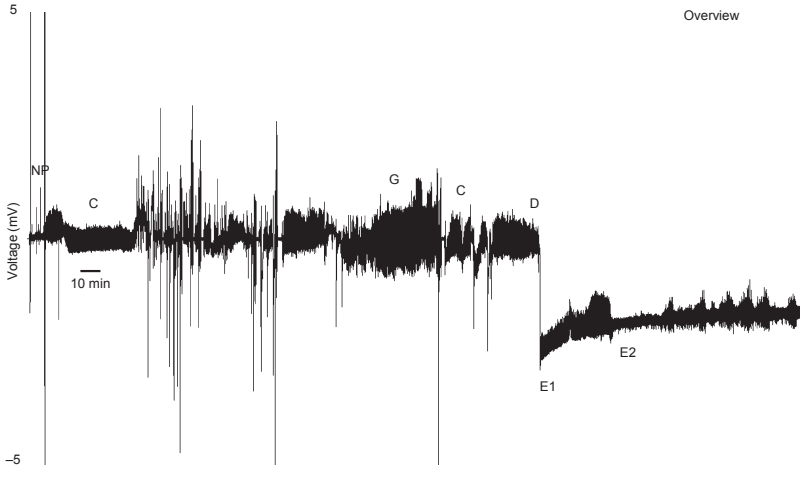

Figure 1 General overview of electrical penetration graph (EPG) waveforms produced by the potato psyllid on untreated potato plant during the 1st week of the experiment (see first paragraph of the Results for explanation of letters and waveform types).

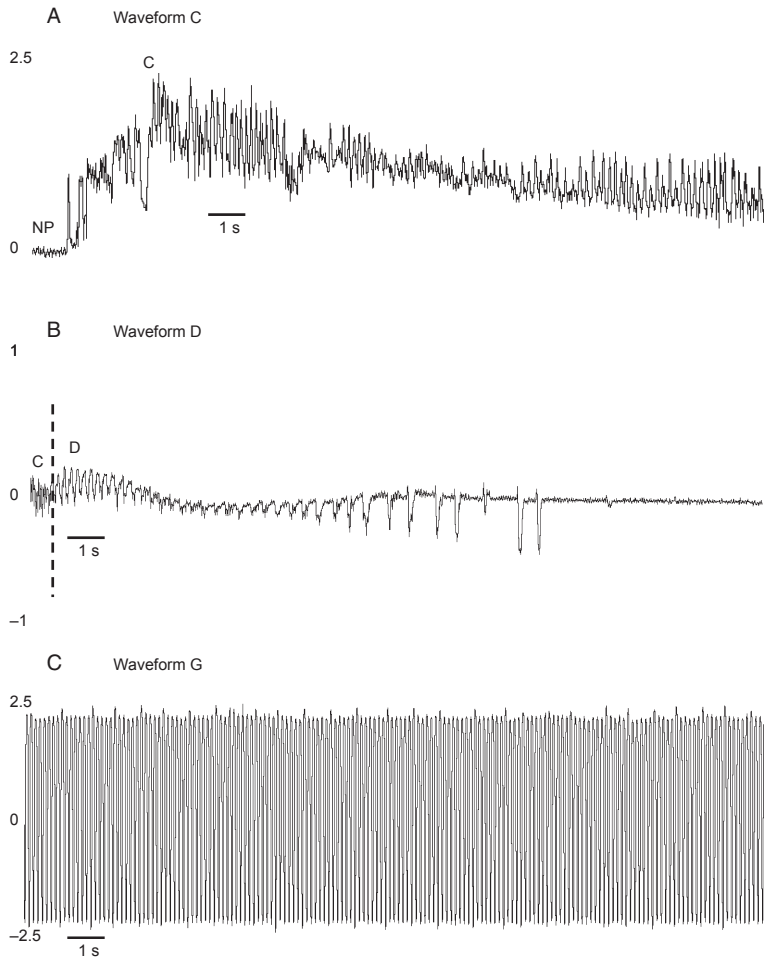

Figure 2 Representative waveforms (A) type C, (B) type D, and (C) type G produced by the potato psyllid on untreated potato plant during the 1st week of the experiment.

