Investigating behavior of the potato psyllid *Bactericera cockerelli* (Šulc) (Hemiptera: Triozidae) on three potato genotypes with putative resistance to “*Candidatus* Liberibacter solacearum”

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Abstract

Zebra chip disease (ZC) in potato is associated with “*Candidatus* Liberibacter solanacearum” (Lso), which is transmitted by the potato psyllid *Bactericera cockerelli* (Šulc) (Hemiptera: Triozidae). ZC can cause large economic losses when disease incidence is high. ZC management is currently focused on managing populations of the psyllid vector with insecticides. Host plant resistance to Lso and ZC has been investigated, but no commercial potato variety has been found resistant to the pathogen or the disease symptoms. Three Lso-resistant breeding clones with reduced ZC symptoms have been derived from a potato relative *Solanum chacoense* Bitter. Our study was designed to screen these genotypes for their effects on the psyllid’s host acceptance behavior and oviposition. The breeding clones selected were: ‘A07781-10LB’ (‘10LB’), ‘A07781-3LB’ (‘3LB’) and ‘A07781-4LB’ (‘4LB’). ‘Russet Burbank’ (*Solanum tuberosum* L.) was used as a Lso-susceptible control. We conducted no-choice assays with intact potato leaflets and observed the following behaviors: probing, walking, cleaning and leaving the leaf. We also compared oviposition and egg fertility for psyllids held on these genotypes. Probing frequency and female walking duration were highest on Russet Burbank, suggesting greater activity on Russet Burbank than on the three resistant genotypes. The number of eggs did not differ among genotypes but declined on all genotypes during the last period of observation (18-20 days after pairing with a male). Egg fertility did not differ among genotypes for the first three observation periods (16-18 days after pairing with a male) but was higher on Russet Burbank than 10LB or 3LB during the last observation period (18-20 days after pairing with a male). For these genotypes with putative resistance to Lso, we found antibiotic effects on egg fertility. Our study found little to no evidence of antixenotic or antibiotic effects on psyllid settling behavior.

# Introduction

The potato/tomato psyllid, *Bactericera cockerelli* (Šulc) (Hemiptera: Triozidae), is a small sternorrhynchan insect pest of solanaceous crops such as potato, tomato, cape gooseberry, tobacco, pepper, eggplant and tamarillo (Knowlton and Thomas [1934](#ref-Knowlton1934), Liefting et al. ([2008](#ref-Liefting2008)), Wallis [1955](#ref-Wallis1955), Martin [2008](#ref-Martin2008), [2009](#ref-Liefting2009), Aguilar et al. [2013](#ref-Aguilar2013)). First discovered in Colorado (Šulc [1909](#ref-Sulc1909)), potato psyllids have a history closely tied to potato growing regions and potato diseases (Richards and Blood [1973](#ref-Richards1973)). *B. cockerelli*’s geographical distribution ranges from southern Canada to Central America, throughout the western United States (Munyaneza et al. [2007](#ref-Munyaneza2007a), Rehman et al. [2010](#ref-Rehman2010), Butler and Trumble [2012](#ref-Butler2012a)) and a recent introduction to New Zealand (Martin [2008](#ref-Martin2008), Liefting et al. [2009](#ref-Liefting2009), Teulon et al. [2009](#ref-Teulon2009)).

Publications regarding the psyllid initially emerged from 1926-1928, due a condition affecting solanaceous plants known as ‘psyllid yellows’ (Richards [1928](#ref-Richards1928), Eyer and Crawford [1933](#ref-Eyer1933), Richards and Blood [1973](#ref-Richards1973)).

Potato psyllids have recently been identified as vectors of “*Candidatus* Liberibacter solanacearum” (Lso) (Rhizobiaceae: Alphaproteobacteria) (Goolsby et al. [2007](#ref-Goolsby2007a), Munyaneza et al. [2007](#ref-Munyaneza2007a), Liefting et al. [2009](#ref-Liefting2009), Cicero et al. [2016](#ref-Cicero2016)). Lso is an uncultured gram-negative -proteobacterium (Liefting et al. [2009](#ref-Liefting2009)) that infects solanaceous plants. Lso is transmitted to the plant’s phloem by the psyllid’s saliva while feeding (Cooper and Bamberg [2014](#ref-Cooper2014)). Symptoms in potato include stunting, swollen axillary buds, aerial tubers, leaf purpling, chlorosis and reduced yield (Munyaneza et al. [2007](#ref-Munyaneza2007a), [2008](#ref-Munyaneza2008)). Infection also alters tuber sugars and phenolics, resulting in brown stripes which char and blacken when fried (Navarre et al. [2009](#ref-Navarre2009), Alvarado et al. [2012](#ref-Alvarado2012), Buchman et al. [2012](#ref-Buchman2012)). This condition is known as ‘zebra chip’ disease (ZC) (Hansen et al. [2008](#ref-Hansen2008), Liefting et al. [2009](#ref-Liefting2009), Lin et al. [2009](#ref-Lin2009), Crosslin et al. [2011](#ref-Crosslin2011)). ZC-affected tubers are unmarketable, which results in large economic losses for growers (Rosson et al. [2006](#ref-Rosson2006), Munyaneza et al. [2007](#ref-Munyaneza2007a)). Yield reduction from Lso infection has ranged from 43% to 93% in some cases (Munyaneza et al. [2008](#ref-Munyaneza2008), [2011](#ref-Munyaneza2011)).