examined produced waveforms NP and C. There were significant differences in the number of potato psyllid adults that produced the waveforms D, E1, and E2 on potato plants treated with imidacloprid for the 1st and 2nd weeks post-application compared with untreated controls (Table 1). For up to 2 weeks, imidacloprid significantly reduced the number of psyllids that produced waveforms D (Fisher's exact test: week 1: $P = 0.0038$; week 2: $P = 0.0012$), E1 (week 1: $P = 0.0036$; week 2: $P = 0.0002$), and E2 (week 1: $P = 0.0036$; week 2: $P = 0.0001$). One week after imidacloprid treatment, the numbers of adults that displayed waveforms D, E1, and E2 was reduced by 67, 71, and 71%, respectively, compared with the untreated controls. In the 2nd week after imidacloprid application, similar reductions of waveforms D (73%), E1 (86%), and E2 (92%) were evident. However, 4 weeks after imidacloprid application, the numbers of adults that produced these waveforms were not significantly different from the controls (Table 1). In addition, imidacloprid did not significantly impact the number of adults that produced waveform G for any of the weeks tested.

The total mean numbers of waveform events per potato psyllid are listed in Table 2. For NP, potato psyllids produced significantly fewer NP events on control plants (mean ± SE = 9.7 ± 0.9 events) than imidacloprid-treated plants (13.0 ± 1.1) ($F_{1,114} = 5.65$, $P = 0.019$). There were no significant effects of time ($F_{2,114} = 1.18$, $P = 0.31$) or the interaction treatment*time ($F_{2,114} = 0.42$, $P = 0.66$). For C, the mean numbers of waveform events were not significantly different by treatment ($F_{1,114} = 1.01$, $P = 0.32$), time ($F_{2,114} = 0.18$, $P = 0.84$), or treatment*time ($F_{2,114} = 0.32$, $P = 0.73$). Potato psyllids produced significantly fewer waveform D events on imidacloprid-treated plants than on control plants (0.8 ± 0.2 vs. 2.5 ± 0.3; $F_{1,114} = 25.60$, $P<0.0001$). There were no significant effects of time ($F_{2,114} = 1.13$,

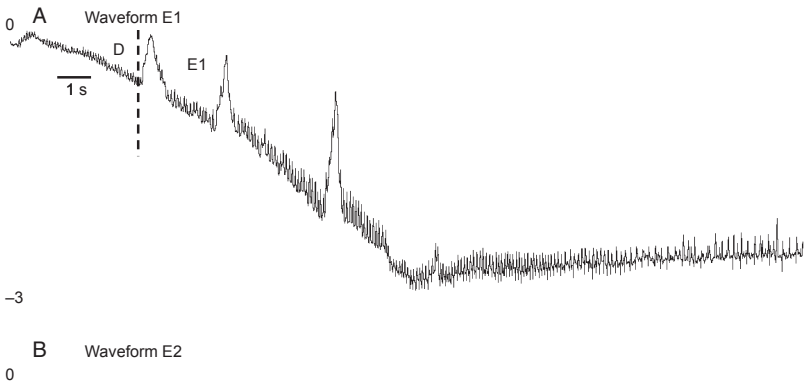

Figure 3 Representative waveform (A) type E1 and (B) type E2 produced by the potato psyllid on untreated potato plant during the 1st week of the experiment.

Table 1 Number of potato psyllids (n = 20) that produced each waveform type (see first paragraph of the Results for explanation of letters and waveform types) on control or imidacloprid-treated plants tested at weeks 1, 2, and 4 post-application

		NP			C			D			E1			E2			G		
Time (week)	Treatment	Y	N	P	Y	N	P	Y	N	P	Y	N	P	Y	N	P	Y	N	P
1	Control	20	0	nt[1]	20	0	nt	15	5	0.0038	14	6	0.0036	14	6	0.0036	8	12	0.16
	Imidacloprid	20	0		20	0		5	15		4	16		4	16		3	17	
2	Control	20	0	nt	20	0	nt	15	5	0.0012	14	6	0.0002	13	7	0.0001	13	7	0.056
	Imidacloprid	20	0		20	0		4	16		2	18		1	19		6	14	
4	Control	20	0	nt	20	0	nt	13	7	0.75	12	8	0.53	11	9	0.53	11	9	0.11
	Imidacloprid	20	0		20	0		11	9		9	11		8	12		5	15	

Y = number of psyllids that produced the waveform; N = number of psyllids that did not produce the waveform; P = probability that there was a difference between the control and imidacloprid-treated plants for each week of testing (Fisher's exact test: $\alpha = 0.05$).
[1]nt = not tested, data identical for both treatments.

Table 2 Total mean (± SE; n = 20) number of waveform events (see first paragraph of the Results for explanation of letters and waveform types) during the 5-h recording per potato psyllid on control or imidacloprid-treated plants tested at weeks 1, 2, and 4 post-application

Time (week)	Treatment	NP	C	D	E1	E2	G
1	Control	10.8 ± 2.0a	11.9 ± 1.9a	1.6 ± 0.4a	3.0 ± 1.1a	2.5 ± 0.8a	0.5 ± 0.1a
	Imidacloprid	15.2 ± 2.0b	15.2 ± 2.0a	0.8 ± 0.4b	0.8 ± 0.5b	0.7 ± 0.4b	0.2 ± 0.1a
2	Control	9.0 ± 1.5a	12.3 ± 1.6a	3.2 ± 0.7a	4.7 ± 1.3a	3.5 ± 1.1a	0.8 ± 0.2a
	Imidacloprid	12.6 ± 2.2b	13.0 ± 2.3a	0.2 ± 0.1b	0.1 ± 0.1b	0.1 ± 0.1b	0.7 ± 0.3a
4	Control	9.2 ± 1.4a	12.1 ± 1.6a	2.7 ± 0.6a	2.9 ± 0.7a	1.6 ± 0.4a	0.8 ± 0.2a
	Imidacloprid	11.2 ± 1.6b	12.8 ± 1.9a	1.4 ± 0.4b	1.2 ± 0.4b	0.9 ± 0.4b	0.8 ± 0.4a

Means within a column followed by different letters are significantly different (Scheffé's test: $P<0.05$).

P = 0.33) or treatment*time ($F_{2,114} = 2.25$, P = 0.11). For E1, potato psyllids produced significantly more phloem salivation events on control plants than on imidacloprid-treated plants (3.5 ± 0.6 vs. 0.7 ± 0.2; $F_{1,114} = 25.60$, $P<0.0001$). There was no significant effect of time ($F_{2,114} = 1.13$, P = 0.33) or treatment*time ($F_{2,114} = 2.26$,

P = 0.41). For E2, potato psyllids produced significantly fewer phloem ingestion events on imidacloprid-treated plants than on control plants (0.5 ± 0.2 vs. 2.5 ± 0.5; $F_{1,114}$ = 30.66, P<0.0001). There were no significant effects of time ($F_{2,114}$ = 0.70, P = 0.50) or treatment*time ($F_{2,114}$ = 3.02, P = 0.053). For G, the mean number of xylem ingestion events was not significantly different by treatment ($F_{1,114}$ = 0.46, P = 0.50), time ($F_{2,114}$ = 2.20, P = 0.12), or treatment*time ($F_{2,114}$ = 0.09, P = 0.91).