Lso and ZC symptoms were first described in 1994 in Mexico (Secor and Rivera-Varas [2004](#ref-Secor2004), Munyaneza et al. [2009](#ref-Munyaneza2009)) and was detected in the United States in 2000 (Secor and Rivera-Varas [2004](#ref-Secor2004)). Lso and ZC were first detected in the Pacific Northwest (PNW) states of Idaho, Washington, and Oregon in 2011 (Crosslin et al. [2012](#ref-Crosslin2012), Murphy et al. [2012](#ref-Murphy2012)). Since 2011, Lso and ZC continue to threaten potato production in the PNW, increasing production costs for growers (Guenthner et al. [2012](#ref-Guenthner2012), Greenway [2014](#ref-Greenway2014), Wenninger et al. [2017](#ref-Wenninger2017), Greenway and Rondon [2018](#ref-Greenway2018)).

Traditional management of the potato psyllid vector relies on multiple applications of insecticides (Guenthner et al. [2012](#ref-Guenthner2012), Greenway [2014](#ref-Greenway2014), Echegaray and Rondon [2017](#ref-Echegaray2017)). In 2018, around half of Eastern Idaho growers’ insecticide expenditures were related to ZC control (Greenway and Rondon [2018](#ref-Greenway2018)). Chemicals such as abamectin, imidacloprid, spiromesifen, thiamethoxam and dinotefuran (Goolsby, Adamczyk, et al. [2007](#ref-Goolsby2007b), Vega-Gutiérrez et al. [2008](#ref-Vega-Gutierrez2008), Gharalari et al. [2009](#ref-Gharalari2009), Guenthner et al. [2012](#ref-Guenthner2012)) are commonly used but, some psyllid populations are starting to develop resistance to common neonicotinoids and abamectin (Liu and Trumble [2004](#ref-Liu2004), Hernández-Bautista et al. [2013](#ref-Hernandez-Bautista2013), Prager et al. [2013](#ref-Prager2013), Chávez et al. [2015](#ref-Chavez2015)). The difficulty and large expense of psyllid control emphasizes the need for alternative and improved pest management strategies such as host plant resistance.

Host plant resistance is a valuable part of integrated pest management (Kogan [1988](#ref-Kogan1988), Butler and Trumble [2012](#ref-Butler2012a) a, Munyaneza [2012](#ref-Munyaneza2012b) b, Diaz-Montano et al. [2013](#ref-Diaz-Montano2013)). Even a small amount of resistance/tolerance of a plant to a vector or it’s pathogen can reduce damage below action thresholds and reduce pesticide applications (Kennedy et al. [1987](#ref-Kennedy1987)). Host plant resistance increases pesticide efficiency and helps to delay insecticide resistance (Gharalari et al. [2009](#ref-Gharalari2009)). Currently no commercial potato varieties have been found with acceptable resistance to Lso. (Munyaneza et al. [2011](#ref-Munyaneza2011), Anderson et al. [2012](#ref-Anderson2012)).

Potatoes which have been bred with closely related plants such as *Solanum chacoense* Bitter (Rashidi et al. [2017](#ref-Rashidi2017)) and *Solanum berthaultii* Hawkes (Butler et al. [2011](#ref-Butler2011)) have shown less Lso infection and/or ZC symptoms than other genotypes tested. By determining how these genotypes resist/tolerate Lso or to the psyllid vector (Kennedy et al. [1987](#ref-Kennedy1987), Putten et al. [2001](#ref-Putten2001), Butler et al. [2011](#ref-Butler2011)), we can decide which traits should be bred or cloned into commercial cultivars to create resistant potatoes (Kaloshian [2004](#ref-Kaloshian2004), Casteel et al. [2006](#ref-Casteel2006), [2007](#ref-Casteel2007)).

We examined psyllid host acceptance behaviors and oviposition on three potato breeding clones derived from *Solanum chacoense*: ‘A07781-10LB’ (‘10LB’), ‘A07781-3LB’, (‘3LB’) and ‘A07781-4LB’ (‘4LB’) (Rashidi et al. [2017](#ref-Rashidi2017)). These genotypes exhibit high tolerance and low susceptibility to Lso (Rashidi et al. [2017](#ref-Rashidi2017)), possibly due to resistance/tolerance to the psyllid vector. Our results will help clarify potato-psyllid interactions on these genotypes, which will help plant breeders to develop Lso-resistant potatoes (Kennedy et al. [1987](#ref-Kennedy1987)).

# Materials and Methods

## Plant Characteristics and Living Conditions

Potato clones were provided by the USDA-ARS, Small Grains and Potato Germplasm Research Unit Aberdeen, ID, USA. We used three sibling clones derived from *Solanum chacoense* Bitter with putative tolerance/resistance to Lso: A07781-3LB, A07781-4LB, and A07781-10LB (Rashidi et al. [2017](#ref-Rashidi2017)). ‘Russet Burbank’ was used because it is susceptible to Lso (Munyaneza et al. [2011](#ref-Munyaneza2011)) and because of its large impact on potato production in the Pacific Northwest (NASS Northwest Regional Field Office [2017](#ref-NASSNorthwestRegionalFieldOffice2017)). The selected potatoes were grown in a greenhouse maintained between 25-32°C, 32% RH, with a photoperiod of 16:8 (L:D). Plants were grown in pots of approximately 8.5 cm length 8.5 cm width 9.5 cm height, with a soil mixed in ratios of 4:4:4:1 peat moss: compost: coconut coir: perlite. Fertilizer was not used on experimental plants to avoid nitrogen increases which may alter insect feeding behaviors (Pfeiffer and Burts [1983](#ref-Pfeiffer1983), [1984](#ref-Pfeiffer1984)). We used plants in their vegetative growth stage (growth stage II) (Dwelle et al. [2003](#ref-Dwelle2003)).

## Insect Characteristics and Living Conditions

A Lso-positive potato psyllid colony was reared in the same greenhouse conditions as described above to avoid phenological asynchrony (Hodkinson et al. [2015](#ref-Hodkinson2015)). Psyllids were allowed free access to both Russet Burbank potatoes and ‘Yellow Pear’ tomatoes (*Solanum lycopersicum* L.). Colony plants were fertilized once weekly with approximately 17 g of 24:8:16 NPK fertilizer per gallon of water (MiracleGro All Purpose Plant Food, Scotts Company, Marysville, OH). Plants were replaced as needed.

## Lso Detection

Idaho harbors four haplotypes of the potato psyllid: Northwestern, Western, Central and Southwestern and two haplotypes of Lso: Lso A and Lso B (Dahan et al. [2017](#ref-Dahan2017), Wenninger et al. [2017](#ref-Wenninger2017)). Our lab colony was determined to be comprised of ‘Central’ psyllids infected with Lso ‘B’ via the methods described in Swisher and Crosslin ([2014](#ref-Swisher2014a) a). A sample of forty psyllids taken from the colony were transferred to individual microcentrifuge tubes filled with 70% ethanol. Lso incidence was tested at the Aberdeen Research and Extension Center (Aberdeen, ID, USA). DNA extraction was based on the methods described by Marzachi et al. ([1998](#ref-Marzachi1998)). Individual psyllids were ground by a homogenizer (Omni International Inc., Kennesaw, GA), macerating each psyllid for 1 minute at high speed and an additional minute at medium speed in 500 of Cetyl Trimethylammonium Bromide 2% (Alpha Teknova, Inc., Hollister, CA, Cat. No. C2190) (Composition: 2% CTAB, 100mM Tris-HCl, pH 8.0, 20mM EDTA, pH 8.0, 1.4M Sodium Chloride (NaCl). Microcentrifuge tubes were then incubated at 60 for 30 minutes and gently mixed by inversion every 10 minutes while incubating. Tubes were then spun in a centrifuge at 14,000 rpm for 5 minutes and then the supernatant was transferred to clean 2 ml tubes. The supernatant was vortexed for approximately 20 seconds with 500 ml of chloroform:isoamyl alcohol (24:1 v:v) (Sigma-Aldrich, Inc., Atlanta, GA: Catalogue number C0549), then centrifuged at 14,000 rpm for 5-10 minutes at 4. The clean supernatant was transferred to a new tube, then refrigerated isopropanol (Sigma-Aldrich, Inc., Atlanta, GA: Catalogue number I9516) was added at a rate of 2/3 of the volume of the supernatant. The mixture was then refrigerated at -20 for 20-30 minutes. DNA was precipitated by centrifuging the mixture for 20 minutes at 14,000 rpm at 4, gently pouring off the supernatant and keeping the precipitated DNA pellet. The pellet was washed in 300 of 70% ethanol and centrifuged for 5 mins at 10,000 rpm. The pellet was then dried overnight in a fume hood. Once dry, 30 of nuclease-free water was added. DNA was stored at -20.

Extracted DNA samples were then processed using a Sybgreen method. SsoAdvanced Universal SYBR Green Supermix (Biorad, Hercules, CA) was mixed in a CFX Connect Real-Time PCR Detection System (Biorad, Hercules, CA). HLBr (5’-GCG TTA TCC CGT AGA AAA AGG TAG-3’) and LsoF (5’-GTC GAG CGC TTA TTT TTA ATA GGA-3’) were used as primers (Li et al. [2006](#ref-Li2006), [2009](#ref-Li2009)) and 10 of Sybgreen supermix was added to 150 nM of each primer with 1 of DNA template. The program cycle was as follows: one cycle at 98 for 2 mins followed by 40 cycles of 95 for 10 sec and 62 for 20 sec. The melt curve was 65 to 95, with increments of 0.5 sec-1. DNA of a healthy tuber was used as a negative control. DNA of a Lso-infected tuber was used as a positive control and water was used as a no-template control in all tests. pIDTSmart Kan (Synthetic Genomics, SGI-DNA, CA) with a 250 bp region was amplified with the primer HLBr. The plasmid was diluted 10-fold and used with the following dilutions: 1 10-2, 1 10-3, 1 10-4, 1 10-6, 1 10-7, and 1 x 10-8 ng. Pathogen quantity was reported as copy number of Lso, copy numbers were determined using the methods of (Levy et al. [2011](#ref-Levy2011)).