The mean waveform durations per potato psyllid are reported in Table 3. For NP, there was a significant interaction between treatment and time for the duration of NP ($F_{2,114}$ = 3.68, P = 0.028). Psyllids spent ca. 60 min NP on untreated controls, which was not significantly different among weeks. In contrast, potato psyllids on plants treated with imidacloprid spent significantly more time NP (160.9 ± 11.2 min). For C, the mean duration of pathway phase by potato psyllids was significantly shorter on plants during the first than during the fourth week post-application (100.0 ± 9.7 vs. 164.8 ± 11.3 min; $F_{2,114}$ = 8.03, P = 0.0005). There were no significant effects of treatment ($F_{1,114}$ = 0.83, P = 0.37) or the interaction treatment*time ($F_{2,114}$ = 0.24, P = 0.79). Potato psyllids produced significantly longer waveform D durations on control than on imidacloprid-treated plants (2.5 ± 0.4 vs. 1.2 ± 0.4 min; $F_{1,114}$ = 19.27, P<0.0001). There were no significant effects of time ($F_{2,114}$ = 1.45, P = 0.24) or treatment*time ($F_{2,114}$ = 2.76, P = 0.067). For E1, potato psyllids spent significantly more time salivating into the phloem on control than on imidacloprid-treated plants (12.8 ± 3.4 vs. 2.3 ± 1.2 min; $F_{1,114}$ = 26.27, P<0.0001). There were no significant effects of time ($F_{2,114}$ = 0.15, P = 0.86) or treatment*time ($F_{2,114}$ = 2.10, P = 0.13). For E2, potato psyllid adults spent significantly more time ingesting phloem on untreated than on imidacloprid-treated potato plants (66.0 ± 10.7 vs. 5.6 ± 2.4 min; $F_{1,114}$ = 37.31, P<0.0001). There were no significant effects of time ($F_{2,114}$ = 0.47, P = 0.62) or treatment*time ($F_{2,114}$ = 1.75, P = 0.18). For G, potato psyllid adults spent significantly more time ingesting xylem fluid on untreated than on imidacloprid-treated plants (17.5 ± 3.9 vs. 2.8 ± 2.1 min; $F_{1,114}$ = 19.50, P<0.0001). There were no significant effects of time ($F_{2,114}$ = 1.08, P = 0.34) or treatment*time ($F_{2,114}$ = 0.12, P = 0.89).

The mean waveform duration per event is listed in Table 4. For NP, the average duration of a NP event for

Table 3 Mean (± SE; n = 20) waveform duration (min) (see first paragraph of the Results for explanation of letters and waveform types) during the 5-h recording per potato psyllid on control or imidacloprid-treated plants tested at weeks 1, 2, and 4 post-application

Time (week)	Treatment	NP[1]	C	D	E1	E2	G
1	Control	57.6 ± 13.6c	111.0 ± 14.1a	1.2 ± 0.3a	10.7 ± 4.4a	96.0 ± 21.5a	21.3 ± 9.8a
	Imidacloprid	202.6 ± 14.1a	89.0 ± 13.3a	1.8 ± 1.0b	0.1 ± 0.1b	3.7 ± 2.1b	0.5 ± 0.4b
2	Control	60.0 ± 14.3c	127.7 ± 15.9ab	3.1 ± 0.7a	20.2 ± 8.4a	57.6 ± 15.5a	18.5 ± 5.5a
	Imidacloprid	163.7 ± 21.4ab	127.8 ± 20.7ab	0.2 ± 0.1b	0.9 ± 0.9b	0.9 ± 0.9b	1.0 ± 0.6b
4	Control	59.9 ± 11.6c	171.8 ± 15.1b	3.1 ± 0.9a	7.5 ± 3.7a	45.0 ± 17.3a	12.7 ± 3.7a
	Imidacloprid	116.3 ± 17.5b	157.7 ± 17.1b	1.7 ± 0.5b	5.8 ± 3.6b	12.1 ± 6.7b	6.8 ± 6.3b

Means within a column followed by different letters are significantly different (Scheffé's test: P<0.05).
[1]Means within the NP column followed by different letters are significantly different (LSMEAN/PDIFF option: P<0.05).

Table 4 Mean (± SE) waveform duration (min) per waveform event (see first paragraph of the Results for explanation of letters and waveform types) on control or imidacloprid-treated plants tested at weeks 1, 2, and 4 post-application

Time (week)	Treatment	NP	C	D	E1	E2	G
1	Control	7.2 ± 2.2a (20)	11.5 ± 1.6a (20)	0.8 ± 0.1a (15)	4.9 ± 1.8a (14)	64.4 ± 16.7a (14)	52.4 ± 20.3a (8)
	Imidacloprid	21.7 ± 5.1b (20)	6.7 ± 1.1a (20)	2.7 ± 1.6b (5)	0.2 ± 0.03a (4)	5.0 ± 1.9b (4)	1.9 ± 0.9b (3)
2	Control	9.2 ± 3.2a (20)	11.9 ± 1.7a (20)	1.3 ± 0.4a (15)	3.6 ± 0.9a (14)	22.5 ± 5.4a (13)	17.2 ± 4.0a (13)
	Imidacloprid	23.3 ± 5.7b (20)	14.0 ± 3.3a (20)	1.1 ± 0.2b (4)	8.8 ± 8.5a (2)	18.8[1] (1)	1.4 ± 0.3b (6)
4	Control	7.7 ± 1.9a (20)	17.0 ± 2.2b (20)	1.0 ± 0.1a (13)	2.0 ± 0.7a (12)	38.0 ± 13.1a (11)	17.1 ± 3.5a (11)
	Imidacloprid	22.7 ± 7.4b (20)	18.1 ± 3.4b (20)	1.4 ± 0.3b (11)	6.6 ± 4.9a (9)	11.1 ± 5.2b (8)	4.6 ± 3.3b (5)