Each psyllid tested positive for Lso, suggesting a 100% rate of infection for the colony.

## No-Choice Behavior Assays

No-choice assays were conducted in a climate-controlled room maintained at 26. Assays were conducted on a wire shelving unit which allowed the testing arena to be lit both from above and below. Three Smith-Victor Digilight fixtures (Smith-Victor Corporation, Bartlett, IL) were used with three Azlo (Akces Media LLC dba ALZO Digital, Bethel, CT) full-spectrum CFL bulbs per light fixture (100-240 volts, 60 Hz, color temp 5500K CRI 91, 750 lumens, 15 watts). Two lights were placed with their light sources 35 cm above the testing arena and the light was softened with a diffusion material. The remaining light fixture was placed so that its light source was 45 cm below the testing arena and was softened with diffusion material as well. Illuminance was 3600 lx at the surface of the arena (Sekonic L-308DC-U Light Meter, Sekonic Corporation, Tokyo, Japan).

The observation arena (*Fig. 1*) was modeled after the design described by Liu et al. ([2004](#ref-Liu2004)), but modified to use leaflets of intact, potted plants like Butler et al. ([2011](#ref-Butler2011)). This permitted us to observe the psyllids with minimal interference to plant physiology and avoided altering plant volatiles or chemical defenses activated by damaging plant tissues (Klingler et al. [2005](#ref-Klingler2005)). A recording arena was formed by sandwiching a panel of glass, a wetted filter paper, a leaf, and a piece of Plastazote polyethylene foam (Zotefoams Inc., Croydon, UK), with a circular opening in the center (28 mm diameter). The arena was held together with two clips. This arena was then suspended by a suction cup held by an adjustable burette clamp. We used leaves from the upper canopy of the plants. The filter paper was discarded between observations. The glass pane and foam were replaced with each new plant and washed and dried at 90 before reuse to remove potential volatile accumulation. Recordings were done with a L3CMOS C-mount USB camera and ToupView recording software (L3CMOS14000KPA, Hangzhou ToupTek Photonics Co., Ltd, Hangzhou, Zhejiang, China).

We collected psyllids from the colony by aspiration and transferred them to 8 35 mm glass shell vials. All psyllids were used within 90 minutes from the time of collection. Psyllids were introduced to the arena and recorded for five minutes. Psyllid sex was identified and psyllids were preserved in 95% ethanol for later testing for Lso by PCR. We recorded similar categories as Butler et al. ([2011](#ref-Butler2011)): probing, walking, cleaning, and whether the psyllid was on or off the leaf. Probing behaviors have putative significance with disease transmission and host selection (Prager, Esquivel, et al. [2014](#ref-Prager2014a) a, [2014](#ref-Prager2014b) b). Behavior was scored using CowLog3 (Hänninen and Pastell [2009](#ref-Haenninen2009)), which recorded incidence and timestamps for the behaviors observed.

## Oviposition Assays

Oviposition assays were conducted with greenhouse conditions, plants, and insects as previously described. A female/male pair of teneral psyllids (identified by their green body color) was introduced to a plant covered with an insect rearing sleeve (MegaView Science Co., Ltd., Taiwan). Rearing sleeves were supported over the plant using two lengths of galvanized steel wire with a diameter of 1.63 mm. Each wire was curved into a parabolic shape and each end of the wire was inserted into the soil on opposite corners of the plant pot (*Fig. 2*). Plants were blocked by germplasm accession in rows of four and placed inside 60 cm length 60 cm width 60 cm height mesh-covered PVC-framed cages. Plants were watered on alternating days by soaking pots in 56 cm length 28 cm width 6 cm height plastic trays until the soil became saturated (approximately 45 mins). After a period of six to eight days the males were removed from the plants and the female transferred to a new plant of the same accession. The female psyllid was then transferred to a new plant every four days at three intervals. Eggs were counted on each plant after the female was removed. Nymphs were counted four days, eight days and twelve days later to allow time for hatching (Knowlton and Janes [1931](#ref-Knowlton1931)). Each nymph was removed as it was counted. The number of nymphs that hatched was considered an indicator of egg fertility. Fertility percentages were calculated as the ratio of nymphs divided by egg counts for each sample.

## Statistical Analysis

Statistical analysis was performed using R Version 3.5.1 (R Core Team [2013](#ref-RCT2013)) Assumptions of normality were investigated with qqplots and Cullen and Frey graphs from the R package fitdistrplus (Delignette-Muller and Dutang [2015](#ref-Delignette-Muller2015)). No-choice experiments and egg count data were analyzed using generalized linear mixed modeling techniques (GLMM) (Stroup [2015](#ref-Stroup2015)) from the glmer function (Bates et al. [2015](#ref-Bates2015)). A Poisson distribution and log link were used to model count data. Egg fertility was modeled with a binomial distribution and log link to account for ratios. Behavioral models had fixed factors of germplasm accession, sex and the interaction of accession sex. Psyllid replicate was treated as a random factor. The interaction of accession sex was excluded from the off-leaf model to low occurrences (n = 20 out of 181 observations), which did not allow an interaction to be estimated by the model. Oviposition models had fixed factors of accession, period and accession period. Psyllid replicate was considered the random factor. Egg fertility was modeled with accession and period as fixed factors and individual psyllids as the random factor. All data were tested with Wald’s 2 tests, followed by least-squares means with Tukey’s adjustments to test for multiple comparisons. Statistical significance was considered at = 0.05.



**Fig. 1.** No-choice arena used for behavioral recordings



**Fig. 2.** Sleeve cage with potato used in oviposition assays

# Results

## No-Choice Assays

The number of probing events observed was significantly different among genotypes (*Table 1*). Psyllids probed more frequently on Russet Burbank than on A07781-10LB and A07781-3LB, which did not differ between each other (*Table 2*). Probing frequency on A07781-4LB did not differ among the other genotypes. This effect appeared to reflect the trend of more probing by females on Russet Burbank (*Table 2*). However, the genotype sex interaction was not significant (*Table 1*). Probing frequency did not was not affected by sex (*Table 2*). Overall, psyllids spent more time engaged in probing behavior than in the other activities recorded (*Tables 2-5*). Probing duration did not differ among genotypes, between sexes or by their interaction (*Table 1*).

The number of walking events differed significantly among genotypes as well as by the interaction of genotype sex (*Table 1*). Psyllids walked more on Russet Burbank than 10LB (*Table 3*). Female psyllids on Russet Burbank walked significantly more often than males and females on 10LB and females on 3LB (*Table 3*). The other means did not differ among each other. Walking duration did not differ among genotypes or between sexes, but the interaction term was significant (*Table 1*). Female psyllids walked significantly longer on Russet Burbank than for all other genotype sex combinations (*Table 3*).

Cleaning behaviors generally were uncommon and of short duration. The frequencies and durations of cleaning behaviors were not significantly different among genotypes, between sexes, or by their interaction (*Table 1*, *Table 4*).

Off-leaf behaviors also tended to occur rarely. Frequency of off-leaf behaviors did not differ among genotypes, between sexes or by their interaction (*Table 1*). However, the duration of off-leaf behaviors differed significantly among genotypes (*Table 1*). Psyllids spent more time off-leaf in the 3LB treatment relative to the 4LB and Russet Burbank treatments. Time spent off-leaf in the 10LB treatment did not differ among the other genotypes (*Table 5*). Off-leaf duration did not differ by sex (*Table 1*). The interaction between genotype and sex could not be analyzed due to the low number psyllids observed leaving the leaf (n = 20 out of 181).

## Oviposition Assays

Neither the number of eggs nor percent viable eggs differed significantly among genotypes (*Table 6*). However, both the number of eggs and egg fertility were significantly different by period and the interaction of genotype period (*Table 6*). For oviposition, this interaction effect was an artifact of calculating multiple comparisons of different genotypes across observation periods. There were no significant differences among genotypes within a given period (*Table 7*). For egg fertility during the last period, there were significantly more fertile eggs on Russet Burbank than 10LB or 3LB and there were significantly more eggs on 4LB than 10LB (*Table 7*). There were no significant differences among genotypes within periods 1-3 (*Table 7*). Overall oviposition (with genotype pooled) was significantly lower during period 4 than for the first (*Table 7*). Similarly, egg fertility (with genotype pooled) tended to decline during the last observation period for all genotypes except for Russet Burbank (*Table 7*).

# Discussion

It is difficult to separate the mechanisms of host plant resistance or tolerance and how these correlate with psyllid host acceptance (Diaz-Montano et al. [2006](#ref-Diaz-Montano2006), Butler et al. [2011](#ref-Butler2011)). Our visual observations of settling behavior lack the precision of electrical penetration recordings used in similar studies (Butler et al. [2012](#ref-Butler2012b), Sandanayaka et al. [2014](#ref-Sandanayaka2014), Mustafa et al. [2015](#ref-Mustafa2015b)), but requires less expensive equipment. Our results are like other investigations of putatively resistant potato genotypes. Our study found more probing and walking on Russet Burbank than on the putatively resistant genotypes, which is consistent with results reported by Butler et al. ([2011](#ref-Butler2011)) and Prager et al. [Prager, Lewis, et al. ([2014](#ref-Prager2014b)); b]. However, in contrast to Butler et al. ([2011](#ref-Butler2011)), we found cleaning and leaf-leaving behaviors to be rare. Russet Burbank received more probes than two other genotypes, but the psyllids still probed the other genotypes, often for long periods. Sandanayaka et al. ([2014](#ref-Sandanayaka2014)) and Mustafa et al [Mustafa et al. ([2015](#ref-Mustafa2015b)); b] both suggest that it takes *B. cockerelli* approximately two hours to access the phloem and acquire Lso. This suggests that very long recordings may be necessary to determine when probing becomes true feeding. Minimal overnight recordings revealed little activity besides apparent feeding on the genotype where they were placed (ANF, unpublished data). In addition, psyllids rarely abandoned the plants where they began to probe. A single psyllid is enough to transmit Lso and the disease progresses independently of bacterial titer (Buchman et al. [2011](#ref-Buchman2011a), a; Rashed et al. [2012](#ref-Rashed2012)). Therefore, it is unlikely that we were observing phloem feeding which would result in pathogen transmission within the span of our short observation periods. These factors underscore that psyllid probing behavior would have to be nearly eliminated to truly reduce the risk of Lso transmission. We found no evidence for such reductions in probing behavior on these genotypes.