Means within a column followed by different letters are significantly different (Scheffé's test: P<0.05). The numbers of psyllids that produced the waveform are given in parentheses.
[1]Excluded from analysis because there was only one observation.

potato psyllids was significantly longer on plants treated with imidacloprid than on untreated controls for all three observation periods (22.6 ± 3.5 vs. 8.0 ± 1.4 min; $F_{1,114} = 25.29$, $P<0.0001$). There was no significant effect of time ($F_{2,114} = 0.12$, $P = 0.89$) or the interaction treatment*time ($F_{2,114} = 0.95$, $P = 0.39$). The average duration of waveform C events was 9.1 ± 1.0 and 12.9 ± 1.9 min during the 1st and 2nd weeks (pooled treated and untreated), respectively, both of which were significantly shorter than during the 4th week post-application (17.5 ± 2.0 min) ($F_{2,114} = 9.15$, $P = 0.0002$). There was no significant effect of treatment ($F_{1,114} = 3.14$, $P = 0.067$) or treatment*time ($F_{2,114} = 1.90$, $P = 0.15$). The average duration of a waveform D event was significantly shorter on control plants than on plants treated with imidacloprid (1.1 ± 0.2 vs. 1.7 ± 0.4 min) ($F_{1,57} = 4.74$, $P = 0.034$). There was no significant effect of time ($F_{2,57} = 0.33$, $P = 0.72$) or treatment*time ($F_{2,57} = 0.89$, $P = 0.42$). The mean durations of phloem salivation events were not significantly different between treated and control plants ($F_{1,49} = 2.16$, $P = 0.15$), weeks ($F_{2,49} = 0.58$, $P = 0.56$), or treatment*time ($F_{2,49} = 0.27$, $P = 0.76$). Bouts of phloem ingestion (E2) were significantly longer on control plants than on plants treated with imidacloprid (42.4 ± 7.8 vs. 9.0 ± 3.5 min; $F_{1,45} = 12.37$, $P = 0.0010$). There was no significant effect of time ($F_{2,45} = 1.87$, $P = 0.17$) or treatment*time ($F_{1,45} = 1.35$, $P = 0.25$). For waveform G, the durations of individual xylem ingestion events were significantly longer on control plants than on plants treated with imidacloprid (25.8 ± 5.9 vs. 2.7 ± 1.3 min; $F_{1,39} = 19.84$, $P<0.0001$). There was no significant effect of time ($F_{2,39} = 1.35$, $P = 0.27$) or treatment*time ($F_{2,39} = 1.47$, $P = 0.24$).