Studies on the Asian citrus psyllid, *Diaphorina citri* Kuwayama (Hemiptera: Liviidae), a vector of a similar liberibacter pathogen (Teixeira et al. [2005](#ref-Teixeira2005)) have examined how host plant volatiles can alter psyllid behaviors (Wenninger et al. [2009](#ref-Wenninger2009), Davidson et al. [2014](#ref-Davidson2014)). Plant volatiles can induce probing in combination to visual and chemical cues from host plants (Patt et al. [2011](#ref-Patt2011)).

It is possible that Lso infection has altered *B. cockerelli*’s attraction to leaf volatiles (Mayer et al. [2008](#ref-Mayer2008)), and their settling behavior as well (Mas et al. [2014](#ref-Mas2014)). Lso infection can increase psyllid preferences for undamaged, uninfected hosts for oviposition and settling (Davis et al. [2012](#ref-Davis2012)) – a behavior which has been seen in other insect-plant-vector relationships (Cao et al. [2016](#ref-Cao2016), Eigenbrode et al. [2018](#ref-Eigenbrode2018)). It may be that this encouraged greater acceptance of genotypes which would be rejected by an uninfected psyllid. A high percentage of the psyllids in our colony were infected and our plants were all uninfected, so psyllid infection does not entirely explain the patterns we have seen. Infection status also fails to explain the minor trend we saw between male and female probing on Russet Burbank.

Another explanation for differences between genotypes is that the female psyllids are more influenced by familiar cues while selecting host plants for oviposition or feeding (Prager et al. [2014](#ref-Prager2014a)). Russet Burbank was one of the plants used to rear our colonies, so it is possible that the volatiles from this variety were more stimulating for female psyllids. Further studies into potato psyllid’s attraction to plant volatiles while infected can help clarify if these possible explanations correlate with host plant acceptance.

Although leaf-leaving duration differed significantly among genotypes, the incidence and duration of leaf-leaving behaviors was very small and probably not biologically significant. It is also important to note that leaf-leaving was defined in the context of leaving the leaf in our small observation arena. On a plant in the field there is a much larger surface area for a psyllid to explore, so the leaf-leaving events might represent questing behavior rather than host rejection. It also is possible that the duration between a psyllid’s initial encounter and settling behaviors or eventual plant rejection is longer than the time we allotted for recording.

Contrary to previously published studies (Butler et al. [2011](#ref-Butler2011), Diaz-Montano et al. [2013](#ref-Diaz-Montano2013), Cooper and Bamberg [2014](#ref-Cooper2014), Rubio-Covarrubias et al. [2017](#ref-Rubio-Covarrubias2017)) our study showed similar oviposition rates among genotypes, consistent with results reported by (Prager et al. [2017](#ref-Prager2017)). Other studies have found psyllids will oviposit on a variety of hosts (Diaz-Montano et al. [2013](#ref-Diaz-Montano2013), Thinakaran et al. [2015](#ref-Thinakaran2015)), even when it is not beneficial for their survival (Prager, Lewis, et al. ([2014](#ref-Prager2014b)) b). Psyllids oviposited on every type of potato offered, like observations by Prager et al. ([2017](#ref-Prager2017)), giving little evidence of antixenosis.

We selected the number of days for our observations to correlate with the periods of maximum oviposition reported in the life history tables of Abdullah (Knowlton and Janes [1931](#ref-Knowlton1931), [2008](#ref-Abdullah2008)) and Yang et al. ([2010](#ref-Yang2010), [2013](#ref-Yang2013)). Therefore, it was surprising to see the large reduction of egg fertility for some psyllids in period four (18-24 days). Fertility declined on the resistant genotypes as opposed to the Russet Burbank variety, which suggests that these genotypes may have antibiotic effects over time. Over the course of a growing season, these reductions may have a cumulative effect on psyllid populations. Longer observation periods could help to better quantify these effects.

It is possible that Lso infection status played a role in the fertility observed: Lso has been reported to negatively impact female fertility ([2012](#ref-Nachappa2012a) a, Nachappa, Shapiro, et al. [2012](#ref-Nachappa2012), [2014](#ref-Nachappa2014), Yao et al. [2016](#ref-Yao2016), Frias et al. [2018](#ref-Frias2018)). The antibiotic effects we observed may have different effects on uninfected psyllids.

We saw a large degree of variability in fertility for psyllids on all genotypes. We only permitted male access to the female psyllids during the initial period to increase female longevity by preventing possible harassment (Abdullah [2008](#ref-Abdullah2008), Wenninger and Hall [2008](#ref-Wenninger2008), Arnqvist [2013](#ref-Arnqvist2013)). Abdullah ([2008](#ref-Abdullah2008), and Yang and Liu [2009](#ref-Yang2009), and Yang et al. [2013](#ref-Yang2013)) all kept female and male psyllids together to freely mate for the duration their observations, which may explain why they observed greater fertility than we did. It is possible that potato psyllids may require multiple mates and/or multiple matings over time to maintain egg fertility (Wenninger and Hall [2008](#ref-Wenninger2008), Arnqvist [2013](#ref-Arnqvist2013)). Knowlton and Janes ([1931](#ref-Knowlton1931)) reported (with a limited number of observations) reductions in egg fertility over time after a single mating. There also may be some variability in female reproductive output created by the physiological interactions of male spermatophores, female spermathecae and/or spermatodose (Marchini et al. [2011](#ref-Marchini2011)), which all influence how long females are able to remain fertile (Qazi and Hogdal [2010](#ref-Qazi2010), Schnakenberg et al. [2011](#ref-Schnakenberg2011), Wolfner [2011](#ref-Wolfner2011), Abe and Kamimura [2015](#ref-Abe2015)).

In conclusion, we found little evidence of antixenosis or antibiosis with respect to settling behavior, but we saw a reduction in egg fertility on the resistant genotypes 18-24 days after mating. Taken together, these results suggest that the modality of resistance to Lso for the A07781 genotypes (Rashidi et al. [2017](#ref-Rashidi2017)) is not likely related to psyllid settling behaviors, but that reduced Lso symptoms may be due to resistance to the pathogen itself, and not the psyllid vector. Further work will be required to clarify the modality of resistance to Lso in the A07781 genotypes.

Table 1. Wald’s tests comparing psyllid behaviors between sexes and among four genotypes: A07781-10LB, A07781-3LB, A07781-4LB and Russet Burbank.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Behavior** | **Factors** | **Incidence** | | |  | **Duration** | | |
|  |  | df |  |  |  |  |  | |
| Probing | Genotype | 3 | 27.46 |  |  | 2.51 | 0.473 | |
|  | Sex | 1 | 3.24 |  |  | 0.00 | 0.959 | |
|  | Genotype Sex | 3 | 6.49 |  |  | 4.74 | 0.192 | |
|  |  |  |  |  |  |  |  | |
| Walking | Genotype | 3 | 16.17 |  |  | 4.66 | 0.199 | |
|  | Sex | 1 | 1.65 | 0.200 |  | 0.036 | 0.850 | |
|  | Genotype Sex | 3 | 11.13 |  |  | 10.73 |  | |
|  |  |  |  |  |  |  |  | |
| Cleaning | Genotype | 3 | 5.98 | 0.113 |  | 2.23 | 0.525 | |
|  | Sex | 1 | 0.45 | 0.503 |  | 0.48 | 0.490 | |
|  | Genotype Sex | 3 | 0.33 | 0.955 |  | 0.09 | 0.993 | |
|  |  |  |  |  |  |  |  | |
| Off-Leaf | Genotype | 3 | 1.15 | 0.765 |  | 2.23 |  | |
|  | Sex | 1 | 0.71 | 0.401 |  | 0.48 | 0.832 | |
|  | Genotype Sex | 3 | — | — |  | — | — | |

indicates values which are significant at P > 0.05  
The interaction genotype sex was unable to be analyzed due to the low number of psyllids which left the leaf (n = 20 out of 181)

Table 2: Mean ± SEM potato psyllid probing durations recorded during 300-second no-choice tests compared between sexes on four different genotypes.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Genotype** | **Sex** | **N** | **Incidence** |  |  | **Duration (s)** |
| 10LB | Female | 21 | 1.4 0.26 | A |  | 182 28.2 |
|  | Male | 25 | 1.3 0.23 |  | 242 34.0 |
|  |  |  |  |  |  |  |
| 3LB | Female | 27 | 1.5 0.24 | A |  | 248 33.6 |
|  | Male | 21 | 1.4 0.26 |  | 183 28.2 |
|  |  |  |  |  |  |  |
| 4LB | Female | 25 | 1.7 0.27 | AB |  | 244 34.1 |
|  | Male | 18 | 1.9 0.34 |  | 215 35.6 |
|  |  |  |  |  |  |  |
| Russet Burbank | Female | 26 | 3.4 0.38 | B |  | 250 34.4 |
|  | Male | 18 | 1.8 0.32 |  | 285 47.0 |

Least-squares means. Means in the same column which share a letter are not significantly different (P > 0.05)

Table 3: Potato psyllid walking behaviors recorded during 300s no-choice tests on four different genotypes: A07781-10LB, A07781-3LB, A07781-4LB and Russet Burbank

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Walking** |  | Incidence |  | Duration (s) |
| Genotype | N | Mean SEM |  | Mean SEM |
| **10LB** | 21 *F* | 0.7 0.19 **a** | **A** | 0.9 0.8 **a** |
|  | 25 *M* | 0.3 0.12 **a** | **A** | 0.6 0.5 **a** |
|  |  |  |  |  |
|  | 27 *F* | 0.5 0.15 **a** | **AB** | 0.4 0.4 **a** |
|  | 21 *M* | 0.8 0.21 **ab** | **AB** | 4.0 3.3 **a** |
|  |  |  |  |  |
|  | 25 *F* | 0.9 0.21 **ab** | **AB** | 1.6 1.3 **a** |
|  | 18 *M* | 1.1 0.28 **ab** | **AB** | 5.7 5.0 **a** |
|  |  |  |  |  |
|  | 26 *F* | 1.8 0.33 **b** | **B** | 10.5 7.5 **b** |
|  | 18 *M* | 0.6 0.20 **ab** | **B** | 0.6 0.6 **a** |

Least-squares means. Means in the same column which share a letter are not significantly different (P > 0.05)