Table 5 lists sequential parameters related to the per hour probing behavior of the potato psyllid (after Sarria et al., 2009; Bonani et al., 2010). For the number of probes produced by potato psyllids during the 1st hour of the experiment, there were no significant effects of treatment ($F_{1,114} = 0.38$, $P = 0.54$), time ($F_{2,114} = 1.33$, $P = 0.27$), or treatment*time ($F_{2,114} = 0.49$, $P = 0.61$). During the 2nd hour of the experiment, potato psyllids produced significantly more probes on imidacloprid treated than on control plants (2.3 ± 0.3 vs. 1.7 ± 0.4; $F_{1,114} = 4.28$, $P = 0.041$). There was no significant effect of time ($F_{2,114} = 0.16$, $P = 0.86$) or treatment*time ($F_{2,114} = 1.38$, $P = 0.26$). For the number of probes produced by potato psyllids during the 3rd hour of the experiment, there were no significant effects of treatment ($F_{1,114} = 2.63$, $P = 0.11$), time ($F_{2,114} = 0.19$, $P = 0.83$), or treatment*time ($F_{2,114} = 0.49$, $P = 0.90$). During the 4th hour of the experiment, potato psyllids produced significantly more probes on imidacloprid treated than on control plants (1.7 ± 0.2 vs. 1.1 ± 0.2; $F_{1,114} = 4.36$, $P = 0.039$). There was no significant effect of time ($F_{2,114} = 0.41$, $P = 0.66$) or treatment*time ($F_{2,114} = 1.44$, $P = 0.24$). For the number of probes produced by potato psyllids during the 5th hour of the experiment, there were no significant effects of treatment ($F_{1,114} = 0.25$, $P = 0.62$), time ($F_{2,114} = 1.93$, $P = 0.15$), or treatment*time ($F_{2,114} = 1.42$, $P = 0.25$). Before the first E1, potato psyllids produced significantly more probes on control plants than on plants treated with imidacloprid (3.9 ± 0.7 vs. 1.5 ± 0.5; $F_{1,114} = 24.01$, $P<0.0001$). There was no significant effect of time ($F_{2,114} = 0.71$, $P = 0.49$) or treatment*time ($F_{2,114} = 2.92$, $P = 0.058$). After the first E1/E2, there were no significant effects of treatment ($F_{1,114} = 0.10$, $P = 0.75$), time ($F_{2,114} = 0.98$, $P = 0.38$), or treatment*time ($F_{2,114} = 1.65$, $P = 0.20$).

Table 6 lists selected sequential parameters related to probing, salivation, and ingestion behaviors of the potato psyllid (Sarria et al., 2009; Bonani et al., 2010). For the time of the first probe from the start of the EPG recording, there were no significant effects of treatment ($F_{1,113} = 0.25$, $P = 0.62$), time ($F_{2,113} = 2.14$, $P = 0.12$),

Table 5 Mean (± SE; n = 20) number of probes per hour, and before and after E1 of potato psyllids on control or imidacloprid-treated plants tested at weeks 1, 2, and 4 post-application

	Week 1		Week 2		Week 4	
No. probes	Control	Imidacloprid	Control	Imidacloprid	Control	Imidacloprid
In the 1st hour	5.2 ± 1.1a	6.0 ± 1.0a	4.2 ± 0.7a	5.0 ± 0.9a	3.7 ± 0.5a	3.6 ± 0.5a
In the 2nd hour	2.3 ± 1.0a	2.7 ± 0.6b	1.1 ± 0.3a	2.5 ± 0.7b	1.8 ± 0.5a	1.6 ± 0.4b
In the 3rd hour	1.4 ± 0.5a	1.8 ± 0.5a	1.4 ± 0.4a	2.2 ± 1.4a	1.2 ± 0.5a	2.3 ± 0.8a
In the 4th hour	0.8 ± 0.3a	2.2 ± 0.5b	1.0 ± 0.4a	1.4 ± 0.4b	1.4 ± 0.4a	1.4 ± 0.4b
In the 5th hour	0.6 ± 0.2a	0.7 ± 0.2a	1.2 ± 0.4a	0.5 ± 0.3a	0.9 ± 0.2a	1.6 ± 0.5a
Before first E1	4.4 ± 1.6a	1.0 ± 0.6b	3.9 ± 1.0a	0.4 ± 0.3b	3.3 ± 1.1a	3.1 ± 1.2b
After first E1/E2	0.5 ± 0.2a	1.2 ± 0.9a	2.1 ± 0.8a	0.3 ± 0.3a	1.7 ± 0.9a	2.2 ± 1.1a

Means within a row followed by different letters are significantly different (Scheffé's test: $P<0.05$).