Table 4: Potato psyllid cleaning behaviors recorded during 300s no-choice tests on four different genotypes: A07781-10LB, A07781-3LB, A07781-4LB and Russet Burbank

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Cleaning** |  | Incidence |  | Duration (s) |
| Genotype | N | Mean SEM |  | Mean SEM |
| **10LB** | 21 *F* | 0.34 0.15 |  | 0.008 0.017 |
|  | 25 *M* | 0.33 0.13 |  | 0.023 0.048 |
|  |  |  |  |  |
| **3LB** | 27 *F* | 0.13 0.07 |  | 0.002 0.003 |
|  | 21 *M* | 0.20 0.10 |  | 0.003 0.005 |
|  |  |  |  |  |
| **4LB** | 25 *F* | 0.20 0.10 |  | 0.002 0.003 |
|  | 18 *M* | 0.26 0.13 |  | 0.008 0.018 |
|  |  |  |  |  |
| **Russet Burbank** | 26 *F* | 0.09 0.05 |  | 0.001 0.001 |
|  | 18 *M* | 0.13 0.08 |  | 0.001 0.002 |

Least-squares means. Means in the same column which share a letter are not significantly different (P > 0.05)

Table 5: Potato psyllids leaving the leaf surface during 300s no-choice tests on four different genotypes: A07781-10LB, A07781-3LB, A07781-4LB and Russet Burbank

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Off-Leaf** |  | Incidence |  | Duration (s) |  |
| Genotype | N | Mean SEM |  | Mean SEM |  |
| **10LB** | 21 *F* | 0.03 0.02 |  | 1449.9 2934.1 | **AB** |
|  | 25 *M* | 0.05 0.03 |  | 1873.6 3716.9 | **AB** |
|  |  |  |  |  |  |
| **3LB** | 27 *F* | 0.06 0.03 |  | 2229.5 4272.9 | **B** |
|  | 21 *M* | 0.09 0.05 |  | 2881.0 5700.0 | **B** |
|  |  |  |  |  |  |
| **4LB** | 25 *F* | 0.05 0.04 |  | 10.6 31.6 | **A** |
|  | 18 *M* | 0.08 0.06 |  | 13.7 41.6 | **A** |
|  |  |  |  |  |  |
| **Russet Burbank** | 26 *F* | 0.03 0.02 |  | 9.1 27.1 | **A** |
|  | 18 *M* | 0.05 0.03 |  | 11.7 35.7 | **A** |

Least-squares means. Means in the same column which share a letter are not significantly different (P > 0.05)  
 Off-leaf interactions were unable to be analyzed statistically due to low numbers of replicates (n = 20 out of 181).

Table 6: Wald’s tests comparing psyllid oviposition and fertility among four genotypes: A07781-10LB, A07781-3LB, A07781-4LB and Russet Burbank

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  |  | **Total Eggs** |  |  | **Egg Fertility** |  |
| Factors |  | df |  |  | df |  |
| Genotype | 0.84 | 3 | 0.84 | 0.21 | 3 | 0.976 |
| Period | 70.23 | 3 |  | 25.60 | 3 |  |
| Genotype Period | 51.00 | 9 |  | 81.93 | 9 |  |

Table 7 Mean ( SEM) egg totals and egg fertility of psyllids on four different genotypes. A mating pair of psyllids was placed on a caged plant for six to eight days after which the male was removed. The remaining female was transferred every four days to a new plant of the same genotype until 12 more days had elapsed.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Total Eggs** | **N** | **Period 1** | **Period 2** | **Period 3** | **Period 4** |
| 10LB | 20 | 6.3 1.5 | 7.0 1.7 | 9.4 2.3 | 3.8 1.0 |
| 3LB | 13 | 4.8 1.4 | 9.5 2.8 | 9.1 2.7 | 4.3 1.3 |
| 4LB | 19 | 8.4 2.0 | 10.5 2.6 | 8.0 2.0 | 6.9 1.8 |
| Russet Burbank | 14 | 5.8 1.7 | 7.6 2.2 | 7.0 2.0 | 6.6 1.9 |
|  |  |  |  |  |  |
|  | **66** | 9.5 1.6 | 12.5 1.8 | 12.5 2.0 | 8.2 1.5 |
| **Percent Fertile** | **N** | **Period 1** | **Period 2** | **Period 3** | **Period 4** |
| 10LB | 20 | 68.8 9.2 | 59.5 10.9 | 61.8 10.7 | 3.2 2.0 **a** |
| 3LB | 13 | 65.9 12.8 | 61.0 12.6 | 55.7 13.3 | 11.9 6.8 **ab** |
| 4LB | 19 | 62.3 10.5 | 64.1 10.1 | 49.6 12.2 | 29.2 10.4 **bc** |
| Russet Burbank | 14 | 47.0 13.0 | 50.9 12.7 | 63.9 11.9 | 70.1 10.9 **c** |
|  |  |  |  |  |  |
|  | **66** | 66.8 4.2 **a** | 68.2 4.0 **ab** | 66.0 5.5 **ab** | 43.8 6.2 **b** |

Letters represent differences among periods (*P* > 0.05)

Means in the same column which share a letter are not significantly different (*P* > 0.05)`

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