Table 6 Mean (± SE; n = 20) duration (min) of sequential parameters related to probing behavior (after Bonani et al., 2010) of potato psyllids on control or imidacloprid-treated plants tested at weeks 1, 2, and 4 post-application

	Week 1		Week 2		Week 4	
Time elapsed to	Control	Imidacloprid	Control	Imidacloprid	Control	Imidacloprid
First probe from start of EPG	5.7 ± 1.7a	4.1 ± 0.7a	4.2 ± 0.9a	2.8 ± 0.7a	4.9 ± 1.5a	6.2 ± 1.6a[1]
First E1 from start of EPG	159.4 ± 25.0a	255.8 ± 20.7b	159.4 ± 23.8a	285.8 ± 10.7b	188.2 ± 25.0a	217.4 ± 24.9b
First sustained E2 (>10 min) from start of EPG	193.7 ± 23.4a	275.9 ± 14.3b	213.1 ± 21.7a	296.8 ± 3.2b	221.0 ± 22.8a	264.6 ± 18.7b
First probe to first E1	154.7 ± 25.8a	255.2 ± 20.9b	156.2 ± 24.3a	285.1 ± 11.1b	187.3 ± 25.1a	214.9 ± 25.6b
First probe to first sustained E2 (>10 min)	193.2 ± 23.5a	275.3 ± 14.5b	209.9 ± 22.2a	296.3 ± 3.7b	219.2 ± 22.9a	262.1 ± 19.5b

Means within a row followed by different letters are significantly different (Scheffé's test: $P<0.05$).
[1]n = 19.

or the interaction between treatment and time ($F_{2,113} = 1.13$, $P = 0.33$). Thus, potato psyllids first probed a potato plant within 2.8–6.2 min. For the first E1 from the start of the EPG, potato psyllids took significantly longer on imidacloprid treated than on control plants to begin the first successful salivation event (253.0 ± 11.7 vs. 169.0 ± 14.1 min; $F_{1,114} = 21.32$, $P<0.0001$). There was no significant effect of time ($F_{2,114} = 0.43$, $P = 0.65$) or treatment*time ($F_{2,114} = 2.50$, $P = 0.087$). Likewise, for the first E2 from the start of the EPG, potato psyllids took significantly longer on imidacloprid treated than on control plants to begin the first successful phloem ingestion event (279.1 ± 8.0 vs. 209.3 ± 13.0 min; $F_{1,114} = 20.83$, $P<0.0001$). There was no significant effect of time ($F_{2,114} = 0.59$, $P = 0.56$) or treatment*time ($F_{2,114} = 0.73$, $P = 0.48$). For the start of E1 from the first successful probe, potato psyllids took significantly longer on imidacloprid treated than on control plants to begin the first successful salivation event (251.7 ± 12.0 vs. 166.1 ± 14.4 min; $F_{1,114} = 21.27$, $P<0.0001$). There was no significant effect of time ($F_{2,114} = 0.42$, $P = 0.66$) or treatment*time ($F_{2,114} = 2.64$, $P = 0.076$). For the start of E2 from the first successful probe, potato psyllids took significantly longer on imidacloprid treated than on control plants to begin the first successful phloem ingestion event (277.0 ± 8.3 vs. 207.4 ± 13.0 min; $F_{1,114} = 20.57$, $P< 0.0001$). There was no significant effect of time ($F_{2,114} = 0.51$, $P = 0.60$) or treatment*time ($F_{2,114} = 0.79$, $P = 0.46$).

Discussion

Imidacloprid caused a variety of significant effects on potato psyllid EPG parameters and waveforms examined. One measure of the anti-feedant effects of imidacloprid is evident from the NP waveform. The number of NP events significantly increased on plants treated with imidacloprid as well as the durations of single NP events compared with controls. However, the mean waveform duration of NP per psyllid produced a significant interaction between treatment and time post-application. The anti-feedant effects of imidacloprid have been documented with the psyllid *D. citri*, the aphids *Myzus persicae* (Sulzer), *Myzus nicotianae* (Blackman), *Schizaphis graminum* (Rondani), the leafhopper *Nephotettix cincticeps* (Uhler), and the whitefly *Bemisia tabaci* (Gennadius) at lethal and sublethal doses (Nauen, 1995; Devine et al., 1996; Nauen & Elbert, 1997; Widiarta et al., 1997; Nauen et al., 1998; Isaacs et al., 1999; Boina et al., 2009; Costa et al., 2011; Serikawa et al., 2010). Research by Butler et al. (2011) found that imidacloprid acted as a repellent to the potato psyllid and systemic application of imidacloprid significantly reduced *Ca.* L. psyllaurous infection to potatoes by up to 64% when compared with controls. Our present study provides evidence that imidacloprid can significantly increase the NP behavior of this insect, which would limit time available for transmission.

Imidacloprid appeared to have little impact on the pathway phase of potato psyllids. Both the number of adult psyllids and number of pathway phase events were not significantly different based on treatments and over the course of the experiments. However, significant increases were detected for the duration of pathway phase and the duration of a pathway phase per event based on the age of the plant, in which psyllids produced waveform C significantly longer on plants that were older. In addition, it appears that imidacloprid and age of the plant do not impact the sequence of probing behaviors of the potato psyllid on potato plants as psyllids appear to probe a plant within 3 min of being placed on the plant.

The systemic effects of imidacloprid were detected most often with waveforms associated with penetration of

phloem and xylem tissue. Similar effects of neonicotinoids have been reported with aphids and thrips using the EPG technique (Joost & Riley, 2005; Daniels et al., 2009; Costa et al., 2010). In our study, imidacloprid significantly decreased the number of adult psyllids that produced waveforms D, E1, and E2 for up to 2 weeks post-application, but the number of psyllids exhibiting each of these waveforms was not significant at 4 weeks post-application. For the Asian citrus psyllid, waveform D appears to be associated with phloem tissue (Bonani et al., 2010). For the potato psyllid, waveform D showed significant decreases in the number of waveform D events and a shorter waveform duration on imidacloprid-treated plants; however, the average bout of an individual waveform D event appears to be significantly increased. Further experiments will be needed to determine the exact behavioral activity of waveform D (Bonani et al., 2010).

Candidatus L. psyllaurous is assumed to be inoculated during phloem salivation (Cicero et al., 2009; Lin et al., 2011) and potato psyllids on plants treated with imidacloprid produced significantly fewer salivation events (E1) and significantly decreased waveform durations, but the average duration per event did not significantly differ between treated and control plants. The E2 waveform (phloem sap ingestion) has been associated with bacterial acquisition of *Candidatus* L. asiaticus by *D. citri* (Bonani et al., 2010). The numbers of waveform events, waveform duration, and waveform duration per phloem ingestion bout for E2 were significantly different between psyllids on treated and control plants. With these parameters, E2 duration significantly decreased on plants treated with imidacloprid compared with untreated controls, and this lasted throughout the duration of the experiments. Imidacloprid also increased the amount of time it took the potato psyllid to reach the phloem tissues as evident with the significant increases in the amount of time for this psyllid to begin its first salivation and phloem ingestion. Research by Butler et al. (2011) found that applications of imidacloprid significantly reduced *Ca.* L. psyllaurous infection by 59–64% compared with untreated controls. Thus, although imidacloprid may not provide 100% protection of potatoes from transmission of *Ca.* L. psyllaurous, as seen in the citrus-*D. citri*-*Ca.* L. asiaticus system (Serikawa et al., 2010), this compound can significantly decrease salivation into and ingestion from phloem, which can greatly reduce the likelihood of transmission. Future EPG experiments will be needed to study potato psyllid acquisition and inoculation of *Ca.* L. psyllaurous on potato plants.

Xylem ingestion was also impacted by imidacloprid. Although there was no difference for the number of adults that produced the xylem ingestion waveform (G), psyllids on plants treated with imidacloprid produced significantly more G waveform events. However, waveform duration per psyllid and per event significantly declined on plants treated with imidacloprid.

This study provides detailed information regarding the effects of imidacloprid on potato psyllid feeding behavior. Imidacloprid appears to have both pre-phloem effects (i.e., it takes longer for the psyllid to reach the phloem) as related to the increase in NP behaviors, and impacts on the psyllid once it reaches the phloem (i.e., it decreased salivation and phloem ingestion events, and shorter phloem ingestion durations). The EPG technique could be used in further studies regarding other insecticides, host plant resistance, and transmission of *Ca.* L. psyllaurous. The information generated on the number of weeks that behavior is modified following imidacloprid application can be used to improve recommendations for potato psyllid and ZC disease management.

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